Clemson University
3 1604 003 618 404




GOVT. DOCUMENTS
DEPOSITORY

MAY

CLEMSON
LIBRARY

# PROCEEDINGS OF THE FIRST CONFERENCE ON

# SCIENTIFIC RESEARCH IN THE NATIONAL PARKS

## Volume I

Digitized by the Internet Archive
in 2013

http://archive.org/details/proceedingsoffir00linn

Proceedings of the

# First Conference on Scientific Research in the National Parks

## Volume I

New Orleans, Louisiana
November 9 - 12, 1976

Edited by Robert M. Linn

Sponsored By:
National Park Service and American Institute of Biological Sciences

U.S. Department of the Interior
National Park Service Transactions and Proceedings Series • Number Five • 1979

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interests of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in Island Territories under U.S. administration.

**Note:** This publication contains all Conference papers received by the editor's deadline.

**Library of Congress Cataloging in Publication Data**

Conference on Scientific Research in the National Parks, 1st, New Orleans, 1976.
Proceedings of the First Conference on Scientific Research in the National Parks, New Orleans, Louisiana, November 9-12, 1976.

(Transactions and proceedings series – National Park Service; no. 5)
Includes bibliographies.
1. Natural history–United States–Congresses. 2. Science–United States–Congresses. 3. National parks and reserves–United States–Congresses. I. Linn, Robert M. II. United States. National Park Service. III. American Institute of Biological Sciences. IV. Series: United States. National Park Service. Transactions and proceedings series – National Park Service; no. 5.

QH104.C59 1976 500.9'73'072 78-21700

For sale by the Superintendent of Documents, U.S. Government Printing Office
Washington, D.C. 20402

Stock No. 024-005-00743-1

CONTENTS

VOLUME I

Opening Remarks - ROBERT M. LINN ..... xv
Welcome to the Conference - RICHARD TRUMBULL ..... xvii
Introduction of Nathaniel P. Reed - THEODORE W. SUDIA ..... xix
Keynote Address - GARY EVERHARDT ..... xxi
Closing Remarks - ROBERT M. LINN ..... xxvii
Summary of Conference - STANLEY A. CAIN ..... xxix
TV Editorial ..... xxxiii

PLENARY AND DISCIPLINARY SESSIONS

YOUR MOVE! THE CHANCE AND CHOICE OF SCIENCE IN THE NATIONAL PARKS
Robert C. Euler ..... 1

THE HOLE IN THE SYSTEM: A GREAT PLAINS NATIONAL PARK
Durward L. Allen ..... 5

RESEARCH ON ENDANGERED FISHES IN THE NATIONAL PARKS WITH SPECIAL EMPHASIS ON THE DEVILS HOLE PUPFISH
James E. Deacon and Maxine S. Deacon ..... 9

THE NPS AND INFORMATION: A NEEDED PARTNERSHIP
Charles Douglas ..... 21

ECOLOGY OF YELLOWSTONE THERMAL EFFLUENTS: THE BLUE-GREEN ALGAE-BRINE FLY COMMUNITY
Richard G. Wiegert ..... 27

ENERGY ANALYSIS OF THE EVERGLADES NATIONAL PARK
Edward DeBellevue, Howard T. Odum, Joan Browder and George Gardner ..... 31

MARINE BIOLOGICAL RESEARCH IN THE VIRGIN ISLANDS NATIONAL PARK
John E. Randall, Helen A. Randall and Alan H. Robinson ..... 45

CLIMATOLOGICAL STUDIES IN YELLOWSTONE AND GRAND TETON NATIONAL PARKS
Richard A. Dirks ..... 49

NATIONAL PARK SERVICE ARCHEOLOGICAL PROGRAMS: AN HISTORICAL OVERVIEW
Wilfred D. Logan and F.A. Calabrese ..... 57

A RESOURCE BASIC INVENTORY TO SUPPORT LAND USE PLANNING FOR DELAWARE WATER GAP NATIONAL RECREATION AREA
J. Robert Stottlemyer ..... 65

THE SAGUARO GIANT CACTUS: AN ECOLOGICAL PERSPECTIVE
Warren F. Steenbergh and Charles H. Lowe ..... 71

PREDICTING SPECIES CHANGES IN ISOLATED WILDLIFE PRESERVES
Ronald I. Miller and Larry D. Harris ..... 79

INSULARITY AND MAMMAL SPECIES NUMBER IN TWO NATIONAL PARKS
A.R. Weisbrod ..... 83

APPLICATION OF ISLAND BIOGEOGRAPHY THEORY TO REFUGE DESIGN: MAKING THE RIGHT DECISION FOR THE WRONG REASONS
L.G. Abele and Edward F. Connor ..... 89

TERRESTRIAL BIOLOGY – BOTANY

PROSPECTIVE CONTRIBUTIONS OF A COMPUTER-BASED CONTINENTAL FLORA TO SCIENTIFIC INFORMATION NEEDS OF THE NATIONAL PARK SERVICE
Larry E. Morse and Jane I. Lawyer ..... 95

THE IMPACT OF EXOTIC PLANTS ON THE NATIVE VEGETATION OF THEODORE ROOSEVELT ISLAND
L.K. Thomas, Jr. ..... 97

THE STATUS OF FIVE EXOTIC WOODY PLANTS IN THE TENNESSEE DISTRICT OF GREAT SMOKY MOUNTAINS NATIONAL PARK
Jill Baron, Christine Dombrowski and Susan Power Bratton ..... 101

THE ORIGINAL SURVEY NOTES OF THE PICTURED ROCKS AND APOSTLE ISLANDS NATIONAL LAKESHORES AND THEIR USE IN RECONSTRUCTING ORIGINAL FORESTS
D.J. Frederick, L. Rakestraw, C.R. Eder, R.A. Van Dyke, B.J. Griewe and M.A. Anderson ..... 107

ORIGINAL FOREST VEGETATION AND LAND USE HISTORY OF THE APOSTLE ISLANDS NATIONAL LAKESHORE
L. Rakestraw, D.J. Frederick, C.R. Eder, R.A. Van Dyke, B.J. Griewe ..... 111

ECOLOGY OF THE SAND VEGETATION OF THE APOSTLE ISLANDS
Carol A. Jefferson ..... 115

PLANT DISTRIBUTION IN RELATION TO GEOMORPHIC PROCESSES ON PRESQUE ISLE TOMBOLO, STOCKTON ISLAND, LAKE SUPERIOR
Barbara Ann Coffin ..... 119

THE *SEQUOIADENDRON GIGANTEUM* EXHIBIT AT THE WORLD'S COLUMBIAN EXHIBITION IN CHICAGO, 1893
Donald J. McGraw ..... 133

PALEOECOLOGY OF HOLOCENE AND PLEISTOCENE LACUSTRINE SEDIMENTS FROM ZION NATIONAL PARK, UTAH
Richard H. Hevly ..... 151

PALYNOLOGY OF THE GALLATIN MOUNTAIN "FOSSIL FORESTS" OF YELLOWSTONE NATIONAL PARK, MONTANA: PRELIMINARY REPORT
Phillip L. DeBord ..... 159

THE ECOLOGY OF SAWGRASS IN THE EVERGLADES OF SOUTHERN FLORIDA
Ronald H. Hofstetter and Frances Parsons ..... 165

SEASONAL DIFFERENCES IN NITROGEN AND PHOSPHORUS CONCENTRATIONS IN SAWGRASS IN SOUTHERN FLORIDA
Frances Parsons ..... 171

THE MAJOR PLANT COMMUNITIES OF THE FIRE ISLAND NATIONAL SEASHORE
Richard Stalter ..... 177

RE-ESTABLISHMENT OF PRAIRIE VEGETATION AT PEA RIDGE NATIONAL MILITARY PARK, BENTON COUNTY, ARKANSAS
Edward E. Dale, Jr. and James W. Gibbons ..... 183

AIR POLLUTION – VEGETATION EFFECTS STUDIES IN TWO NATIONAL PARKS
S.V. Krupa, R.J. Kohut and J.A. Laurence ..... 189

VEGETATION IN RELATION TO ENVIRONMENTS OF CANYONLANDS NATIONAL PARK
Walter L. Loope and Neil E. West ..... 195

DISTRIBUTION AND ECOLOGICAL RELATIONSHIPS OF TWO MOUNTAIN HEATHS (*PHYLLODOCE*) IN OLYMPIC NATIONAL PARK
Ingrid Olmsted ..... 200

OBSERVATIONS ON SNOW ALGAE IN CALIFORNIA
William H. Thomas ..... 200

FOREST ECOSYSTEMS OF MOUNT RAINIER NATIONAL PARK
W.H. Moir, F.D. Hobson, M. Hemstrom and J.F. Franklin ..... 201

ECOLOGY OF ALPINE TIMBERLINE IN OLYMPIC NATIONAL PARK
R.W. Fonda ..... 209

PRIMARY VERSUS SECONDARY SUCCESSION AT GLACIER BAY NATIONAL MONUMENT, SOUTHEASTERN ALASKA
Donald B. Lawrence ..... 213

SEEDS IN SOILS OF FORMER EVERGLADES FARMLANDS
John Ewel and Louis Conde ..... 225

FACTORS ASSOCIATED WITH TREE FAILURE OF GIANT SEQUOIA – PATHOLOGICAL ASPECTS
Douglas D. Piirto ..... 235

FACTORS ASSOCIATED WITH TREE FAILURE OF GIANT SEQUOIA – ENTOMOLOGICAL ASPECTS
C.T. David, D.A. Tilles and D.L. Wood ..... 239

PROBLEMS OF REVEGETATION OF ALPINE TUNDRA
David R. Stevens ..... 241

TERRESTRIAL BIOLOGY – RIPARIAN BIOLOGY

ECOLOGY OF SHORELINE VEGETATION, LAKE POWELL
Loren D. Potter ..... 247

NATURAL RESOURCES, WHITE WATER RECREATION, AND RIVER MANAGEMENT ALTERNATIVES ON THE COLORADO RIVER, GRAND CANYON NATIONAL PARK, ARIZONA
Steven W. Carothers, Stewart W. Aitchison and R. Roy Johnson ..... 253

INTER-RELATIONSHIPS AMONG VISITOR USAGE, HUMAN IMPACT, AND THE BIOTIC RESOURCES OF THE RIPARIAN ECOSYSTEM IN BIG BEND NATIONAL PARK
David J. Schmidly, Robert B. Ditton, William J. Boeer and Alan R. Graefe ..... 261

OZARK RIVER-USE INVESTIGATIONS
Leo F. Marnell ..... 269

APPLICATION OF RESEARCH DATA TO CARRYING CAPACITY DETERMINATION
Kenneth C. Chilman and John Burde ..... 275

TERRESTRIAL BIOLOGY – ZOOLOGY

ENVIRONMENTAL VARIABLES AND MULTI-ANNUAL CYCLES IN POPULATION DENSITY OF THE MONTANE VOLE, *MICROTUS MONTANUS*, IN GRAND TETON NATIONAL PARK – A PRELIMINARY REPORT
Aelita J. Pinter ..... 279

EFFECTS OF PRESCRIBED BURNING ON SMALL-MAMMAL COMMUNITIES IN LAVA BEDS NATIONAL MONUMENT, CALIFORNIA
R.W. Frenzel, E.E. Starkey and H.C. Black ..... 287

POPULATION ORGANIZATION AND REGULATORY MECHANISMS OF PINE MARTENS IN GRAND TETON NATIONAL PARK, WYOMING
Tim W. Clark and Tom M. Campbell ..... 293

MAMMALS OF GUADALUPE MOUNTAINS NATIONAL PARK
John E. Cornely, Hugh H. Genoways and Robert J. Baker ..... 297

RHYOLITE RADIONUCLIDE UPTAKE BY SELECTED PLANT SPECIES AND POCKET GOPHERS IN YELLOWSTONE NATIONAL PARK
Kenneth L. Diem and Garth S. Kennington ..... 301

RABBITS AND OTHER MAMMALS OF SAN JUAN ISLAND NATIONAL HISTORICAL PARK
A.R. Weisbrod, W.F. Stevens and G.E. Nordquist ..... 307

DISTRIBUTION AND RICHNESS OF MAMMAL SPECIES IN MOUNT RAINIER NATIONAL PARK
A.R. Weisbrod and J.A. Dragavon ..... 315

MAN-CAUSED MORTALITIES OF COYOTES RADIO-MARKED IN GRAND TETON NATIONAL PARK
Walter M. Tzilkowski and Frederick F. Knowlton ..... 319

HUMAN DISTURBANCE AT WOLF DENS — A MANAGEMENT PROBLEM
Richard C. Chapman ..... 323

THE ROLE OF WOLF PREDATION IN A MOOSE POPULATION DECLINE
Rolf O. Peterson ..... 329

SUMMER SCAVENGING ACTIVITY IN NORTHEASTERN ALASKA
Audrey J. Magoun ..... 335

PRODUCTION OF AQUATIC MACROPHYTES AND ITS UTILIZATION BY MOOSE ON ISLE ROYALE NATIONAL PARK
Robert W. Aho and Peter A. Jordan ..... 341

STREAM FLOW EFFECTS ON BEAVER POPULATIONS IN GRAND TETON NATIONAL PARK
Thomas C. Collins ..... 349

POPULATION STUDIES OF BEAVERS IN ISLE ROYALE NATIONAL PARK, MICHIGAN
Philip C. Shelton ..... 353

BEHAVIOR OF THE EUROPEAN WILD BOAR IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK
Mark L. Shaffer ..... 357

THE FERAL PIG IN HAWAII VOLCANOES NATIONAL PARK
James K. Baker ..... 365

THE BEHAVIOR, ECOLOGY AND SOCIAL ORGANIZATION OF THE FERAL PONIES OF ASSATEAGUE ISLAND
Ronald R. Keiper ..... 369

ECOLOGICAL STUDIES OF FERAL BURROS IN DEATH VALLEY
Charles L. Douglas and Christopher Norment ..... 373

FERAL BURRO MANAGEMENT AT BANDELIER NATIONAL MONUMENT, NEW MEXICO
Milford R. Fletcher ..... 385

INVERTEBRATE FAUNA OF THE EARTH CRACKS OF WUPATKI NATIONAL MONUMENT, ARIZONA
W. Calvin Welbourn ..... 387

A YEAR IN THE LIFE OF *ORTHOPORUS ORNATUS*, A DESERT MILLIPEDE
Clifford S. Crawford ..... 393

REPRODUCTIVE CHARACTERISTICS AND MANAGEMENT POTENTIAL OF THE SEA TURTLE ROOKERY AT CANAVERAL NATIONAL SEASHORE, FLORIDA
L.M. Ehrhart ..... 397

HERPETOLOGICAL RESEARCH IN THE NATIONAL PARK SYSTEM
David J. Morafka ..... 401

SPECIES-ORIENTED MATRIX STUDIES TO INVESTIGATE ECOSYSTEMS IN A CANADIAN NATIONAL PARK
L.N. Carbyn ..... 409

DEPLOYMENT, DISPERSAL, AND ADAPTIVE STRATEGIES OF LAND VERTEBRATES ON ATLANTIC AND GULF BARRIER ISLANDS
James D. Lazell, Jr. ..... 415

ECOLOGY OF ELK ON ALPINE TUNDRA IN ROCKY MOUNTAIN NATIONAL PARK
David R. Stevens ..... 421

A POPULATION MODEL OF THE NORTHERN YELLOWSTONE ELK HERD
Charles W. Fowler and William J. Barmore ..... 427

DESERT BIGHORN SHEEP, LIVESTOCK, AND LANDFORMS IN CANYONLANDS NATIONAL PARK
Clay Dean ..... 435

MOVEMENTS OF DESERT BIGHORN SHEEP IN THE RIVER MOUNTAINS OF LAKE MEAD NATIONAL RECREATION AREA
David M. Leslie, Jr. and Charles L. Douglas ..... 439

EWE-LAMB VOCALIZATION AND RECOGNITION IN CAPTIVE DESERT BIGHORNS AT ZION NATIONAL PARK, UTAH
Henry E. McCutchen ..... 443

DALL SHEEP IN MOUNT MCKINLEY NATIONAL PARK: IMPLICATIONS FOR CONSERVATION
Edward C. Murphy ..... 449

ECOLOGICAL RELATIONSHIPS OF MOUNTAIN GOATS (*OREAMNOS AMERICANUS*) IN GLACIER NATIONAL PARK, MONTANA
Douglas H. Chadwick ..... 451

APPLICATION OF A RUMINANT ENERGETICS MODEL TO A STUDY OF ELK WINTER RANGE CARRYING CAPACITY
D.M. Swift, J.E. Ellis and N.T. Hobbs ..... 457

JUNCO HABITATS IN THE WESTERN UNITED STATES
John R. Haldeman ..... 461

COLIMA WARBLER STATUS AT BIG BEND NATIONAL PARK, TEXAS
Roland H. Wauer ..... 469

CONCENTRATED AVIAN UTILIZATION OF AN EARLY FLOWERING CENTURY PLANT (*AGAVE HAVARDIANA*)
Robert L. Neill and Therese M. Allen ..... 475

AVIFAUNAL ASSOCIATES OF *AGAVE HAVARDIANA* TREL., IN BIG BEND NATIONAL PARK
Therese M. Allen and Robert L. Neill ..... 479

WADING BIRD PRESERVATION IN EVERGLADES NATIONAL PARK
James A. Kushlan ..... 483

WHITE PELICAN REPRODUCTIVE FAILURES IN THE MOLLY ISLANDS BREEDING COLONY IN YELLOWSTONE NATIONAL PARK
Kenneth L. Diem ..... 489

THE COLUMBIAN SHARPTAILED GROUSE: WITH SPECIAL REFERENCE TO THEIR POTENTIAL REINTRODUCTION TO LAVA BEDS NATIONAL MONUMENT
E.E. Starkey and R.A. Schnoes ..... 497

HISTORICAL SURVEY OF PEREGRINE FALCON EYRIES IN NATIONAL PARK SERVICE LANDS BORDERING LAKE SUPERIOR
Frank B. Isaacs and Norman F. Sloan ..... 501

FOREST FIRES AND THE TREE-HOLE NESTING CYCLE IN GRAND TETON AND YELLOWSTONE NATIONAL PARKS
Dale L. Taylor ..... 509

COMPARATIVE ECOLOGY OF TWO AVIAN PREDATOR GUILDS: A DISCUSSION ON THE USE OF ADAPTIVE SYNDROMES IN STUDIES OF PREDATION
Robert C. Eckhardt ..... 513

THE INFLUENCE OF FOX PREDATION ON RING-BILLED AND HERRING GULL NESTING SUCCESS
William E. Southern, Francesca J. Cuthbert and Stephen R. Patton ..... 519

AQUATIC BIOLOGY

ASSOCIATION OF PHYTOPLANKTON PHOTOSYNTHETIC RATES WITH VERTICAL TEMPERATURE AND LIGHT TRANSMISSION GRADIENTS IN CRATER LAKE, OREGON
Douglas W. Larson ..... 525

SPATIAL AND TEMPORAL DISTRIBUTION OF ALGAE AND SELECTED WATER QUALITY PARAMETERS IN THE BUFFALO RIVER, ARKANSAS
Richard L. Meyer and Laura L. Rippey ..... 531

PRELIMINARY STUDIES INTO THE AQUATIC RESOURCES OF GULPHA GORGE CREEK, HOT SPRINGS NATIONAL PARK, ARKANSAS
M.S. Ogra, A.C. Sims and G.S. Rai ..... 539

BACTERIOLOGICAL INDICATORS AND EVALUATION OF BATHER CONTAMINATION IN FRESHWATER PONDS IN THE CAPE COD NATIONAL SEASHORE
Jessie S. Ortiz, Stephen A. Souza and William L. Levine ..... 545

WARMING PROCESSES IN THE KAWEAH RIVER, SEQUOIA NATIONAL PARK, CALIFORNIA
Dana L. Abell ..... 553

ACID DRAINAGE TOXICITY AND ASSESSMENT OF SODIUM HYDROXIDE NEUTRALIZATION IN STREAMS OF THE GREAT SMOKY MOUNTAINS
R.C. Mathews, J.D. Sinks and E.L. Morgan ..... 559

THE CHEMISTRY OF THE COLORADO RIVER AND ITS TRIBUTARIES IN MARBLE AND GRAND CANYONS
Dennis M. Kubly and Gerald A. Cole ..... 565

A LIMNOLOGICAL SURVEY OF BASS LAKE, POINT REYES NATIONAL SEASHORE, 1976
Carl Widmer ..... 573

THE LIMNOLOGY OF FRESHWATER KETTLE PONDS IN THE CAPE COD NATIONAL SEASHORE
Michael Soukup ..... 577

THE LIMNOLOGY OF FOUR SMALL RESERVOIRS IN MISSISSIPPI
Luther A. Knight, Jr. and Jack Herring ..... 585

THE SIGNIFICANCE OF CRATER LAKE AS A SCIENTIFIC BENCHMARK FOR LIMNOLOGICAL RESEARCH
F.O. Hoffman and J.R. Donaldson ..... 591

AN ANALYSIS OF THE DISTRIBUTION AND ABUNDANCE OF *BAETIS* IN THE KAWEAH RIVER BASIN, CALIFORNIA
Dana L. Abell ..... 595

FISHES OF THE COLORADO RIVER IN GRAND CANYON NATIONAL PARK
Royal D. Suttkus and Glenn H. Clemmer ..... 599

ENDANGERED AND THREATENED FISH IN THE YAMPA AND GREEN RIVERS OF DINOSAUR NATIONAL MONUMENT
K.H. Seethaler, C.W. McAda and R.S. Wydoski ..... 605

SPECIES RELATIONSHIPS AMONG FISHES OF THE GENUS *GILA* IN THE UPPER COLORADO RIVER DRAINAGE
Gerald R. Smith, Robert Rush Miller and W. Daniel Sable ..... 613

REPRODUCTIVE ECOLOGY OF THE QUITOBAQUITO PUPFISH FROM ORGAN PIPE CACTUS NATIONAL MONUMENT, ARIZONA
Boyd Kynard and Robert Garrett ..... 625

A REVIEW OF CIRCUMSTANCES AFFECTING THE ABUNDANCE OF *GAMBUSIA GAIGEI*, AN ENDANGERED FISH ENDEMIC TO BIG BEND NATIONAL PARK
Clark Hubbs and John G. Williams ..... 631

POSTGLACIAL DISPERSION AND PRESENT DISTRIBUTION OF SALMONID FISHES IN THE NORTHERN CASCADES RANGE
Robert Wasem ..... 637

MAN INDUCED ACID DRAINAGE IMPACT ON BENTHIC MACROINVERTEBRATE COMMUNITIES IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK
William F. Trumpf, Eric L. Morgan and Ray Herrmann ..... 643

AGE STRUCTURE, AS DETERMINED BY VERTEBRAL SECTIONING, AND SEX RATIO OF BROOK TROUT (*SALVELINUS FONTINALIS*) FROM COSBY CREEK, GREAT SMOKY MOUNTAINS NATIONAL PARK
Michael H. Hoff and Eric L. Morgan ..... 649

THE ENVIRONMENT OF SOUTH FLORIDA, A SUMMARY REPORT
B.F. McPherson, G.Y. Hendrix, Howard Klein and H.M. Tyus ..... 653

ESTUARINE AND COASTAL MARINE FISHERY MANAGEMENT IN EVERGLADES NATIONAL PARK
Gary E. Davis ..... 657

SEASONAL BIOMASS ESTIMATES OF MARINE AND ESTUARINE FISHES WITHIN THE WESTERN FLORIDA BAY PORTION OF EVERGLADES NATIONAL PARK, MAY 1973 TO JULY 1974
Thomas W. Schmidt ..... 665

DISTRIBUTION AND ABUNDANCE OF MARINE MAMMALS IN THE WATERS OF THE EVERGLADES NATIONAL PARK
Daniel K. Odell ..... 673

ENVIRONMENTAL STUDIES OF BUCK ISLAND REEF NATIONAL MONUMENT
Elizabeth H. Gladfelter and Rosemary K. Monahan ..... 679

VOLUME II

METEOROLOGY

ATMOSPHERIC MEASUREMENTS AT GRAND CANYON
R.G. Layton, W.C. Malm, K.D. O'Dell and W.R. Willis ..... 683

RADON 222 AND AIR EXCHANGE IN THE CARLSBAD CAVERNS
Marvin H. Wilkening ..... 687

ALPHA RADIATION MONITORING AT CARLSBAD CAVERNS
Gary M. Ahlstrand and Patricia L. Fry ..... 691

GEOLOGY

THE INFLUENCE OF PRESCRIBED FIRES ON WATER-REPELLENCY OF MIXED-CONIFER FOREST FLOOR
James K. Agee ..... 695

INVESTIGATION OF RADIATION PRODUCED BY RADON AND THORON IN NATURAL CAVES ADMINISTERED BY THE NATIONAL PARK SERVICE
Keith A. Yarborough, Milford R. Fletcher, Joseph McGown and Patty Fry ..... 703

ALUMINUM PRECIPITATION, BEECH FLATS AND WALKER'S PRONG CREEKS, GREAT SMOKY MOUNTAINS NATIONAL PARK
R. Herrmann, E.L. Morgan and R.L. Green ..... 715

HAVASU CANYON – A NATURAL GEOCHEMICAL LABORATORY
Robert Giegengack, Elizabeth K. Ralph and Alan M. Gaines ..... 719

STRATIGRAPHY AND MICROFOSSILS OF THE PRECAMBRIAN ALTYN FORMATION OF GLACIER NATIONAL PARK, MONTANA
Brian White ..... 727

PALEOECOLOGY OF THE PALEOCENE BLACK PEAKS FORMATION, BIG BEND NATIONAL PARK, TEXAS
Judith A. Schiebout ..... 737

PALEOECOLOGY OF PETRIFIED WOODS FROM THE AMETHYST MOUNTAIN "FOSSIL FOREST," YELLOWSTONE NATIONAL PARK, WYOMING
William J. Fritz and Lanny H. Fisk ..... 743

COASTAL PARAMETERS RELATIVE TO HARBOR DESIGN
William F. Rittschof, Albert B. Dickas and John J. Fisher ..... 751

CASE HISTORY OF A COASTAL INVESTIGATION AT THE CAPE COD NATIONAL SEASHORE
Maurice L. Schwartz ..... 757

SPIT DYNAMICS AND MANAGEMENT PROBLEMS OF SANDY HOOK, GATEWAY NATIONAL RECREATION AREA
Karl F. Nordstrom, Norbert P. Psuty, James R. Allen, Lynn R. Sherman and Jonathan R. Pawlow ..... 761

ASSATEAGUE ISLAND: A CASE STUDY OF BARRIER ISLAND DYNAMICS
Stephen P. Leatherman ..... 769

INTERACTIONS OF PLANT COMMUNITIES AND OCEANIC OVERWASH ON THE MANIPULATED BARRIER ISLANDS OF CAPE HATTERAS NATIONAL SEASHORE, NORTH CAROLINA
Richard W. Travis and Paul J. Godfrey ..... 777

BARRIER ISLAND STUDIES, MISSISSIPPI-ALABAMA GULF COAST
Ervin G. Otvos, Jr. ..... 781

ACTIVE GEOLOGIC PROCESSES, PADRE ISLAND NATIONAL SEASHORE — IMPACT ON PARK MANAGEMENT
Christopher C. Mathewson and Robert M. McHam ..... 787

GEOLOGY, PARKS AND OIL: ENERGY WITH PRESERVATION?
John A. Barnett and Raymond Herrmann ..... 791

GLACIAL GEOLOGY OF RECENTLY DEGLACIATED BEDROCK AREAS
B. Hallet ..... 795

OBSERVATIONS OF GLACIER VARIATIONS IN GLACIER BAY NATIONAL MONUMENT
William O. Field ..... 803

GLACIER FLUCTUATIONS IN GLACIER BAY, ALASKA, IN THE PAST 11,000 YEARS
Garry D. McKenzie ..... 809

RESEARCH BY THE INSTITUTE OF POLAR STUDIES IN GLACIER BAY NATIONAL MONUMENT, ALASKA
Richard P. Goldthwait and Garry D. McKenzie ..... 815

AEOLIAN THEORY REEXAMINED FOR THE WHITE RIVER GROUP
J.C. Harksen, D.K. Olson and E.A. Gordon ..... 823

GENESIS OF THE EROSIONAL FORMS OF BRYCE CANYON NATIONAL PARK
Robert C. Lindquist ..... 827

HOLOCENE AND PLEISTOCENE LAKES IN ZION NATIONAL PARK, UTAH
Wayne L. Hamilton ..... 835

CHANGES IN THE FLUVIAL DEPOSITS OF THE COLORADO RIVER IN THE GRAND CANYON CAUSED BY GLEN CANYON DAM
Alan D. Howard and Robert Dolan ..... 845

ANTHROPOLOGY

MONTANE COCHISE CULTURE SITES IN CORONADO NATIONAL MEMORIAL
Yvonne G. Stewart ..... 853

NAVAJO ARCHEOLOGY IN CANYON DEL MUERTO: THE HISTORIC STUDY OF THE MODERN INHABITANTS OF CANYON DE CHELLY NATIONAL MONUMENT, ARIZONA
Pamela C. Magers ..... 859

NEW INTERPRETATIONS OF CANYON DE CHELLY PREHISTORY — SUMMARY OF THE ANTELOPE HOUSE PROJECT
Don P. Morris ..... 865

PREHISTORIC SETTLEMENT PATTERNS IN CANYON DE CHELLY NATIONAL MONUMENT
James A. McDonald ..... 869

ATLATL CAVE: ARCHAIC-BASKETMAKER II INVESTIGATIONS IN CHACO CANYON NATIONAL MONUMENT
T.W. Mathews and E.H. Neller ..... 873

STRANGE BEDFELLOWS? TANGENT POINTS OF IN-PARK CULTURAL AND NATURAL RESOURCES RESEARCH
Roger E. Kelly ..... 875

STEPS AND TRAILS IN THE GLEN CANYON AREA
Natalie B. Pattison ..... 879

OCMULGEE NATIONAL MONUMENT: PERIPHERAL SITES TUFT SPRINGS #1 (13Bi25) AND #2 (13Bi19)
James W. Stoutamire ..... 881

HOMAGE TO GUSTAVUS CHENEY DOANE: SCIENCE IN OUR NATIONAL PARKS
Gary A. Wright ..... 887

HOW OLD IS CAPULIN MOUNTAIN?: CORRELATION BETWEEN CAPULIN MOUNTAIN VOLCANIC FLOWS AND THE FOLSOM TYPE SITE, NORTHEASTERN NEW MEXICO
Adrienne B. Anderson and C. Vance Haynes, Jr. ..... 893

THE DEVELOPMENT OF A COMPLEX CULTURAL ECOSYSTEM IN THE CHACO BASIN, NEW MEXICO
W. James Judge ..... 901

ARCHAEOLOGICAL RESEARCH IN NATIONAL PARK SERVICE AREAS: THE UNIVERSITY OF COLORADO EXAMPLE
David A. Breternitz ..... 907

PREHISTORIC SETTLEMENT PATTERNS IN THE BIGHORN CANYON NATIONAL RECREATION AREA, SOUTH CENTRAL MONTANA
Lawrence L. Loendorf ..... 911

CURRENT ANTHROPOLOGICAL RESEARCH – GRAND CANYON NATIONAL PARK
Robert C. Euler ..... 917

ETHNOHISTORY OF THE KALTAG PORTAGE, WEST CENTRAL ALASKA
Elizabeth Andrews and Kathryn Koutsky ..... 921

ARCHAEOLOGICAL SAMPLING TECHNIQUES IN ALASKA
Harvey M. Shields ..... 925

WHAT'S COOKING IN THE CALDERA: MULTIPLE USE ON THE ANIAKCHAK COASTLINE OF ALASKA
Merry Allyn Tuten ..... 927

CHEMICAL METHODS OF RUINS STABILIZATION
Dennis B. Fenn and Raymond E. Burge ..... 929

PRESERVATION OF ROCK ART
Christy G. Turner II, Richard L. Bradshaw and William J. Burke ..... 935

MAGNETIC SURVEYING OF ARCHAEOLOGICAL SITES
John W. Weymouth ..... 941

THE INUNDATION STUDY: A UNIQUE APPROACH TO CULTURAL RESOURCES MANAGEMENT
Toni Carrell ..... 949

COMPOSITE MAPPING FOR ARCHAEOLOGY
John E. Ehrenhard ..... 955

IMPLICATIONS OF RAINFALL RECORDS AT MESA VERDE NATIONAL PARK
J.E. Ingmanson and M.A. Colyer ..... 959

THE IMPACT OF MAN ON NATIONAL PARK SERVICE AREAS FROM PREHISTORY TO THE PRESENT
John L. Cotter ..... 961

SOCIOLOGY

DISPERSED WINTER RECREATION IN THE CRATER LAKE – DIAMOND LAKE AREA
Kent Downing and Terry Jo Thompson ..... 965

ECONOMIC IMPACT OF PROPOSED KLONDIKE GOLD RUSH NATIONAL HISTORIC PARK ON SKAGWAY, ALASKA
Ken L. Casavant and James C. Barron ..... 971

STRATEGIES FOR THE ASSESSMENT OF SOCIAL-PSYCHOLOGICAL CARRYING CAPACITIES OF WHITEWATER RIVERS: A COMPARATIVE ANALYSIS
Richard M. Schreyer and Joseph W. Roggenbuck ..... 975

A POPULATION OF LOCAL FISHERMEN AND THEIR PERCEPTIONS OF CHANGE IN A RIVER ENVIRONMENT
Kenneth C. Chilman and Marvin Brown ..... 985

ASSESSING USER SPATIAL DENSITY PREFERENCE: TOWARD A SOCIAL CARRYING CAPACITY MODEL
Robert H. Becker ..... 991

PREVALENCE OF SOCIAL INTERACTION IN A NATIONAL PARK FAMILY-CAMPGROUND
Glenn E. Haas ..... 999

MULTIDIMENSIONAL BELIEFS OF YOUTH TOWARD NATIONAL PARKS
F.P. Noe and Kirk Elifson ..... 1003

PAY AS YOU PLAY: AN ANALYSIS OF ATTITUDES TOWARD A FEE-FOR-USE APPROACH TO OUTDOOR RECREATION
Michael D. Grimes, Thomas K. Pinhey and Daniel E. Campos ..... 1013

A REVIEW OF FOREST SERVICE RECREATION RESEARCH RESULTS
Elwood L. Shafer ..... 1021

INTERPERSONAL BEHAVIOR IN CITIZEN INVOLVEMENT WORKSHOPS
D.Q. Brodie and Susan F. Taylor ..... 1023

INFORMATION SCIENCES

YOSEMITE NATIONAL PARK PLANNING: COMPUTERIZED DATA RETRIEVAL AND ANALYSIS
Gregory Schalliol, Margaret Morgan, John Reynolds, Robert Schiller and Thomas Fake ..... 1027

A CONCEPTUAL BACKCOUNTRY CARRYING CAPACITY MODEL
Jan W. van Wagtendonk ..... 1033

USE OF A WILDERNESS SIMULATOR FOR MANAGEMENT DECISIONS
Jan W. van Wagtendonk ..... 1039

ANALYSIS OF RHYOLITE CANYON WATERSHED, CHIRICAHUA NATIONAL MONUMENT: A PROTOTYPE STUDY TO IMPROVE THE EFFICIENCY OF NATURAL RESOURCE DECISION MAKING
Michael M. McCarthy, Anne F. Frondorf and Lewis S. Albert ..... 1041

MULTISPECTRAL SCANNER DATA: USEFUL FOR PLANNING AND MANAGING THE NATIONAL PARK SYSTEM?
Harvey Fleet, Kenneth Muth and Nancy Fries ..... 1049

COMPUTER-AIDED PARKLAND RESEARCH OPTIMIZATION
R.H. Giles, Jr., A.R. Tipton, T.L. Sharik, G.J. Buhyoff and K.A. Argow ..... 1051

PREDICTING IMPACTS OF PROPOSED FACILITIES IN PARKS
Robert H. Giles, Jr., A.B. Jones III, A.R. Tipton and T.L. Sharik ..... 1061

THE USE OF SIMULATION MODELS IN PROJECTING POTENTIAL VISITATION TO NEW NATIONAL PARK AREAS IN ALASKA
R. Gerald Wright ..... 1067

THE USE OF SPATIAL SIMULATION MODELS IN EVALUATING LAND-USE AND RESOURCE MANAGEMENT STRATEGIES IN THE PROPOSED ALASKAN PARKS
R. Gerald Wright ..... 1077

RESOURCES MANAGEMENT

MONITORING EMERGENCE PERIODS OF THE SMALLER EUROPEAN ELM BARK BEETLE *SCOLYTUS MULTISTRIATUS* IN THE NATIONAL CAPITAL REGION, WITH MULTILURE BAITED TRAPS
James L. Sherald ..... 1081

THE IMPACT OF DEFOLIATION BY GYPSY MOTHS ON THE FOREST AT MORRISTOWN NATIONAL HISTORIC PARK, NEW JERSEY
Joan G. Ehrenfeld ..... 1085

DUTCH ELM DISEASE THERAPY IN THE NATIONAL CAPITAL PARKS — A PROGRESS REPORT
James L. Sherald ..... 1089

COMPARATIVE STUDIES ON GROWTH AND DEVELOPMENT OF ST. AUGUSTINE GRASS TURF AS AFFECTED BY COMMERCIALLY AVAILABLE RETARDANTS
G.A. Rai, M.S. Ogra, L.Y. Yatsu and J.D. Tallant ..... 1091

ROOT DISEASE, HAZARD, AND FOREST PROTECTION IN YOSEMITE VALLEY
J.R. Parmeter, Jr., M. Srago, N.J. MacGregor and F.W. Cobb, Jr. ..... 1097

COMPOSTING — AN ATTRACTIVE AND ECONOMICAL WAY TO RECYCLE URBAN-PRODUCED ORGANIC MATERIALS
J.C. Patterson and J.R. Short ..... 1101

UTILIZATION OF URBAN-PRODUCED WASTES FOR SOIL RENOVATION
J.R. Short and J.C. Patterson ..... 1107

USE OF COMPOSTED SEWAGE SLUDGE FOR THE ESTABLISHMENT OF TURFGRASS SOD
Jay S. Angle, Duane C. Wolf and John R. Hall III ..... 1111

SOIL COMPACTION — EFFECTS ON URBAN VEGETATION
James C. Patterson and John R. Short ..... 1115

MODIFICATION OF BULK DENSITY ON SANDY LOAM AND SILTY LOAM SOILS IN WASHINGTON, D.C.
J.R. Short and J.C. Patterson ..... 1116

EFFECTS OF OFF-ROAD VEHICLES ON THE GEOMORPHOLOGY OF DUNES IN CAPE COD NATIONAL SEASHORE
Stephen P. Leatherman ..... 1119

ASPEN UTILIZATION BY LARGE HERBIVORES IN ROCKY MOUNTAIN NATIONAL PARK AND ITS IMPLICATIONS FOR MANAGEMENT
Charles E. Olmsted ..... 1125

LAND USE HABITS AND CHANGES IN VEGETATION ON EASTERN OREGON RANGELANDS: AN HISTORICAL PERSPECTIVE
D.A. Shinn ..... 1135

ALPINE AND SUBALPINE VEGETATION UNDER THE INFLUENCE OF NON-NATIVE MOUNTAIN GOATS, OLYMPIC NATIONAL PARK
Ingrid C. Olmsted ..... 1143

SUCCESSION FOLLOWING GOAT REMOVAL IN HAWAII VOLCANOES NATIONAL PARK
Dieter Mueller-Dombois ..... 1149

THE USE OF UNIFORM ECOSYSTEM PARAMETERS TO CHARACTERIZE NATURAL AREAS
G. Bradford Shea ..... 1155

THE NATURAL LANDMARKS PROGRAM
Gary S. Waggoner ..... 1161

NATURAL AREA CLASSIFICATION SYSTEM: A STANDARDIZATION SCHEME, II
Albert E. Radford and J. Dan Pittillo ..... 1165

A METHOD FOR EVALUATING NATIONAL PARKS AND NATURAL AREAS
George A. Petrides ..... 1173

THE HALEAKALA CRATER ECOSYSTEM
Clifford W. Smith ..... 1179

BASELINE ECOLOGICAL STUDIES AND PLANNING IN APOSTLE ISLANDS NATIONAL LAKESHORE
R.T. Brown, R.M. Linn, W.L. Kowalski, W.C. Larsen and R.A. Schulz ..... 1183

RESOURCE MONITORING SYSTEM, CHIRICAHUA NATIONAL MONUMENT, ARIZONA
William H. Moir and William M. Lukens ..... 1189

WHAT WOULD YOU DO WITH, SAY, SAN MIGUEL ISLAND?
Milton C. Kolipinski ..... 1201

PLANT COMMUNITY RESPONSES TO THE USE OF PRESCRIBED BURNING AS AN ALTERNATIVE TO MOWING IN THE MANAGEMENT OF BIG MEADOWS, SHENANDOAH NATIONAL PARK
W.D. Cocking, E.E. Baxter and S.L. Lilly ..... 1205

FIRE MANAGEMENT OF LAVA BEDS NATIONAL MONUMENT
Robert E. Martin and Arlen H. Johnson ..... 1209

SPATIAL AND TEMPORAL DISTRIBUTION OF NATURAL FUELS IN GLACIER PARK
Bruce W. Jeske and Collin D. Bevins ..... 1219

FIRE MODELING FOR NATURAL FUEL SITUATIONS IN GLACIER NATIONAL PARK
Collin D. Bevins ..... 1225

THE FIRE MANAGEMENT PLAN FOR PINNACLES NATIONAL MONUMENT
James K. Agee and Harold H. Biswell ..... 1231

FIRE RESILIENT FORESTS OF DOUGLAS FIR IN OLYMPIC NATIONAL PARK: AN HYPOTHESIS
R.W. Fonda ..... 1239

MOOSE-FOREST-FIRE ECOLOGY IN ISLE ROYALE NATIONAL PARK
Robert A. Janke ..... 1243

FIRE MANAGEMENT IN EVERGLADES NATIONAL PARK
William L. Bancroft ..... 1253

PATTERNS OF SOIL EROSION AND VEGETATION DAMAGE ASSOCIATED WITH TRAILS AND CAMPSITES IN GREAT SMOKY MOUNTAINS NATIONAL PARK
Matthew G. Hickler and Susan Power Bratton ..... 1261

CULTURAL INFLUENCES ON SUBALPINE AND ALPINE MEADOW VEGETATION IN YOSEMITE NATIONAL PARK
Daniel O. Holmes ..... 1267

MANAGEMENT STUDIES OF HUMAN IMPACT AT BACKCOUNTRY CAMPSITES IN OLYMPIC NATIONAL PARK, WASHINGTON
Bruce B. Moorhead and Edward S. Schreiner ..... 1273

VISITOR IMPACT ON SUBALPINE MEADOW VEGETATION IN GLACIER NATIONAL PARK, MONTANA
Ernest Hartley ..... 1279

VISITOR USE IMPACT IN A SUBALPINE MEADOW, YOSEMITE NATIONAL PARK, CALIFORNIA
John Lemons ..... 1287

GEOLOGY, SOILS, AND RECREATIONAL LIMITATIONS OF BEAR ISLAND, WISCONSIN, APOSTLE ISLANDS NATIONAL LAKESHORE
William L. Kowalski ..... 1293

MOUNTAIN MEADOW MANAGEMENT AND RESEARCH IN SEQUOIA AND KINGS CANYON NATIONAL PARKS: A REVIEW AND UPDATE
Steven H. DeBenedetti and David J. Parsons ..... 1305

WILDERNESS PROTECTION IN THE HIGH SIERRA: EFFECTS OF A 15-YEAR CLOSURE
David J. Parsons and Steven H. DeBenedetti ..... 1313

ANALYSIS OF KAIPAROWITS: POWER PLANT IMPACTS ON NATIONAL RECREATION RESOURCES
Richard V Giamberdine, Alex R. Carter, Douglas D. Faris, John T. Austin and Joel V. Kussman ..... 1319

# OPENING REMARKS

Robert M. Linn[1]

It is my great pleasure to welcome you to this First Conference on Scientific Research in the National Parks, dedicated to George M. Wright who was the first Chief of the Wildlife Division of the National Park Service from 1930 to 1936, and whose personal dedication, enthusiasm and knowledge were largely responsible for the initiation of scientific research and the practice of ecological principles in the management of the national parks of the United States.

I welcome not only the conferees, but also the Natural Science Advisory Committee for Fish and Wildlife and Parks, and the Southwest Regional Advisory Committee, both of whom have meetings adjunct to this Conference and to whom I extend a most cordial welcome to attend any and all Conference sessions as their schedules allow.

[1]National Park Service, Michigan Technological University, Houghton 49931.

## WELCOME TO THE CONFERENCE

Dr. Richard Trumbull, Director
American Institute of Biological Sciences

It is my pleasure to welcome you to this first conference on scientific research in the national parks. I find this most appropriate for a setting in New Orleans, a pleasant reminder that so much of the national park scene of interest to us falls within the Louisiana Purchase. Further, one is reminded of the journal of the LeMornes on their way from Montreal to settle in New Orleans. This journal was filled with notes on the abundance and beauty of both flora and fauna. They commented on six-foot catfish in the Susquehanna and paid little attention to trees under four feet in diameter.

Today's awareness of our responsibility for conservation of our heritage must be heightened by a greater understanding of it. Science, then, becomes the handmaiden of stewardship. There are many benefits to be derived from this gathering, in fine papers, meeting of old friends and discovery of mutual interests. We have hopes that even as your disciplinary interests are awakened, you will also gain a better perspective of the interdisciplinary total.

We would have you experience that which the early painters of the emerging American scene a century ago tried to express. It is said that Thomas Moran (1837-1926) painted the geysers and canyons so beautifully that one of his pictures was purchased by Congress and is given credit for the later founding of the national park system itself.

"These painters were all of the nature-loving and heartier school. They saw big, they painted big, they appealed to those who thought big. If man is meant to have dominion over the earth--this earth, this America--then man must be splendid indeed . . ..

"But then, American artists have always felt that if we study our wondrous landscape, immerse ourselves in it, we can create ourselves anew. We can be powerful. Or we can be serene. Perhaps we can even be both."*

---

*"Eden and Awe: The American Landscape," by Mary Ritchie, Delta Air Lines Magazine, *Sky*, November 1976, pp. 20-23.

Finally, I am pleased to indicate that others appreciate your participation in this conference. Quoting a letter from the White House:

"Of particular interest to the White House are the innovative steps being taken by the American Institute of Biological Sciences and the National Park Service to mobilize the scientific community for some effective, integrated use of the vast scientific and educational resource that is the National Park System.

"The White House extends congratulations to the American Institute of Biological Sciences and to the National Park Service for their joint efforts to promote parks as a national research resource."

Let us do our best to accomplish that in the programs to follow. We are happy to have you all here.

INTRODUCTION OF NATHANIEL P. REED
Assistant Secretary of the Interior for Fish and Wildlife, National Parks, and Outdoor Recreation

by

Theodore W. Sudia, Chief Scientist
National Park Service

If my introductions this morning tend to seem somewhat pedestrian, it's because there appears to exist some confusion in the minds of those of us who are not Park Service as to who is what to whom in our little hierarchy. I am determined to clarify the basics.

Nathaniel P. Reed is the Assistant Secretary of the Interior who is charged with responsibility for Fish, Wildlife, and National Parks. His science overview thus is broader than the Park System, including all Wildlife Refuges as well as the extensive scientific research that goes on within that other Service.

The Secretary of the Interior looks to Nat Reed for advice on how developments elsewhere in the Department will affect the natural land and water systems within the fish and wildlife and park systems. This is not an easy job in a Department that has been aptly nicknamed "the dustbin of government." The conflicts are many and horrendous, and Secretary Reed has had some tough on-the-job training in the past 7 years.

But he did not come unprepared. He had served two governors of two different political persuasions as Florida's consultant on matters of environmental concern. Environmental conflicts of interest do NOT tend to shrink when viewed from the state and local level.

He is here today to wish us well as we launch this historic "first" in science deliberations. We are most pleased to be welcomed by Assistant Secretary of the Interior for Fish, Wildlife, and National Parks, Nathaniel P. Reed.

Secretary Reed's remarks are not available for the Proceedings publication. However, at their conclusion, he awarded the Department of the Interior's Distinguished Service medal to William B. Robertson, Jr., and read the following citation, signed by Interior Secretary Thomas S. Kleppe.

"For distinguished service, to William B. Robertson, Jr., in recognition of his outstanding contributions to the National Park Service in the field of ecology and natural sciences.

"Dr. Robertson's 21 years of Government service have resulted in an enhanced understanding of the complexities of the ecosystem of Everglades National Park and the whole of South Florida. As a research biologist he pioneered in the use of fire to restore natural ecosystems and contributed to the understanding of the role of fire in natural resource management. Dr. Robertson in his long and distinguished career has become a world expert in the ecology of the sooty tern, the wood ibis, and the colonial nesting birds of South Florida. He has served as advisor to numerous natural resource managers in South Florida and was frequently called upon to advise the Office of the Secretary and the State of Florida on matters relating to the ecological well-being of Florida. Dr. Robertson's long list of publications which have appeared in national and international journals is ample testimony of a long and distinguished scientific career. In 1971 Dr. Robertson had conferred upon him the rank of senior scientist. He was elected to the Society of the Sigma Xi, the Phi Sigma Society, and was made a fellow of the American Association for the Advancement of Science. Dr. Robertson's standing in the national and international scientific communities reflects the professionalism with which he has long served the Government and the reputation by which he has earned outside support for Service policies. In recognition of his outstanding contributions as a scientist and researcher, William B. Robertson, Jr., is granted the highest honor of the Department of the Interior, the Distinguished Service Award."

# KEYNOTE ADDRESS

Gary Everhardt
Director
National Park Service

I want to begin this conference by thanking you for extending me the privilege of welcoming you. I represent management of the National Parks and my presence on this platform speaks more eloquently than any words. It says "We've come a long way."

Ten years ago I would not have been here. And if I had been, I wouldn't have looked out into the audience and seen the number of managers I see here today. Ten years ago you would have been scientists talking to scientists. And if that fact implies any fault, that fault lies as much in my court as it does in yours.

But 10 years ago is only a point in time, and today we are here, *together*. And so I submit that we can start this conference on a note of hope, for we have already made progress.

I do not necessarily assume that science and management are superior to science itself. But as long as parks must be managed, then I propose that science *and* management is better for the parks than either is, by itself.

Just as I don't assign all blame to science for the separateness of the past, neither do I award all credit to scientists for the progress we demonstrate here today.

There have been important changes in attitudes.

Managers today--and those who are moving into positions to become managers tomorrow--are a different breed. They are more sophisticated in their overall education and thinking. The new manager has seen the results of decisions which would have been different had more facts been available at the time the decision had to be made.

Today's manager doesn't want to be remembered tomorrow for some monumental blooper. (Or even for some *natural* area blooper.)

I realize that science must be free, but I'm going to risk seeing you flinch by saying that perhaps we haven't managed science enough. And before your howls rise to the heavens, let me add that we managers haven't had enough voice in the choice of research and control of the information flow that results.

I do not mean to say that managers are competent to design specific research projects. That is your field and we leave it to you. But managers are much more aware than scientists of the park problems that *in themselves* are *demanding management answers*. We have a duty to make you aware of these problems--where and when and how they may rear their heads.

And then you, in your infinite scientific wisdom, can go out and slay our dragons--or at least pin them to the mat so that *we* can slay them.

Management and science have in the past been two separate rivers, each contained within its own comfortable banks, both flowing through the National Parks but seldom mixing. Management knew science was there, and presumably was "up to something." But when the tough decisions had to be made, often times the appropriate results of scientific research simply were not available. Maybe science had the answers, but management never asked the questions. Often because it didn't know whom to ask or what to ask.

Today I'm in a choice position to ask questions. I look at this address as an opportunity to throw out some questions--questions that constitute a challenge to both science and management. I hope that in the course of your deliberations here this week you can come up with some answers. Managers have shown a willingness to reassess science in the parks. I would hope that scientists are willing to look at what they do within the context of management problems.

Essentially management's role is to evaluate information and make decisions. We need the information that only science can afford. And public awareness of environmental imperatives is forcing management's hand. If we dig a sewer to serve our visitor loads and happen to hit a wrong soil or rock--if we project an airplane runway or punch an access road through a sage grouse strutting ground, we aren't just criticized any more--we're hauled into the courts--those hallowed halls of justice where good intentions get no brownie points and ignorance is no excuse.

The legal and political ramifications of managing the National parks are helping management hear science better.

We need better integration of scientific research into the mission of park management, and I am here today to put the stamp of management approval on that objective.

We are dealing here with two distinct areas of responsibility

which must somehow, and soon, be fashioned into one strong stand. Management has certain duties; science has others.

It is the duty of management to perceive and assess correctly the problems faced in the parks. Having identified these problems, it is management's continued responsibility to pose appropriate questions for research.

It is the duty of research to move quickly at this point--to acquire the facts, to answer management's questions, to identify the various possible alternatives, to inform about the consequences of each, and them to assess scientifically the impact of implementing the action plan chosen by management.

We need your information all along the line. When we are developing our planning requirements, we need to know what our basic natural resource consists of--how its processes operate--and what visitors will expect of it. The clear focus of potential and of expectations by the public should be made at this point, and it is a joint job for both science and management. It carries an important interpretive element too. *We must know* what a proposed area can deliver, and the *public must be informed* as to what they can expect to gain from its operation as a park site.

The next step--a resource management plan--should stem from a realistic assessment of the natural potential and the human expectations. Information is needed at this point to fine-tune one or the other and bring the two into agreement. Your natural and social science research can help us decide which is the more easily manipulated and how to achieve harmony.

Visitor use plans--another element of the general management process--also depend on what we know about an area and the people it will serve. As managers we have a duty to be specific in the questions we ask, and to ask them within a time frame that allows you to do your best in furnishing answers.

When all these decisions have been made and implemented, we have a park area and we have people using it. We come now to visitor interpretation. This is where science first entered the National Parks. It was naturalists, interpreting the uniqueness of our great natural areas, that were science's first representatives within the National Park Service. The role of science in interpretation is at least as important today as it was in the beginning. And now it has an additional task--the job of interpreting the impact on park areas and visitors of science's own stepchild, technology. The National Park System was founded on the bedrock of nature and history, and if we don't have our interpretive stories straight, we aren't doing our job.

Finally, we come to the DCPs--the development concept plans. Although our area roots are all embedded in the past, we are being dragged into the future willy nilly--and again we are faced with decisions. How do we deal with continuing park processes and changing visitor demands?

Science has a continuing task to keep our information current in *both* areas of science--natural and social. As managers we must remain constantly aware that parks and visitors are never set in any one condition for all time. Everything about a park area is in a constant state of change. Parks are process, and so are visitors, and so most of all is the interaction between them. We need all the information we can get on both parks and visitors, and we need to be alert to their ever changing natures.

One of the roles we share is the effort to *anticipate* problems. This forward-looking role is recognition that *there will be a future*, and that parks are not just for us, now, but also for future generations. A large part of meaningful science in parks is an attempt to project parks into the future.

Today park managers are still heroes. Help us continue to be the guys in the white hats. I think we're moving in the right direction, but let's quit doing it inches at a time. Let's make it meters-kilometers at a time: Park reorganization has put us into the mode of acceleration. Let's take a close look at how we can accelerate the integration of management, science and interpretation. Training, career opportunities, lateral movement between the fields--all of these possibilities are open and being scrutinized right now. Help us with your input.

Still unresolved is the issue of how much science should be done in-house and how much by contracting with outside research capability. A judicious mix of both seems best suited to our present Service needs. The NPS science staff should be developing the basic long-range understanding of natural area processes.

It should provide a clear, stored and retrievable picture of these processes. Then, within this larger context, specific management needs can be defined and urgent short-term research projects answering the needs can be let out on contract to universities or private research groups.

It is clearly necessary that we move toward enlarging our science staffs in the more seriously threatened parks. The kind of ongoing scientific monitoring that an in-house staff can provide is imperative if we are to cut our casualties. Redwoods, Indian Dunes, Everglades--our critical list is getting uncomfortably long.

The direction we are taking is to move massively, one step at a time. Everglades is our first giant step. I recognize that science in the parks as a whole is understaffed and underfunded. But to bring it up to a realistic standard across the board would be financially prohibitive and perhaps premature. A tested overall game plan is needed, and what we are doing in Everglades is being done with an eye to eventual Service-wide application.

At Everglades, we have committed ourselves to the establishment of a model science and resource management program. A building will be staffed by both resource managers and research scientists and dedicated to making these two functions strongly singular.

We hope and expect that this approach will bridge some of the existing gaps between resource management and research. We have created new science positions *in* the park and a science advisory board *outside* it. The integrity of the in-park program will thus be subject to the critical review of outside eyes. We have committed 450,000 additional dollars to the 1977 phase of this thrust, and added $2 million to the fiscal year 1978 budget.

I look upon the Everglades project as the first of what must become a System-wide assessment of our major natural areas. As we strengthen and tighten our research and management programs we expect to become increasingly successful. What we learn in the Everglades will help us formulate plans for the next major area to go the line for similar treatment.

I have recently set up a Task Force, headed by Deputy Director Briggle and including the NPS Chief Scientist and two members of Secretary Reed's Science Advisory Committee--Drs. Durward Allen and A. Starker Leopold. I have asked them to look at the overall NPS science effort--where it came from, where it is today, and where it needs to go in wedding science to resource management. The Task Force has an April 1 report deadline.

Two new opportunities have arisen recently for science to contribute to our Service mission straight across the board--in planning, design, management, operations, maintenance and interpretation. One of these is the Bicentennial Land Heritage proposal and the other is the energy crisis. Our efforts in response to both must clearly be tied to our science capability.

As we add to our System under the Land Heritage Act, and as we manage and interpret that system in energy-conserving ways, we have a chance to pioneer new territory--to discover better "fits" between man and the rest of nature. We can show the way ourselves, by scientifically wise management and maintenance practices, and we

can educate others by sound interpretation.

Advances in energy conservation already are underway. The new Lovell Visitor Center at Big Horn Canyon is solar-heated; at Gateway a windmill will soon be powering electric vehicles and the visitor center; and at Cuyahoga NRA in Ohio we're designing a park that will be entirely energy self-sufficient. Our energy conservation efforts are being coordinated by the Chief Scientist with the Director of Management Services and his Departmental conservation committee.

In conclusion, my specific questions are these: (1) How can management cut down on its mistakes? (2) What can technology do for us as park managers? (3) How can information management be used to launch needed research in a time frame that will coincide with management's need for answers? (4) What science information storage and retrieval technology is available and (5) how can it be adapted specifically to tie science and management into a closer, more productive working relationship?

These are our challenges and our opportunities. Neither science nor management has fully measured up to its responsibilities so far. Perhaps too much time has been spent contending *about* the job and too little in attending *to* it. People roll up their sleeves to do one of two things--fight or work. We've had enough of fighting. As long as our sleeves are rolled up, I suggest we get to work--mesh our efforts--fulfill our responsibilities.

Again, I appreciate the opportunity to welcome you to this gathering, and with your help at every field level I can assure you we can accomplish our goals for science and research in the National Parks. Thank you.

# CLOSING REMARKS

Robert M. Linn[1]

It's been great meeting all the old faces again; and even greater to see all the young scientists who are using the national parks as laboratories for their research. The success of this Conference is indebted to many, especially the following:

Lorraine Tucker and Carol Chisholm of the American Institute of Biological Sciences, who worked very hard (and succeeded admirably) in making a myriad of logistic decisions and arrangements;

All the good folks at the registration desk;

The Audio-Visual guys from Tulane University--I have personally never witnessed audio-visual arrangements that have been done so well and without mishap as the ones at this Conference;

The Program Committee members and session chairmen; and

Those who could not obtain institutional or governmental funds to travel here, but came anyway--sometimes at great personal sacrifice.

We look for and welcome any suggestions for improving the next Conference on Scientific Research in the National Parks, which ought to occur in about 3 years.

---

[1]National Park Service, Michigan Technological University, Houghton 49931.

# SUMMARY OF CONFERENCE

Stanley A. Cain
University of California, Santa Cruz

When I accepted the invitation to make some summary remarks, I had no idea of the magnitude of the program--three and a half days of program with many concurrent sessions, all on results of scientific research projects in the National Parks.

It is a far cry from the time 15 years ago when I wrote a plea for Research by the National Park Service at the request of the Chairman of the Advisory Board, and a far cry from my service as Assistant Secretary of Interior from 1964 to 1968 when I continued to stress the importance of scientific research in the National Parks and direct participation by scientists in the Service.

Therefore although it is a shock to heft the bulk of the abstracts of papers of this Conference, you can imagine how gratifying a shock it is. It is good to know how many scientists are doing research in the Parks, and especially what a relatively high percentage of them are Park employees or are receiving Park assistance.

I have done some counting. I will not impose the details on you, but merely approximate the statistics.

I find that there are about 350 separate contributions to the program and that, importantly, more than 300 of them are based on research in the parks. About 200 of the contributions have biological subject matter. More than 100 of them are by Park Service employees, including supported work at cooperative centers. Looking more closely at the involved Park personnel, I find that they come from throughout the Service: 54 individuals from a total of 18 different parks, 20 from Research and Service Centers, 21 from 9 University Cooperative Research Centers, and 47 from 12 different administrative centers including Washington, Regional Offices and the like. Park Service employed scientists have participated side by side with scientists of non-federal institutions. Papers came from the USDA, eight units including six different National Forests. Contributions have come from

three Atomic Energy Commission laboratories, five U.S. Geological Survey bases, as well as from the Army Corps of Engineers, the Bureau of Land Management, the Fish and Wildlife Service, Bureau of Outdoor Recreation, and the Public Health Service. In addition to the Park Service personnel and those of other federal agencies, I find representation on the program by five different state agencies, five private museums, five non-governmental organizations, six private corporations, one foreign agency, and four private citizens. Looking at the program another way, the contributors have official connections with 106 institutions of higher learning in 39 different states. Counting all kinds of contributions, every state in the Union is represented in the program.

In a sense this, the *First* Conference on Scientific Research in the National Parks, is a new phenomenon. After a very long gestation period, the concept is born fully mature. How ever logical the use of the parks is for appropriate research, it is comparatively recently that the National Park Service itself has employed significant numbers of well-qualified investigators not only to help work out management problems but to increase knowledge of natural conditions and phenomena of which many could be studied only in Parks.

How great has been the change in management's attitude toward research could be documented by many of us, but such comments are now pointless. Today we can and should express our appreciation to the Director, to the Chief Scientist, and to the Co-Chairmen for the Conference, one representing the National Park Service, the other the American Institute of Biological Sciences, as well as to the many cooperative Park Superintendents.

Having listened to as many papers as possible, I have heard a fair cross-section of the presentations in the several subject-matter sections with, however, a bias toward ecological matters. This hasn't been much of a bias, however, because ecological relationships are central to the studies of most of the participants.

Many of the papers might have been reserved for presentation before other forums such as the American Association for the Advancement of Science and the American Institute of Biological Sciences as well as the meetings of the individual specialized sections. I have become convinced that the authors were attracted to this conference because the Parks contain many of the best natural labora-

tories in America; but there seems to be a second strong reason, a desire to be useful as well as grateful to the Service. To this end a surprisingly large number of the studies are directed toward helping solve management problems. This is a double thrust. Many of the studies provide information that helps administrators see their way through complex and sometimes conflicting situations toward supportable decisions. Also many of the studies yield information that is suitable for the public that likes to know more about the attractions of the parks, hence for enriching museum and visitor-center presentations, campfire talks, etc.

In summary of a summary, I trust that it is not amiss for me to draw certain conclusions and make recommendations. You have given me the opportunity and I have tried to see the Conference as a whole and integral part of the Service's concern.

1. A large percentage of the papers on the program were matured recently and based on data gathered during the last 2 or 3 years. This suggests, and I therefore recommend, that the National Park Service plan to follow this conference with similar ones at 3- to 5-year intervals, for there promises to be an abundance of useful and interesting information that should be published promptly.

2. Although many if not most of the present papers would find ready publication elsewhere, they should appear as a Proceedings of this and subsequent conferences.

3. If the Service is to get full benefit from research in the parks, as many top-level management persons as possible should continue to attend future conferences. The "whole show" has a tremendously greater impact than the papers that deal with a specific interest or problem.

4. As soon as the Proceedings become available and NPS personnel have had a chance to peruse them, it would be useful to hold in-park seminars on pertinent subjects as a follow-up to this conference.

TV EDITORIAL

Read over New Orleans TV stations on November 8 and 9, 1976

This week New Orleans is hosting a quiet little conference that holds important and hopeful seeds for the future. The National Park Service and the American Institute of Biological Sciences are meeting with scientists and park managers from all over the United States to take their first joint look at scientific research in the National Parks.

To quote NPS Director Gary Everhardt: "This is our real, tangible way of saying we recognize that the National Park System is just a part of the total world biosphere. The problems we face in parks are only smaller versions of the problems faced by the entire world."

The great natural area parks in our System are there because they exemplify the highest quality environments that Earth has been able to achieve in the course of natural evolution. In today's energy-conscious society, we can look to these parks for vital clues as to how the great natural power systems of Earth function--the sun and wind and tides that keep matter cycling through all the living systems that support us.

National parks are superb examples of energy and matter in dynamic balance. The Park Service has a double mission--to *serve* and to *pre*serve. In its management role, the National Park Service must know as much as possible about how the natural systems work; and it must arrange to fit people and their needs into these systems with the least possible damage to the environment.

The research that goes on in parks is providing baseline information about the power and matter flow of the biosphere--that thin, fragile security blanket that makes all the difference between Earth and the other planets that circle our Sun.

Fitting people into high quality environmental systems and pre-

serving the quality--that, after all, is what we are essentially seeking to do, worldwide. To provide for people, efficiently and economically, taking full advantage of the natural energies that everywhere abound, is the challenge of the day.

As members of a highly technical modern society, we tend to pin our faith on technology. But Lewis Mumford told us 10 years ago that no technology ever invented by man is anything but a faithful imitation or a hideous caricature of some bio-technical process of nature. Instead of piling on another layer of technology, perhaps we ought to be stepping out of the way.

If parks can plug into the sun to heat their visitor centers; if parks can plug into the wind to power batteries for smooth, silent electric buses; if parks can plug into swamps and cypress domes to avoid building tertiary treatment plants, then the rest of the world should be taking a page from the Park Service book.

As usual, Shakespeare said it best: "Tongues in trees, books in the running brooks, sermons in stones and good in everything." The parks are eloquent teachers--especially when the lessons arise from our having stubbed our toe on nature.

New Orleans would do well to pay attention this week as the National Park Service holds its first conference on scientific research in the National Parks.

# YOUR MOVE! THE CHANCE AND CHOICE OF SCIENCE IN THE NATIONAL PARKS

Robert C. Euler[1]

I am most pleased and honored to have this opportunity to address a few brief remarks to this plenary session of the First Conference on Scientific Research in the National Parks. As an anthropologist and scientist who has long been concerned with the topic of this conference, I hope that I can present to you some cogent and productive thoughts based upon this experience.

At the outset, some clarification of my position -- and, hence, my biases -- may serve to place my remarks in a clearer perspective. My tenure in the National Park Service, aside from 1-1/2 years stint as a Ranger in 1948, is only entering its 3rd year. I am new to the internal operations of the Service, and there is much I do not know. Being relatively new, however, perhaps I can offer a relatively new viewpoint.

Secondly, I consider myself as an anthropologist to be scientifically oriented, not only to the social sciences, but especially to the natural sciences. In this, I should like to present a functional, holistic approach to science in the national parks. Natural and social or (cultural) resources must be viewed as functional interdependents, not separately. To put this another way, anthropology, at least cultural anthropology, in my view, is a part of natural science in which we study and attempt to understand human beings and their society and behavior. Since human societies no less than other animal societies are an integral part of nature, we can study them scientifically at all times and places. We do this functionally and holistically, relating each aspect of behavior to the other, to the whole, and to the natural environment. Human behavior thus viewed is a system, or perhaps in some instances a series of subsystems interacting with the natural environment. Scientific resources in our national parks, be they biological, geological, or cultural must be viewed systemically, not as disjointed parts.

Thirdly, I am a firm believer in basic research. Many national parks and monuments, protected as they are, unique as they are, present ideal research potential. Basic research by both Park Service and other professional scientists should be given every possible support and encouragement. This means that research projects should not necessarily be tied to *immediate* management needs but should be supported for their own sake. As has been voiced elsewhere, the significance of scientific resources in our parks cannot be evaluated in a research vacuum.

Intimately related to research is the necessity for an adequate and rapid publication system. I have forgotten now who it was who phrased that old saw: "Not publishing research is like winking at a girl in the dark; no one knows you're doing it."

Important, cogent research in the parks, or for that matter anywhere else, can be carried out only by scientists who possess what some have termed "the scientific spirit." It was Francis Peabody who remarked:

> A greater gain to the world than all the growth of scientific knowledge is the growth of the scientific spirit with its courage and serenity, its disciplined conscience, its habitual response to any disclosure of the truth.

The attainment of this scientific spirit is not easy. But, basic ingredients to its achievement include intellectual honesty, academic stimulation through colleagues and libraries, freedom of thought, inquiry, expression, and flexibility of activity. As G. Spencer Brown, in his book, THE LAWS OF FORM (1969), said a few years ago:

> To arrive at the simplest truth . . . requires years of contemplation. Not activity. Not reasoning. Not calculation. Not busy behavior of any kind. Not reading. Not talking. Not making an effort. Not thinking. Simply bearing in mind what it is one needs to know. And yet, those with the courage to tread this path to real discovery are not only offered practically no guidance on how to do so, they are actively discouraged and have set about it in secret, pretending meanwhile to be diligently engaged in the frantic diversions and to conform with the deadening personal opinions that are being continually thrust upon them.

This may seem to some to be a most unusual and stringent view, but I quote it because the lives of too many of us, scientists and others alike, are far too structured and mechanical.

In sum, my philosophy stresses the interrelationships of the sciences, the undeniable strength of well planned basic research, the dissemination of data through timely publication, and the acquisition and maintenance of the scientific spirit.

How are these thoughts reflected in National Park Service divisions? In looking at and posing questions primarily about *my own discipline* and the roles of scientists within the National Park System, I perceive several areas where innovations may be warranted. By way of introduction to this reflection, let me tell you of an interesting experience I had not long ago.

I had the privilege of speaking to a group of Park Service superintendents attending a seminar in resource management in one of our regions. Some of the stated objectives of that seminar, it seems to me, are germane to our meeting here. For example, one objective was "to reestablish our understanding of the basic values of the National Park System." To my way of thinking, cultural and natural -- that is, scientific -- resources are some of the most important basic values of the system -- the cultural ones being irreplaceable, non-renewable.

[1]National Park Service, Grand Canyon National Park, Arizona, and Southern Illinois University, Carbondale.

Secondly, the formulators of that seminar said that they wanted "to restate the priority position which management of resources holds among total service responsibility." Really, no one should argue with a position that suggests that if these resources are not to be irretrievably lost, their management deserves a very high priority indeed.

Thirdly, the participants of the seminar were asked "to reevaluate the specific responsibilities of park managers in relation to the management of these basic values." I submit that realistic understanding of the nature of scientific resources and planning for needed research is such an important responsibility.

Finally, the conferees were asked "to provide an atmosphere which will allow the reorder of area priorities." I remarked then, and I reiterate it now, that attitudes in our minds come about through interest, through understanding, through excitement, and through effective communication.

Let us look at functionalism in science for a moment. In my own field of anthropology -- especially in its archaeological aspects -- research is impossible without the functioning cooperation of botanists, zoologists, surficial geologists, hydrologists, and a host of other types of scientists. Human societies interact with the plants, animals, soils, water -- indeed with all of nature (unless I totally misunderstand ecology), and the archaeologist cannot begin to comprehend human behavior without close interdigiting with these other disciplines. The effect of human activity on land and water must be of some concern to them also. Hence, I am disturbed -- no, puzzled would be a more apt word -- when I see what I perceive to be a general dichotomy between the archaeologists in the National Park Service and those who are more frequently termed "scientists" or "researchers." I almost missed an opportunity to attend this conference because announcement of it was routed to "the researchers" and not to me because a secretary on our staff did not think a conference on science would be of concern to an anthropologist. In fact, I am told that anthropology was at first not considered an integral part of this conference for somewhat the same reasons.

Western Regional Archaeologist Roger Kelly, in his paper, "Strange Bedfellows?" prepared for presentation at this conference, has made some telling points in focusing on what should be mutual concerns of scientists from different disciplines. He mentions, as just one example, the problem of the effect of controlled forest fires on surface archaeological materials in the area to be burned. At Grand Canyon, anyway, biologists carried out "controlled" burns without any consideration for the impact they might have upon archaeological resources. Without any prior research data upon which to base an opinion, one biologist informed me that the fire would not have any adverse effect. I have just trudged through ankle deep ashes and charred stumps to locate previously unrecorded cultural resources to make at least an expostfacto assessment of his statement.

It should be a concern of managers to urge the dimming of the distinction between natural and cultural areas as much as is practicable in our parks. The administrative separation of scientists such as biologists and anthropologists should be eliminated. And scientists, if they are dynamic, should be in the forefront in proposing such a unification.

I have already alluded to my contention that research seems to be far down the priority list in our parks and that research immediately unrelated to administrative programs appears to be apathetically received if not in considerable disfavor. There seems to be ample funding for research when the administrator perceives a problem, little if any when the scientist perceives one. Let me again give one example. The Congressional passage of Public Law 93-620, the Grand Canyon National Park Enlargement Act, of January 3, 1975, transferred 185,000 acres of national park and national forest land to the Havasupai Indian Reservation. I do not begrudge this; certainly the Havasupai have needed a larger land base. But, long before this transfer, federal managers of the lands in question had been charged, by Executive Order 11593, with the responsibility of conducting a cultural resource inventory thereon. This had not been done. It is safe to say that more than 90 percent of the affected acreage had never been visited by an archaeologist. Furthermore, Executive Order 11593 clearly states that federal lands will not be "transferred" prior to the completion of a cultural resource inventory. But, the lands were transferred in what appears to be a clear violation of the Executive Order. What may be worse is that no one seems disturbed -- not the Park Service, not the Forest Service, not the Bureau of Indian Affairs, AND NOT THE ARCHAEOLOGICAL PROFESSION.

About a year ago, Kenneth Boulding of the Institute of Behavioral Science at the University of Colorado, published in SCIENCE (Boulding 1975) an editorial entitled "Truth or Power?" It dealt with the relationship between science and politics. If I may take the liberty of substituting the word "administrative" for "political" -- in some quarters, there is little if any difference -- Boulding's editorial would read in part as follows:

> The relationship between the scientific and the [administrative] communities is one of constant mutual frustration. There is a feeling on both sides that each ought to be able to help the other. The [administrative] community is constantly faced with making what it thinks are at least important decisions. Every decision involves the selection among an agenda of alternative images of the future, a selection that is guided by some system of values. The values are traditionally supposed to be the cherished preserve of the [administrative] decision-maker, but the agenda which involves fact or at least a projection into the future of what are presumably factual systems, should be very much the domain of science. Bad agendas make it much harder to make good decisions and if the decision-maker simply does not know that the results of alternative actions will be, it is difficult to evaluate unknown results. The decision-maker wants to know what are the choices from which he must choose. It is not surprising, therefore, that there is a demand for a one-armed scientist . . . without that infuriating other hand.

I hope, parenthetically, that you look upon me as neither one-armed nor infuriating.

Perhaps through mutual dialogue that aims at eliminating value judgments and ethnocentric biases on the parts of both the scientist and the administrator we may achieve desired and harmonious results that will benefit the parks and the American people.

Turning to the third concern I wish to discuss, that of the dissemination of information, I sense around me a pride in the results of publication. At least, there is a great deal of talk about it, especially on the part of the scientists. I am afraid that we are deceiving ourselves. The xeroxing of a few copies of a report for the files is not publication, and I suspect that hundreds of reports of potential scientific import lie buried in files where they remain unread by the scientific community. The National Park Service should be playing a leadership role in this area. Again, turning to my own field, I see a minimum effort to publish research results; and a frustration with the imponderable mechanisms through which it may be accomplished. In the western United States, two regions of the U.S. Forest Service are publishing timely and inexpensive offset produced studies based upon research in their areas. The Park Service should take immediate steps to establish editorial boards to judge the merit of and facilities to actually publish the results of scientific studies in its areas. This could be done not only in regional offices, but also in larger parks such as Grand Canyon. I realize that some of this is being done but it is not being accomplished to the degree of volume or timeliness that is neccessary.

I turn now to the final and perhaps the most important of the concerns that I wish to talk about -- that of the establishment and maintenance of the scientific spirit. Here, too, as with the other topics I have mentioned, I direct my attention to managers and scientists alike. This is also a realm that is fraught with frustration in both quarters. Administrators have little conception of how scientists work; scientists feel that administrators expect them to perform like mechanical clerks.

Administrators, through their often apathetic or even hostile attitudes toward science can do much to destroy the morale that comes with the scientific spirit. One brief example that quickly comes to mind is the recent experience of a National Park Service scientist who was invited to present a paper about his in-park research at an international meeting. Knowing that Service funds were not available for support, and deciding to use personal funds for travel following the meeting, the scientist made but one request. That was that annual leave not be charged against the time he was actually in attendance at the meeting. His request was denied in the regional office and he was told that he was not to consider himself a Park Service representative at the meeting. To add to this demoralizing position, the scientist was further told that the international gathering, incidentally celebrating the centennial of its existence, could not be very important or the scientist would have asked for the necessary travel funds to attend. I think that most would agree that that is one good way to dim the spirit and reduce the effectiveness of personnel.

Many scientists also have their professional utility reduced by being shunted into administrative positions that trained and efficient clerks could be performing. Yet it must also be admitted that some have come into federal service because of their inability or unwillingness to compete with their peers in a more professional sphere. I see many individuals who have been trained in the sciences simply vegetating in their secure positions. To those people I would say, if you are an 8 to 5 person, or one who would prefer to sort pencils or construct paper clip fly traps rather than to sublimate your professional life to the scientific spirit, you are in the wrong business. If you cannot accept the responsibility and discipline that comes with the flexible freedom to work as one chooses, you are not a scientist.

My primary suggestion here is for the establishment of any incentive program for scientists who demonstrate that they merit it. I do not mean monetary incentives, but rather I strongly believe that the Park Service should emulate the academic community and provide regularly scheduled sabbatical leaves for deserving professional scientists. In this way, further training, refresher courses, time for writing, and a stimulation of that scientific spirit could be obtained.

Allied to this, I believe that the Park Service should enter into cooperative agreements with colleges and universities to provide short courses, of less than a semester's duration, for Service scientists. This could do much to upgrade the capabilities of many of our intellectual vegetarians.

Let me indicate to you, finally, that these are but my ideas, voiced, I hope, constructively. They run the usual risk of over-generalization and I am sure that my criticisms do not apply to all. Yet, if they stimulate one administrator or one scientist, my effort will be repaid.

It is your move administrators! You can make a choice and not leave to chance the important collaborative decisions that must be made if science in the parks and science and the parks are to flourish. Look realistically at what scientific research can offer you, boost its priorities, take time to understand scientific attitudes, and positive results will accrue.

And it is also your move scientists! You, too, can make the choice rather than gamble about the contributions that you can make. Speak out, take an active part with responsible aggressiveness, seize the scientific spirit, and be excited about your careers.

Together we can enhance our lives and those of untold numbers of visitors to the parks in the future, at the same time, we can make lasting contributions to knowledge.

## LITERATURE CITED


BOULDING, KENNETH. 1975. Truth or Power? Science 190:423.

BROWN, G. SPENCER. 1969. The Laws of Form. London: Geo. A-len and Unwin.

KELLY, ROGER E. 1976. Strange BEdfellows? Tangent Points of in-park cultural and natural resources research. Ms., First Conference on Scientific Research in the National Parks.

# THE HOLE IN THE SYSTEM: A GREAT PLAINS NATIONAL PARK

Durward L. Allen[1]

A widely recognized and traditional purpose of our National Park System is to preserve representative samples of North America's choice scenery and natural land and water types. It is also an acknowledged ideal that the great wilderness parks, most of which qualify under the "national park" category, should be complete and self-operating ecosystems in whatever degree that is possible. According to longstanding criteria, a "national park" is large in size, has several outstanding features, and is inviolate against exploitive uses. This distinguishes it from monuments, which can have a single major preservation feature and be more subject to disturbing influences. Classic examples of national parks are Yellowstone, Mount McKinley, Great Smokies, and Everglades. Good examples of monuments are Saguaro, Organ Pipe, and Death Valley. Obviously, there are areas worthy of preservation in units of other types, for example bogs or tracts of virgin timber in recreation areas.

There are also land reorganizations that could upgrade the National Park System. One that comes immediately to mind is the possibility of a Sonoran Desert National Park that could include Organ Pipe and the Cabeza Prieta National Game Range on the Mexican border in Arizona. There are possibilities for an international park, in case the Government of Mexico wished to participate by adding their outstanding caldera area in the Sierra del Pinacate immediately to the south.

As short-handed as the National Park Service has been in the past decade, it is understandable if everything is not getting done. At present Alaska's problems are taking up slack where there is none, and that will continue for a while. However, we have an historic need that will not go away, and I propose to help keep it before us as an objective for attention as soon as it becomes feasible. We have no major park that truly represents the Great Plains, and the grasslands in general have been neglected.

This is not to ignore the excellent examples of grassland vegetation, with some appropriate animal species, in such areas as Wind Cave National Park, Theodore Roosevelt National Memorial Park, Badlands and Devil's Tower National Monuments, the National Bison Range, and Wichita Mountains and Valentine National Wildlife Refuges. But grassland is not just grass, and its true beauty and productivity cannot be appreciated unless it is complete with its natural complement of forbs and animal life. Grassland animals include the large and small, the vegetarians and the carnivores, and they need space to utilize their range and pursue their seasonal behaviorisms in the natural manner. As true grassland parks, all of the areas mentioned fall short on size and the fauna they contain. Setting aside any area in the west for public use always is complicated by the indigenous attitude that all grass should be grazed by domestic livestock.

To avoid misunderstanding, it should be made clear that I am not discussing the tall-grass prairie that has been under consideration in the Flint Hills of Kansas. This is a particular type of grassland, essentially a phase of what Weaver (1954) and others designated the "true" prairie. It lay adjacent to the forested lands to the east, and on the lower, more moist sites was characterized by the tall grasses such as big bluestem *(Andropogon gerardi)*, Indian grass *(Sorghastrum nutans)*, switchgrass *(Panicum virgatum)*, and sloughgrass *(Spartina pectinata)*. Especially on uplands, it was dominated by many of the not-so-tall midgrasses, most notably little bluestem *(Andropogon scoparius)*.

The true prairie developed some of the most productive agricultural soils on earth, and it is understandable if such areas are almost totally under the plow. In the Flint Hills, rocks at the surface restrict cultivation, and the grazed prairie vegetation could easily be restored to something like its primitive condition. This prospective park would not be of a size to accommodate the larger mammals in a wild state and qualify as a complete ecosystem. However, it could be an attractive sample of the tall-grass vegetation, with many of the smaller animals that belong there. I assume it would be 50-60 thousand acres.

As a generality, we can say that the eastern prairies occupied a region of forest climax, with a moist subsoil, and they were maintained in a grass "disclimax" (disturbance climax) condition by recurring fires. Some of them are hardly recognizable today because the cessation of fires after the beginning of agriculture permitted forest invasion of uncultivated lands. However, the areas of deep, black, level soils in northern Indiana, northern Illinois, and Iowa are obviously of prairie origin. The land is mostly in a one-year "rotation" to corn, and crop ecologists say they are putting back all they take out. In another quarter-century, we may be able to judge that more accurately.

For conceptual purposes I find it convenient to regard the true climatic grassland, if there is such a thing, as beginning (at the mid-states latitude) beyond the Mississippi River in eastern Nebraska, where the tall grasses largely disappear and several kinds of midgrasses become dominant. Westward it includes certain short grasses; hence it is the "mixed prairie", the most extensive of our grassland types. Nearly all of these types include a great array of largely perennial and deep-rooted forbs that made the open lands an ever-changing garden of flowers through the season. Few people of today have any idea what the magnificently attractive prairie flora was like.

The mixed prairie is underlain by a dry subsoil and a mineral hardpan or lime layer usually at a depth of 4 to 5 feet in the east, where annual rainfall is about 25 inches. As we proceed west into regions of lower rainfall the lime layer rises to within a foot or so of the surface.

[1]Department of Forestry and Environmental Sciences, Purdue University, West Lafayette, Indiana 47907.

I regard the mixed prairie north of Nebraska as offering the best possibilities for a Great Plains National Park. Historically the region was highly productive in both diversity and quantity of animal life and offers great interest in terms of seasonal change. It probably was the prime habitat for both buffalo and the Plains Indians of a century and a half ago.

The principal dominant grasses of this region are the needle grasses *(Stipa* spp.*)*, western wheatgrass *(Agropyron smithii)*, Junegrass *(Koeleria cristata)*, the dropseeds *(Sporobolus* spp.*)*, little bluestem and side-oats grama *(Bouteloua curtipendula)*. Short grasses that occupy a lower level in the open stands are mainly blue grama *(B. gracilis)* and buffalo grass *(Buchloe dactyloides)*, the latter being replaced northward by several sedges *(Carex* spp.*)*. Progressively westward onto the high plains, the midgrasses give way to the short grasses. Weaver and Albertson (1956), confirming earlier work by Clements (1916), and Shantz (1923), observed that short grasses gained ground over the midgrasses as a result of heavy grazing. The same factor reduced the short grasses in turn and permitted such inferior forage as big sage *(Artemisia tridentata)*, rabbitbrush *(Chrysothamnus* spp.*)*, and prickly pear *(Opuntia* spp.*)*, to take over. Sagebrush ranges are now particularly prevalent in Wyoming and Montana.

Earlier I indicated some indecision as to whether a "true" grassland climax exists. This is a question hinging largely on whether one considers fire as an intrinsic attribute of climate. In semi-arid lands that can support a vegetation thick enough to burn, fire is a universal occurrence. "Natural" lightning fires are difficult to separate from man-caused fires, since men have been setting fires for many thousands of years. I tend to follow the thinking of Sauer (1950) and Stewart (1951), that practically every grassland would be invaded by woody vegetation in the absence of fire. On our northern prairies the evidence is convincing in the stands of chokecherry *(Prunus virginianum)*, wolfberry *(Symphoricarpus occidentalis)*, buffaloberry (*Shepherdia argentea*), silverberry (*Eleagnus commutata)*, sumac *(Rhus* spp.*)*, and other woody plants that have escaped burning for a number of years. Favorably situated ravines, other rough topography, and upwind-facing waterfronts are taken over by coverts that bespeak the effect of fire dynamics on local sites. Wells (1965), pointed out the role of topography, soils, and bedrock formations in preserving scarp woodlands in the grass country. He concluded that there are species of woody plants that can survive in practically all areas where grass does not produce enough thatch to burn effectively.

Our grasslands develop their most salient characteristics and greatest stability on large, relatively level open spaces, where they have the earmarks of a climax. I am satisfied to regard them as such with the understanding that fire and the normal complement of animal life were built-in maintenance mechanisms. The park we are discussing would need to incorporate these features, although it would not be objectionable if it included some rough lands illustrating the diversity of the region. For this same reason, it should be far enough west to grade into the short grass and sagebrush habitats of the high plains.

The idea of such a park is not new; Shelford (vide 1940) and others were discussing the need for grassland preservation early in the century, and he is reported as suggesting a great plains park to the National Park Service as early as 1930 -- a move that had support in the Ecological Society of America. In 1940 Cahalane described a plan for a Great Plains National Monument in southwestern South Dakota and northwestern Nebraska. I was not aware of Cahalane's detailed plans at the time I carried out my own field reconnaissance during several summers of the early sixties, and it gave me some reassurance to discover that I finally centered my own interest in the area he recommended. It is open and undeveloped, although private and public lands are all grazed. Both Shelford (1940) and Cahalane decided that a million acres would be needed to create a truly representative and self-contained park, a view to which I subscribe.

Extensive field surveys have been carried out in all parts of the country by personnel of the National Park Service in determining the park needs of the country. I am told that they too are in general agreement that the area where South Dakota, Nebraska, and Wyoming come together should have first consideration in locating a great plains park. It could turn out to be a tri-state area. There are butte lands across the Wyoming border that could be an attractive inclusion, and the possibility of taking in a corner of the Nebraska sandhills should not be neglected. A major consideration in the plan offered here is that the park must avoid any towns or primary highways. If the area in question proves to be unfeasible, then the northwest region of South Dakota should be investigated. It seems to offer outstanding opportunities, although I have been through it only once.

Let us visualize an area roughly 26 by 60 miles, with the long axis from east to west. It would need to be west of the Pine Ridge Indian reservation; the exact shape would depend on topography and other considerations. The park probably should center around a height of land, since it would have to be surrounded by a barrier fence -- a development that might cost as much as a county road. Much of this duplicates Cahalane's original plan.

The fence would need to be proof against bison and wolves, which would be, in their wild and unmanaged association, a unique feature of the park. The outflowing drainageways, commonly dry, would require some engineering at the fenceline, and these might include waterholes designed to conform to the scene. The fence would have an interior bordering service trail, but on the outside it should be as far as possible from any access road.

As a preliminary plan, we can assume that this park would have two entrances -- east and west -- connected by a network of strategically located, blacktop, 30 mph, one-way auto trails. There would be many turnouts and rest stops, but no other developments. Except for a visitor center and administrative headquarters, all of the outside public accommodations could be privately owned. In concession stands, native crafts illustrating the rich culture of the Plains Indians should be featured.

This would be a daytime park to which the public could be given almost unlimited access in their own automobiles. They could witness the habits and interrelations of animal life at leisure in open vistas permitting every observational advantage. Experience indicates that nearly all animals would become accustomed to

slow moving vehicles and largely ignore the human presence. Such a park should be closed at night. The roads would serve a valuable management function as fire breaks for the controlled burning that would be required to maintain a healthy grassland community. Under such a regime it is predictable that the vegetation would recover its primitive aspects and composition and that exotic plants now widespread in the region would be reduced through competition with adapted native species.

The dominant animals of this grassland, and its outstanding attraction, would be the free-living, unmanaged plains bison and its only important native predator, the wolf. As a rough estimate, and depending greatly on location and range conditions, I would expect that a million-acre fenced range might support 8,000 buffalo (about 40 bands) and 200 wolves (15 to 20 packs). Numbers would fluctuate with trends in rainfall and other weather factors. Pronghorns would supply a portion of the food of the wolves, as would elk and deer in case wooded ridges and/or stream bottoms were included.

The Great Plains National Park would be a primary refuge for scarce and endangered mammals and birds, including the black-footed ferret, swift fox, prairie falcon, and golden eagle. Inevitably, it would support an attractive and varied display of grassland birds. Jackrabbits, prairie dogs, and many kinds of ground squirrels and other rodents would provide food for aerial predators as well as such carnivores as the coyote, bobcat, and badger.

It needs to be pointed out that a species can be endangered biologically, even though it is not on the official list, and this applies particularly to the plains bison *(Bison b. bison)*. In all our parks this subspecies is being managed like livestock, subject to annual handling, culling, dipping, and brucellosis vaccination. In a state of nature these management functions are performed by the wolf according to criteria largely unknown to human judgment. The plains park would be the one place where the bison could live in the wild, recover its old, wide-ranging habits, develop normal socially organized bands, and have its speciation directed by carnivore selection as it was in primitive times.

Finding a proper wolf for a grasslands park will be a major biological problem. Depending on location, the area probably would be at or near the presently recognized border-line (region of intergradation) between the extinct great plains wolf, *Canis lupus nubilis*, and the northern Rocky Mountain wolf, *Canis l. irremotus* (vide Goldman 1937, Hall and Kelson 1959). Both preyed on the buffalo, and the western form *irremotus* evidently still hangs on as a scattered remnant in the Wyoming-Montana-Idaho region, where Yellowstone and Glacier National Parks are potential sanctuaries. Whether these wolves can be restored naturally to a viable population is only a tenuous possibility at present, but conceivably public attitudes are changing enough to make this possible. If it happened, a source of wild stock would be available.

On the other hand, some captive wolves that probably are *irremotus* or even *irremotus* x *nubilis* have been held and propagated by Jack and Marjorie Lynch at Gardiner, Washington -- the only such animals in existence to my knowledge. Jack Lynch and others are studying the history of these animals, whose progenitors were captured in the wild by Biological Survey trappers in the 'teens and twenties through the urgent requests of the late Dr. E. H. McCleery, of Kane, Pennsylvania. McCleery bred his wolves and is said to have kept the blood lines distinct.

When the current studies are complete, Lynch will be more certain of what he has. Preliminary inspection of some original catch records indicates that the animals came from Montana. This would make their descendants priority number one for introduction to a great plains park, if wild *irremotus* are unavailable. This group of captive wolves is also a potential back-up in case the precariously situated wild wolves of the Yellowstone-Glacier region disappear.

The wolves at Gardiner, Washington, are in excellent condition, kept in large pens and in socially compatible groups. Jack Lynch's study of their origin is being aided by the endangered species staff of the Fish and Wildlife Service. If these animals can be confirmed as *irremotus*, in whole or in part, their preservation is a matter of public concern. It should no longer depend on the practically unfunded E. H. McCleery Lobo Wolf Foundation and the devotion of a few people. The Lynch effort is urgently in need of assistance.

Over the earth, for some thousands of years, men have been changing grasslands into desert. The process continues, although since the drought years of the thirties range scientists have greatly improved their knowledge of provident management in various grazing lands of the western states. Commendably, they have also managed to get some of our plowed-up semiarid lands back into grass before the next drought period.

However, there is much more progress to be made, and one of the primary needs is for control areas where mature grassland communities can be studied -- their natural production, their degree and mechanisms of stability. Aside from being a superlative area for public observation, a Great Plains National Park would have unique scientific value. We have already learned that some of our research on the behavior and relationships of animal life can best be carried out on undisturbed and unmanaged lands and waters. This is a major value of wilderness, and we cannot say now that we have any authentic grassland wilderness.

Even the park I am proposing would not duplicate the primitive because of extinctions (plains wolf and grizzly, Eskimo curlew) and the presence of exotic species. This need not deter an effort to achieve what is possible, and although there are uncertainties, the result could be very good indeed. It must be emphasized that that size is part of the ecology of the grassland community. A million-acre park (nearly half the size of Yellowstone) will be much more than the sum of its parts.

It is a platitude to say that the time to establish national parks was long ago -- when (bless Yellowstone!) some of it actually was done. With some foresight, we could have had a great plains park easily in the drought period of the thirties, an opportunity that could be repeated. The need for recreational open space, scientific reserves, and wilderness preservation has been increasingly recognized -- as it progressively becomes more difficult. With the growth of population, every economic asset on land and water is under competitive demand. This casts no aspersions; it simply states that a nation with too many people, and more to come, could experience a catastrophic mutilation of its natural scene.

Organizations and individuals concerned for the problems and rights of future citizens are increasingly embattled to save anything in its original form. In many areas where parks are being established-- especially urban areas-- local interests must be bought out at prices that are possible only because the government can print dollars. A park in valuable grazing land undoubtedly would be expensive, but it would not compare with some of the other ventures the Congress and the National Park Service have undertaken.

The Great Plains National Park would be like nothing else we have, and for once we could start in an undeveloped area and apply all that has been learned. On at least two occasions recommendations have been made to the Secretary by the National Parks Advisory Board that the National Park Service carry out further surveys and develop plans for the great grassland park that is our most obvious "hole" in the nation's program of wildland preservation. This much, at least, would not be prohibitively expensive, and if it were done, I have no doubt that there are many members of Congress who would be interested in the proposal.

There is much at stake, and it certainly is worth a try.

LITERATURE CITED


CLEMENTS, FREDERIC E. 1916. Plant succession. Carnegie Inst. Washington Publ. 242.

GOLDMAN, EDWARD A. 1937. The Wolves of North America. Jour. Mamm. 18(1):37-45.

HALL, E. RAYMOND and KEITH R. KELSON. 1959. The mammals of North America. Ronald Press, N.Y. 2 vol.

SAUER, CARL O. 1950. Grassland climax, fire, and man. Jour. Range Mgt. 3(1):16-21.

SHANTZ, HOMER L. 1923. The natural vegetation of the Great Plains. Assoc. Amer. Geog. Ann. 13:81-107.

SHELFORD, VICTOR E. 1940. The need for grassland reservations and grassland research. Canadian Field-Nat. 54:5-7.

STEWART, OMAR C. 1951. Burning and natural vegetation in the United States. Georg. Rev. 41: 317-320.

WELLS, PHILIP V. 1965. Scarp woodlands, transported grassland soils, and concept of grassland climate in the Great Plains. Science 148 (3667):246-249.

WEAVER, JOHN E. 1954. North American Prairie. Johnson Publ. Co., Lincoln, Nebraska 348 pp.

_____ and ALBERTSON. 1956. Grasslands of the Great Plains. Johnson Publ. Co., Lincoln, Nebraska 395 pp.

# RESEARCH ON ENDANGERED FISHES IN THE NATIONAL PARKS WITH SPECIAL EMPHASIS ON THE DEVILS HOLE PUPFISH

James E. Deacon and Maxine S. Deacon[1]

Fishes living in National Parks of the Western United States have physically adapted to the torrential currents, and shifting, unstable substrates of the Colorado River. They have developed humps, apparently for stability at the bottom; fusiform bodies, with slender caudal peduncles and expansive fins for maximum power in the swiftly moving current; large size, including the largest minnow in the world at more than eighty pounds; reduced or embedded scales, and relatively small eyes, characteristics of fishes living in silt-laden streams. Most of these features are expressed to varying degrees by the native fishes inhabiting Grand Canyon National Park.

The most extreme hump is exhibited by the humpback chub, *Gila cypha;* the most extreme fusiform shape by the bonytail chub, *Gila elegans;* and the largest size by the Colorado Squawfish, *Ptychocheilus lucius*. Both above and below Grand Canyon National Park the bizarre razorback sucker, *Xyrauchen texanus,* occurs, apparently having adapted to less torrential stretches of the river. This species occupies some reservoirs of the mainstream Colorado. Its decline and extinction in many reservoirs built within its native range, but its persistence in others, remains a puzzle. Some information is available on spawning, feeding, and relative abundance in some areas. It has also been successfully spawned and reared in hatcheries.

At a quite different physical extreme, we also have fishes adapted to the extreme ranges of variability in salinity, temperature, and quantity occurring in the waters of Death Valley National Monument. Here are species of the genus *Cyprinodon* living in waters that occasionally form a thin film of ice in the winter, and reach maximum temperatures of about 43°C (109°F) in summer. The salinities range from relatively low to concentrations several times that of sea water. Salt-encrusting algae form steep-sided, shallow pools which eventually build a roof of salt. Occasional flash floods may sometimes turn an isolated pool, a few meters in length and a few centimeters in depth, into a portion of a river over a hundred miles in length. Seasonal variations in evapotranspiration isolate some portions of a creek as small, warm, increasingly saline pools. In such habitats, the importance of surviving a few hours during the hottest part of the day becomes critical. The zone of resistance (Fry, 1971) or resistance time (Brett, 1956) therefore, may be one of the most important adaptive features of this group. On a longer time scale, in the Death Valley region, climatic shifts have created at Devils Hole what may be the smallest habitat in the world containing the entire genome of a vertebrate species.

Man's competition for water has pervaded every aspect of his occupation of the western United States. Irrigation practices required establishment of a set of societal rules almost as soon as irrigation began. A major portion of our present federal and state water law was developed in response to the demands to formalize the right of landowners to the surface and subsurface waters on their lands. As the resource became reduced, competition for the resource increased and society was forced to establish priorities and make hard decisions relative to its use.

During the expansionist period of settling the west, society's definition of "good" heavily emphasized the values of economic and population growth. More recently we have been shifting our definition of "good" toward more qualitative values. Not surprisingly this shift toward quality involves the necessity to mediate through the courts, the inevitable conflicts that arise between adherents of the expansionist philosophy and those who believe that quality of life is society's most pressing need. The reflection of these societal values in judgments being handed down by the courts is evident in the clear and concise but eloquent language of Federal District Judge Roger Foley of the District of Nevada. In his Findings of Fact and Conclusions of Law which appeared in a permanent injunction granted by him on 9 April, 1974, Judge Foley wrote as follows: "The United States has shown that the public interest lies in the preservation of this endangered species. Congress has enacted the Endangered Species Conservation Act (16 U.S.C. 688aa.), and the Secretary of the Interior pursuant to that statute has identified the Devils Hole pupfish, *Cyprinodon diabolis,* to be an endangered species. Witnesses offered by the United States testified to the importance of the species to mankind. Congress, state legislatures, local governments, and citizens have all recently voiced their expression for the preservation of our environment, and the destruction of the Devils Hole pupfish would go clearly against that theme of environmental responsibility."

Defining, interpreting and demonstrating the benefits to be gained through practicing environmental responsibility may be the most important contribution the National Park Service can make to the future of the U.S.A. The Park Service has played a key role in reorienting the administration of the waters of the West toward increased recognition of qualitative values in the environment. The Devils Hole pupfish case stands as a landmark! The Park Service will continue to play an important role in establishing priorities for the use of water in the West. It is currently widely assumed that if water is needed for people, the people will get it -- somehow! What is less well understood is that the people *need* the water for purposes other than drinking, irrigation and power. These other qualitative needs are beginning to be established, and the National Park Service is and must continue to play a central role in that trend.

It has been well established that the large main-stream dams on the Colorado have caused significant detriment to the native fishes (Vanicek, 1967; Vanicek and Kramer, 1969; Vanicek *et al.*, 1970; Holden and Stalnaker, 1975). In addition to interrupting movements of native fishes which may have been necessary for successful spawning, dams have significantly lowered the water temperatures downstream, in many cases

[1]University of Nevada, Las Vegas, Nevada, 89154.

precluding successful spawning of native fishes. In Grand Canyon, the closure and operation of Glen Canyon Dam has resulted in a significant lowering of water temperatures downstream. Some introduced fishes, such as carp, red shiner, and green sunfish have been pushed downstream by the lower water temperatures. At present, it appears that the introduced forms in Grand Canyon may have been more adversely affected than the native forms (Figure 1). Collections of fishes made in 1968 show most introduced forms occurring upstream to Lee's Ferry, just below Glen Canyon Dam. Summer water temperatures below Glen Canyon Dam dropped from about 20°C in 1968 to about 10°C following achievement of full pool level in Lake Powell, and fish collections subsequent to 1968 show some introduced forms occurring further downstream or restricted to mouths of tributary streams. By contrast, the native fishes have not shown such severe downstream restriction although they have declined somewhat in abundance. This relationship should be watched closely in the future since it could be quite significant to the survival of the threatened and endangered fishes living in Grand Canyon. For example, the native fishes may simply have longer life spans than the introduced forms and, therefore, require a longer period of time to show the detrimental effects of lowering water temperatures. It is also possible, however, that the native species have found suitable spawning areas in tributary streams or elsewhere in the mainstream and that adults are better able to survive in the cold tailwaters than are some of the exotic species. Recent collections leave little doubt that the lower little Colorado River is important to the humpback chub, *Gila cypha* (Suttkus and Clemmer, personal communication; and R.R. Miller, personal communication).

It may be especially significant that Grand Canyon is not being intensively managed to enhance the sport fishery for cold water game fish. Thus, the native fishes are apparently competing primarily with warm water species that have moved upstream from Lake Mead. It is commendable that the National Park Service has sponsored studies that have developed a reasonably good data base on the fishes of Grand Canyon National Park and obvious that additional information on life history of the native species is needed to develop management alternatives that would insure their continued survival.

It seems especially important to examine the thermal ecology of the native forms. Where and at what temperatures they spawn, pass the fry and fingerling stages, and what their thermal tolerance limits at all stages of the life history are. The intriguing point is that there seems to be a possibility that we may be able to manage the waters within Grand Canyon to enhance the native species.

Probably the two most striking features of the environments in which pupfishes of Death Valley have evolved are the highly variable conditions of temperature and salinity. Much attention has been directed to the constancy of the head spring environments. The fact that much tectonic activity is, and for at least the past few million years has been, occurring in the Death Valley region suggests that most head springs are probably quite transitory. The differentiation that has taken place among the pupfishes, therefore, has probably been most influenced by the variable conditions of temperature and salinity characteristic of the marshes.

The critical thermal maxima for *C. diabolis*, *C. milleri*, and various populations of *C. nevadensis* have been determined by Brown and Feldmeth (1971), Otto and Gerking (1973), and James (1968) to be about 42-44°C. Maxima for long term survival probably are near 38°C. Low temperature tolerance is less well documented but in most cases is near 2°C. Brown and Feldmeth *(op. cit.)* viewed C. diabolis as having evolved in a thermally constant environment, similar to the present condition of Devils Hole. This interpretation may be untenable in view of the clear evidence of higher water levels in Devils Hole, and the evidence developed by Mehringer and Warren (1976) of marked changes in water availability in the Ash Meadows area over the past several thousand years. While the species is strongly differentiated and has probably been isolated from other pupfish populations in Death Valley longer than other forms, its habitat may also have been thermally variable.

Observations of responses of *C. n. nevadensis* to thermal variations at Saratoga Springs, Death Valley National Monument (Deacon, 1967, 1968) follow closely results of experimental determination of CTM. Fish have been seen swimming voluntarily at temperatures between 8° and 42°C. They occasionally dart quickly in and out of areas in the marsh with temperatures up to 44°C. At temperatures below 7°C fish are not seen in the marsh but can be collected by seining through the soft bottom mud. Measurements of diel activity as expressed by catch per trap hour in the marsh at Saratoga Springs illustrate the influence of temperature on activity. On 25-26 January, 1967, temperature at the mud-water interface in the marsh fluctuated between 15° and 23°C. These temperatures are within the mid-range of thermal tolerance for *C. nevadensis*. Catch rate shows a distinct bimodal pattern with peak periods of activity in morning and evening (Figure 2). This is also the basic pattern expressed under normal conditions, in the main spring pool (Figure 3) where water temperatures fluctuate narrowly between 26.5° and 31.0°C throughout the year. During summer, water temperatures in the marsh commonly exceed 38°C during mid-day and mid-day depression of activity remains evident, perhaps in this instance enforced by high temperature (Figure 4). While no activity occurs at the minimum winter temperatures, a single daily activity peak occurs in the early spring as the water begins to warm up. This condition is evident from data taken on 24 March, 1967 (Figure 5). Thus, it appears that *C. n. nevadensis* exhibits a bimodal pattern of diel activity under moderate temperature conditions and that at temperatures below 15° and above 38°C, activity is reduced or ceases entirely.

Similar observations have been made on *Crenichthys baileyi* and *Crenichthys nevadae* (Hubbs and Hettler, 1964; Hubbs *et al.*, 1967; and Deacon and Wilson, 1967). In those species activity is restricted at high temperatures and low oxygen concentrations. It seems probable that scope for activity will be reduced as either thermal or oxygen stress is placed on the individual. For example, since reproductive behavior is metabolically demanding it will be abandoned as scope for activity is reduced. Similarly, since feeding probably occurs primarily during peak activity, metabolic demands for assimilation will likely reach a peak a short time after peak activity has occurred. If, as Fry (1971) suggests, the metabolic cost of assimilation reduces the scope for activity, it is reasonable to expect minimum activity during a period of food assimilation, especially when the CTM is closely approached. The same result (reduced activity following feeding) could also be expected under conditions of high salinity if osmoregulatory demands effectively reduce scope for activity. These are both potentially fruitful research opportunities for fishes living in osmotic or thermally stressful environments, such as occur in Death Valley National Monument.

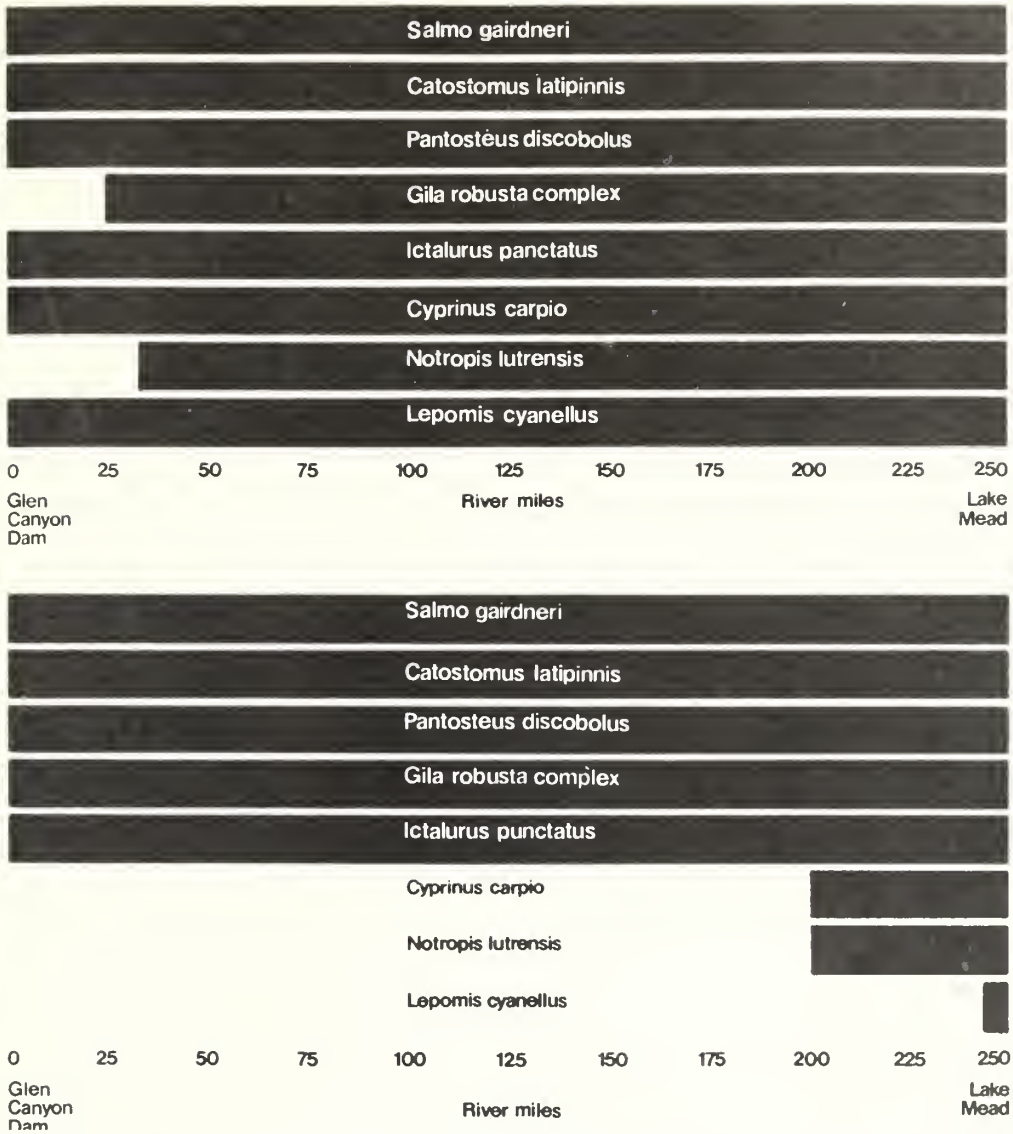



FIGURE 1. Distribution of some native and introduced fishes in the mainstream Colorado River in Grand Canyon, 1968 (upper) and 1975 (lower).

Defense of territories and presence of breeding colors during the summer is common in the marsh at Saratoga Springs until mid-day temperatures rise above 35°C. No fish were seen defending territories or with well-developed breeding colors at temperatures above 38°C (Figure 4). Shrode (1974) showed that eggs of *C. n. nevadensis* would develop at constant temperatures between 20° and 36°C (but not at 38° and 18°C); however, development would occur when temperatures fluctuated between 30-38°C, 20-28°C and 28-36°C. Clark Hubbs (personal communication) has recently shown that *Cyprinodon* eggs will develop up to a constant temperature of 37°C. Thus, it appears that reproductive activity is discontinued at temperatures which rise above those compatible with normal egg development. Furthermore, the primary spawning period occurs during spring and early summer when environmental temperatures never exceed limits compatible with development. Occasionally during mid-summer, environmental temperatures may exceed 38°C and result in egg mortality in the marsh habitat. Shrode's data indicate that developmental temperature tolerance of *C. n. nevadensis* is unusually wide, a situation that is also true for adult pupfish. On the other hand, Gerking (personal communication) has recently shown that critical thermal limits for ovulation of normal ova in this subspecies are quite narrow. Critical thermal maxima for young pupfish exceed that for adults. Thus, under maximum thermal stress, egg mortality will be followed by adult mortality, while young fish will survive the longest. Critical thermal maxima for two-month-old fish acclimated to 36°C was determined by Shrode *(op. cit.)* to fall at about 44°C.

Man induced changes in the Death Valley region have been rapid and with far-reaching consequences. Because all individuals of distinctive species or subspecies occupy very restricted habitats in this area, the changes have more rapidly affected the entire population than has been the case in larger, and more diverse habitats of the Colorado River system. Illustrative of these changes is the extinction in 1958 of both *Empetrichthys latos pahrump,* formerly occurring only at the Pahrump Ranch, Pahrump Valley, Nevada. Irrigation withdrawals resulted in drying up the only springs containing populations of these subspecies (Minckley and Deacon 1968). Except for two transplanted populations, one at Corn Creek Spring, Clark County, Nevada, the other in a plunge pool on the Lake Mead National Recreation Area, the third subspecies, *E. l. latos,* and last remaining representative of the genus living at Manse

(Bowman) Ranch, Pahrump Valley, Nevada, would have suffered the same fate during the summer of 1975 when the last remaining natural habitat occupied by the genus *Empetrichthys* temporarily dried up as a result of irrigation withdrawals.

Except for successful litigation which went through the U.S. Supreme Court, a similar fate would, in all probability, have been the lot of the Devils Hole pupfish. This species is restricted to a single limestone cavern in Ash Meadows, Nevada. The cavern system was made a disjunct portion of Death Valley National Monument in 1952 by President Truman. Information on population sizes is available since 1967. Beginning in April 1972, scuba divers have been used to assist in visually counting the population throughout the entire depth of Devils Hole in which it occurs. The cavern system is quite extensive, and is only incompletely mapped (Figure 6); however, *Cyprinodon diabolis* occurs only in the area of sunlight penetration. While it regularly occurs down to 26 m the population is far more concentrated near the surface. Water temperature in nearly constant at 33°C, and other physical and chemical characteristics of the water are also nearly constant (Dudly and Larson 1974). Since the water surface is about 23 m below the contour of the mountain in which the hole occurs, the water surface receives little sunlight. The time during which sunlight falls on the water surface changes seasonally, resulting in marked seasonal variation in primary productivity.

Beginning in 1969, significant variations in water level were superimposed on the seasonal variations in sunlight as a factor of primary importance in controlling population size of *C. diabolis*. These changes have resulted from ground water pumping in the nearby aquifer (Dudley and Larson, 1974). The purpose of pumping is for irrigation of pasture and hay crops to be used for raising cattle.

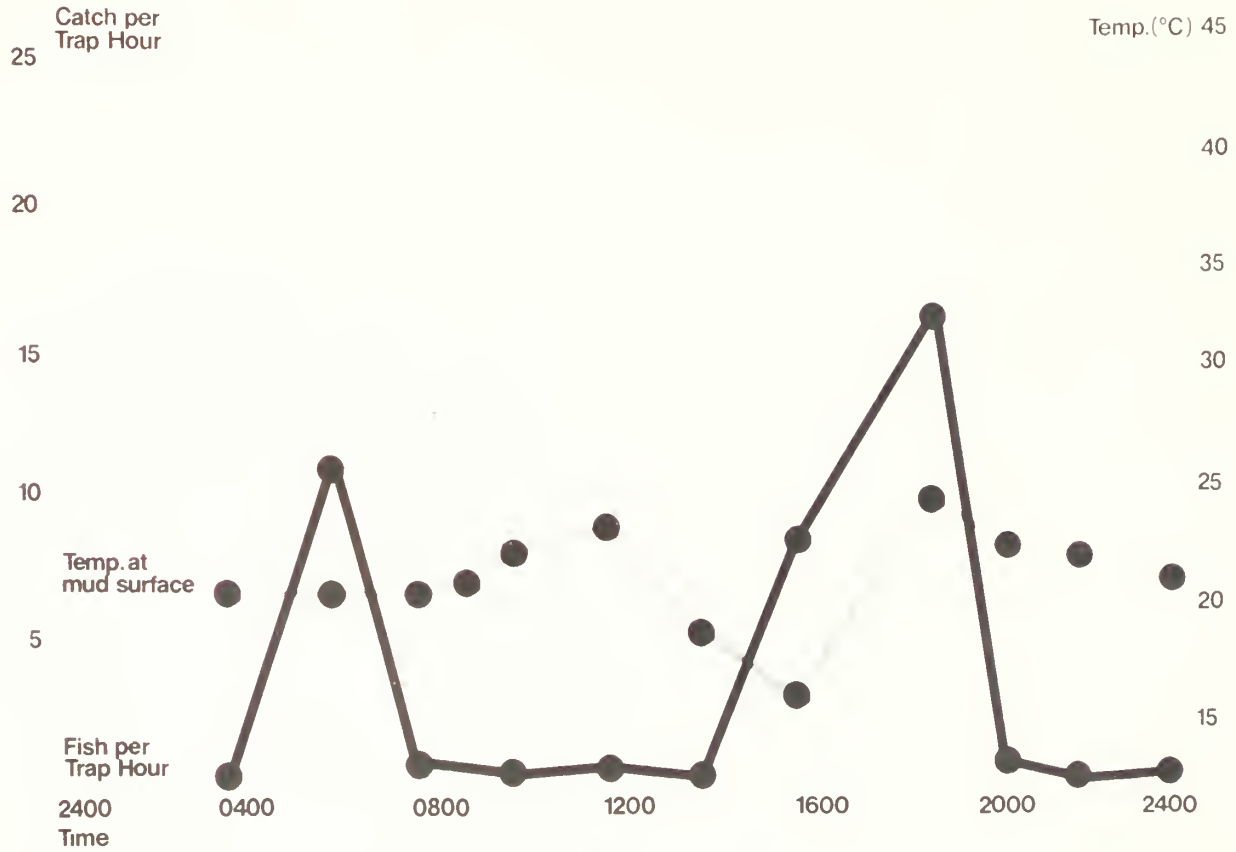



Figure 2. Diel variation in catch per trap hour in the marsh at Saratoga Springs, D.V.N.M. 25-26 Jan. 1967
Water temperature -15 -23 °C.

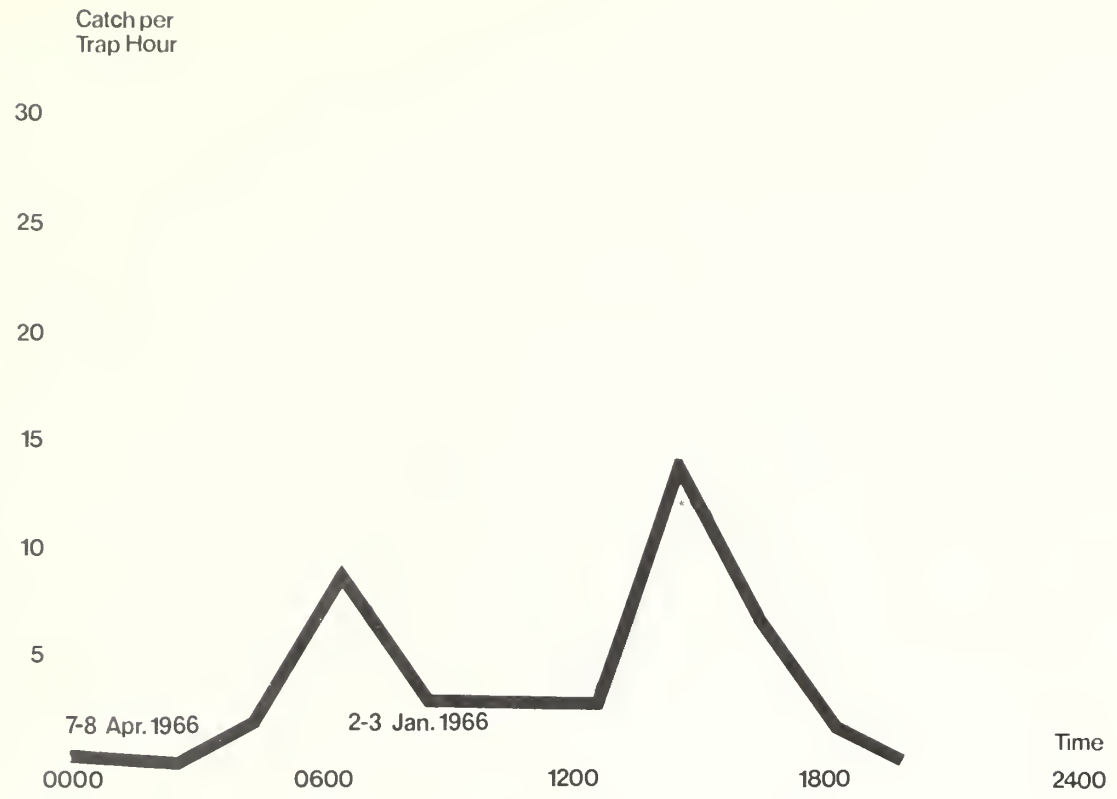



Figure 3. Diel variation in catch per trap hour in the constant temperature main spring pool at Saratoga Springs, Death Valley National Monument. Water Temp. 26.5-29°C.

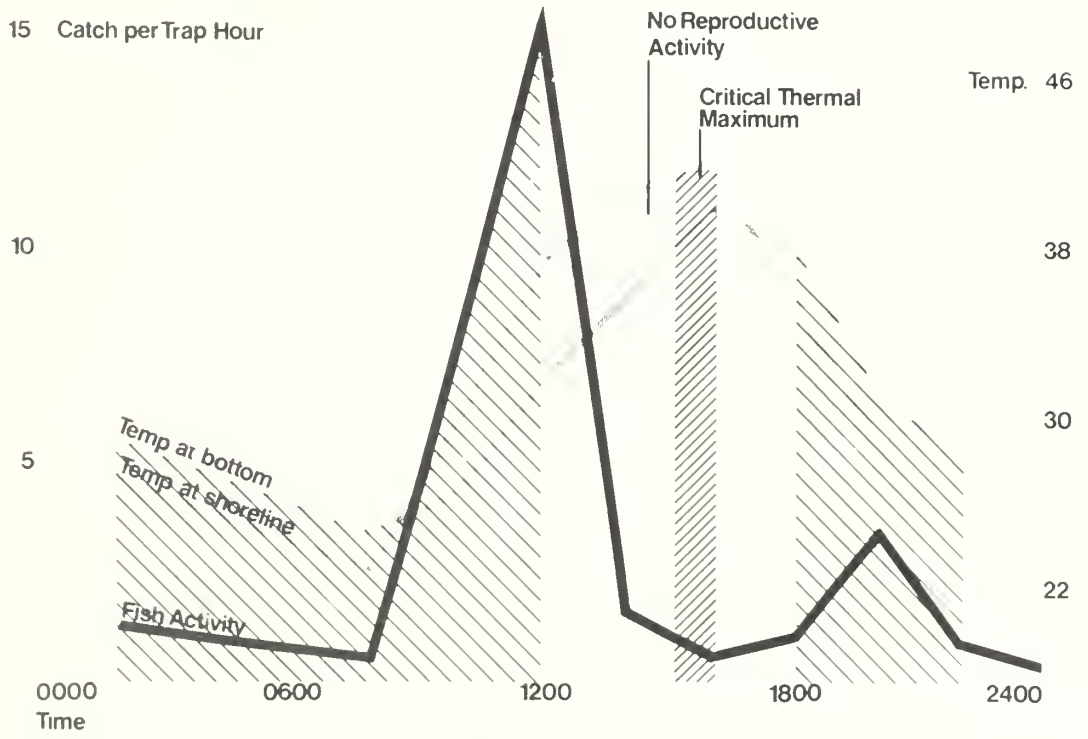



Figure 4 Diel variation in catch per trap hour, reproductive activity and temp. in the marsh at Saratoga Springs, Death Valley National Monument, 18 August, 1966.

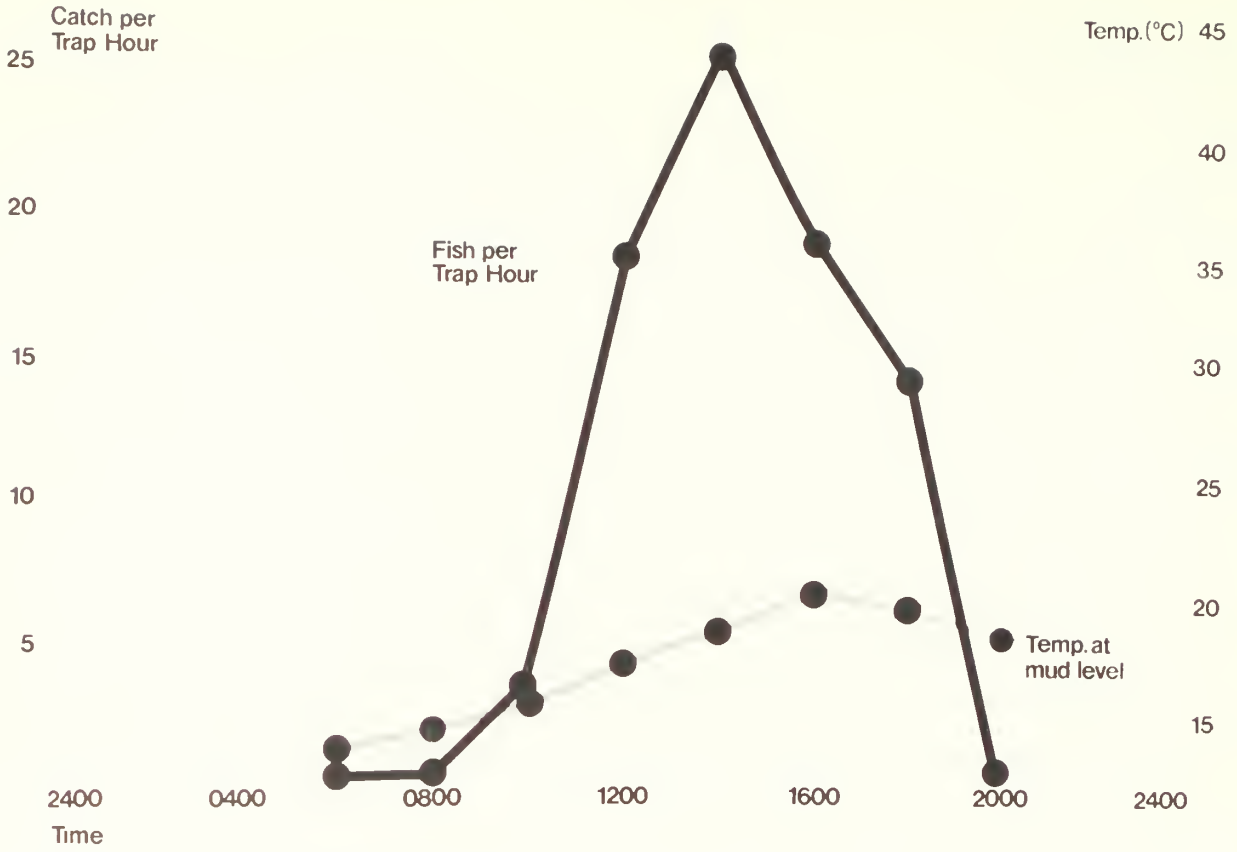



Figure 5 Diel variation in catch per trap hour in the marsh at Saratoga Springs D.V.N.M. 24 March 1967

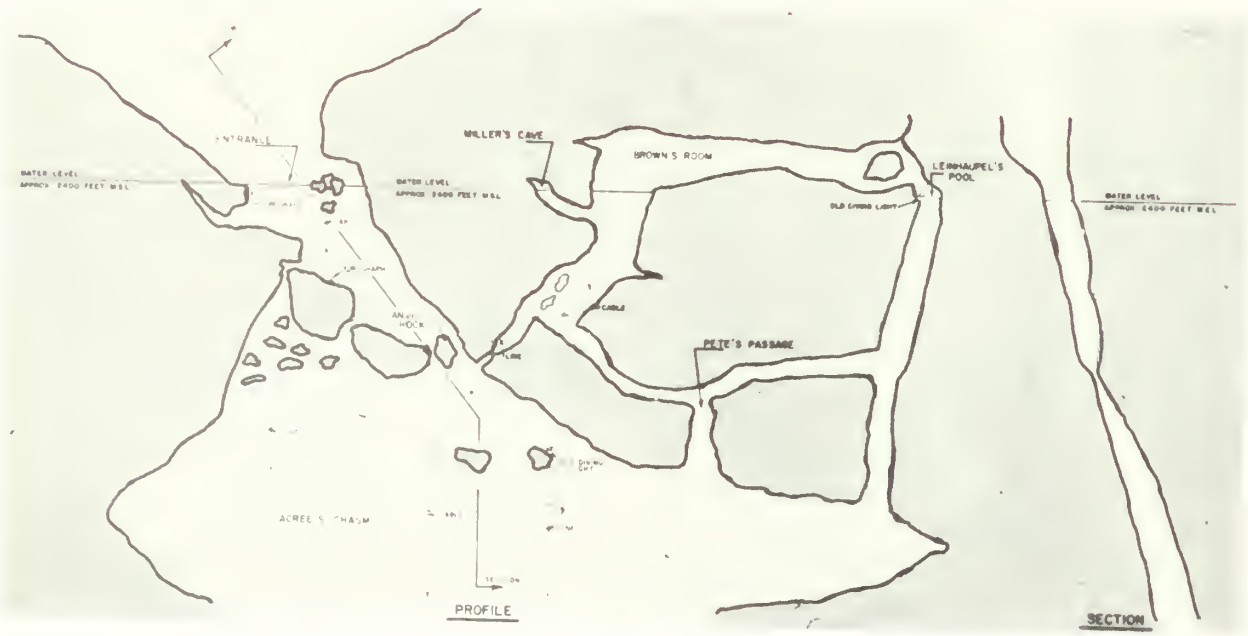



Figure 6 Vertical section of Devils Hole, Death Valley National Monument.




Figure 7. Monthly low water levels at Devils Hole, 1967–73.




Figure 8. Fluctuations in estimated population sizes of juvenile and adult Devils Hole pupfish, April 1972 – Dec. 1976.

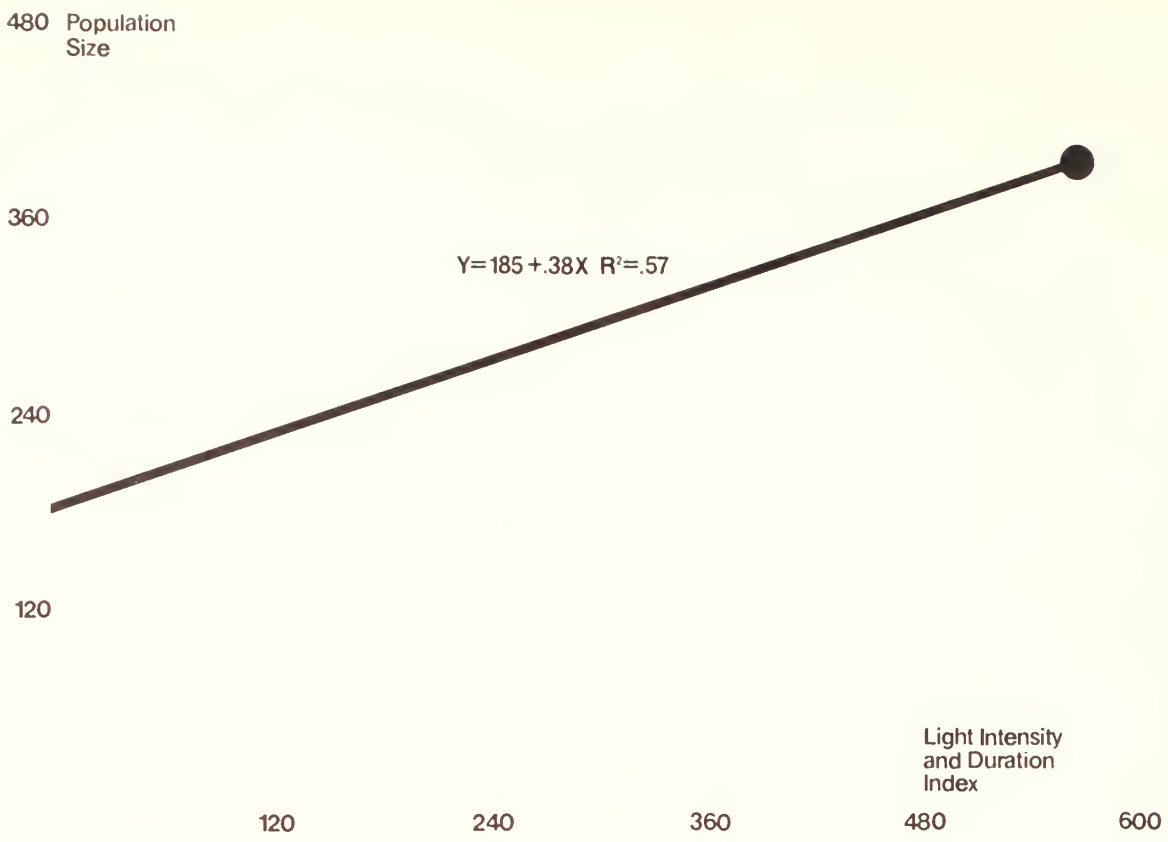



Figure 9 Light intensity and duration correlated with population size two months later.

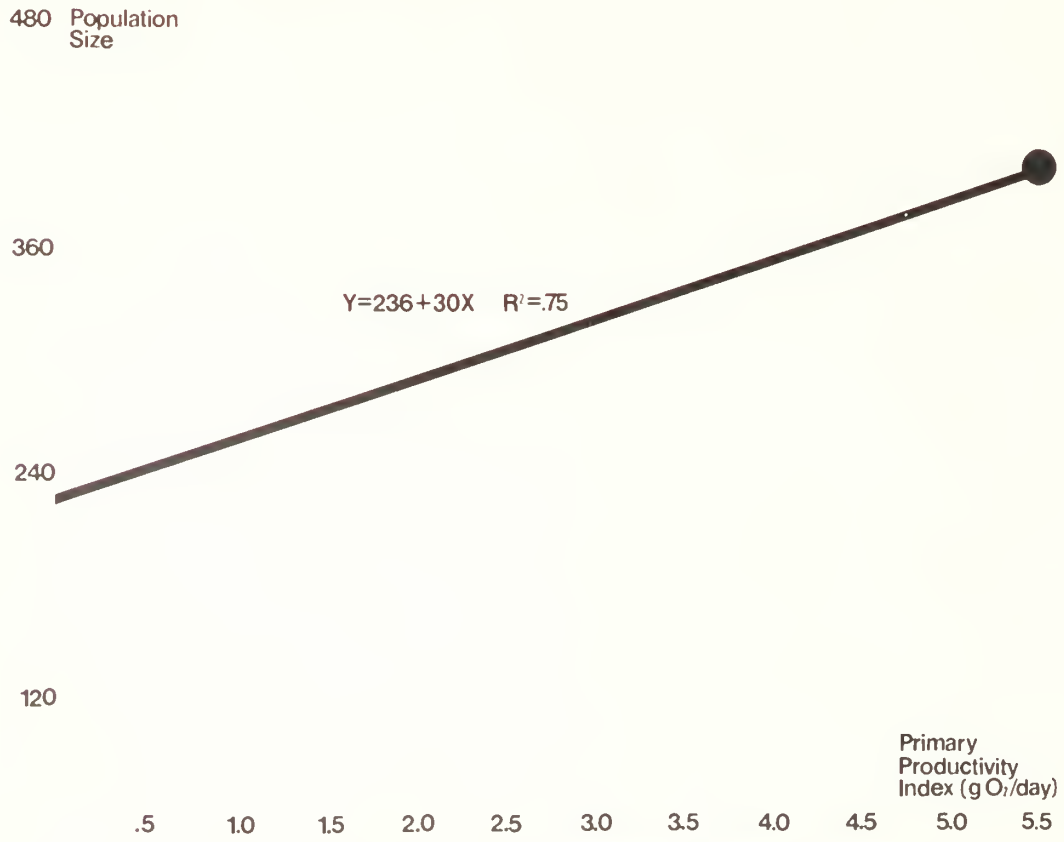



Figure 10 Primary productivity index correlated with population size one month later.

On 20 September, 1972, water level in Devils Hole reached its historic minimum of 1.19 meters below a USGS reference point installed on the rock wall above the water surface. This was the culmination of a downward trend that became evident in 1969 (Figure 7). Frequent census data beginning in April 1972 (Figure 8) shows that, beginning from what was probably an all-time historial low population (of juveniles and adults), the population increased to July 1972. Between July and September, as the water level fell to its lowest point, the fish population also crashed. During this period, subsequent and prior data indicate that a continued population increase would normally be expected. The crash, therefore, is probably attributable to a reduced carrying capacity resulting from low water levels. At the low point, all of the loose gravel and rubble that could reasonably be removed, was removed from the natural shelf in an effort to increase the available habitat. In addition, artifical lights were installed in hopes of increasing the primary production. The fish population responded by increasing its numbers to about 250 by January, 1973. At that point the artificial lights were turned off, and the water level continued to rise. Within a month the population had declined. By March, probably because of the onset of spawning (Minckley and Deacon, 1973), a slight increase was noted. Between March and June when the next census was taken, a flash flood carried large amounts of debris down onto the natural shelf, and NPS personnel, in order to enlarge the habitat, again removed the debris. The result was that during this period, rather than exhibiting its normal spring increase, the population declined. On June 5, 1973, the court appointed a Special Water Master to oversee a permanent injunction granted on that date. The injunction was for the purpose of maintaining sufficient water in Devils Hole to tend to insure the survival of *C. diabolis*. From that time until July 1976, the water level was managed so as not to fall below 1.01 meters below the USGS reference point. The result has been that since June 1973 there has been a relatively regular fluctuation in population size. On 2 July, 1976, the water level began to be managed so as to remain above .91m. Actually water levels rose to about .82m below the reference point. The population responded by increasing to about 400 individuals on September 24, 1976 (Figure 8).

We believe to tend to insure the survival of the species, the minimum population size should not fall below 200 individuals. It appears that the maximum population is about twice the minimum. Therefore, a desirable maximum should fall at about 400 individuals.

We have some information (less precise for 1967-68 than for 1972-76) on maximum population sizes prior to pumping and, therefore, can arrive at some estimates of the requirements for achieving a summer maximum of 400 individuals on the basis of regression analysis. Using data available on maximum population size and water level for 1967, 68, 72, 73, 74, 75 and 76 we find a correlation coefficient of .86 with an $R^2$ of .73 at the 95% level of confidence. This suggests that a maximum population of about 400 individuals could be expected at a water level of about 0.73 meters.

Data on population sizes for 1972-1976 are more accurate as mentioned previously. If we eliminate the less accurate 1967 and 1968 data and examine only the better data, we again find a high correlation coefficient of .81 with an $R^2$ of .65 at the 95% level of confidence. Note that the slope for this line is somewhat steeper than was previously true, indicating a more pronounced effect of water level on population size. Again, however, we find that a maximum population size of about 400 individuals can be expected at a water level of about .73 meters below the reference point.

The influence of seasonal variations in light duration and intensity on population size of *C. diabolis* is evident from data acquired in 1975-76. Pyrheliometer recordings show that, with a lag time of about 2 months, population size increases as sunlight duration and intensity increases. The relationship is strong with a correlation coefficient of .76 and an $R^2$ value of .57 at the 95% level of confidence (Figure 9).

A third and perhaps even more directly influential parameter affecting population size is the total primary productivity of the area circumscribed by the natural shelf. We have developed a PPR index based on diel fluctuations in $O_2$ content of the water. This information, however, is limited to the months of May through October since sunlight intensity and duration on the water surface during other times is insufficient to stimulate sufficient primary productivity to be measureable using our present methods. The data do show, however, that, with a lag time of about 1 month, population size increases as the primary productivity index increases (Figure 10). The correlation coefficient of .86 with an $R^2$ of .75 at the 95% level of confidence again suggests a relatively high correlation for a natural system.

The primary productivity index is based on fluctuations in concentration of dissolved oxygen over the natural shelf. As the volume of water over the natural shelf increases, a larger biomass of plants can be accommodated and, to that extent, the volume of water over the natural shelf may also influence the primary productivity index. In effect, this means that as water volume increases, potential for primary production also increases. This potential is realized only when the sun's rays are able to fall on the water surface. Total production of the pool thus can be maximized only by increasing the water volume during a period of increasing light intensity. Since typically during the period 1970-76 water volumes have been decreasing during periods of increasing light intensity, it is evident that the decreasing water levels have caused a depression in the population size that would have been reached under more stable conditions. The important point demonstrated is that increasing sunlight appears to stimulate increased production which in turn results in increased numbers of fish.

The regression formula of primary production on fish population size suggests that a productivity index of 5.47 grams $0_2$ per day is necessary to achieve a maximum summer population of about 400 individuals. Frequent measurements of the primary productivity index from 26 July - 3 September 1976 show that total production estimates over the shelf ranged between 1.8 and 5.5 $g0_2$/day. The highest sustained productivity index per unit volume (1.9 $g0_2/m^3$) during the period occurred on 26-28 August, 1976. If that index is held constant (probably possible only during periods of maximum sunlight) and water level increased, the regression formula shows that a productivity index of 5.5 $g0_2$/day could be expected at a water level of about .82 meters below the USGS reference point.

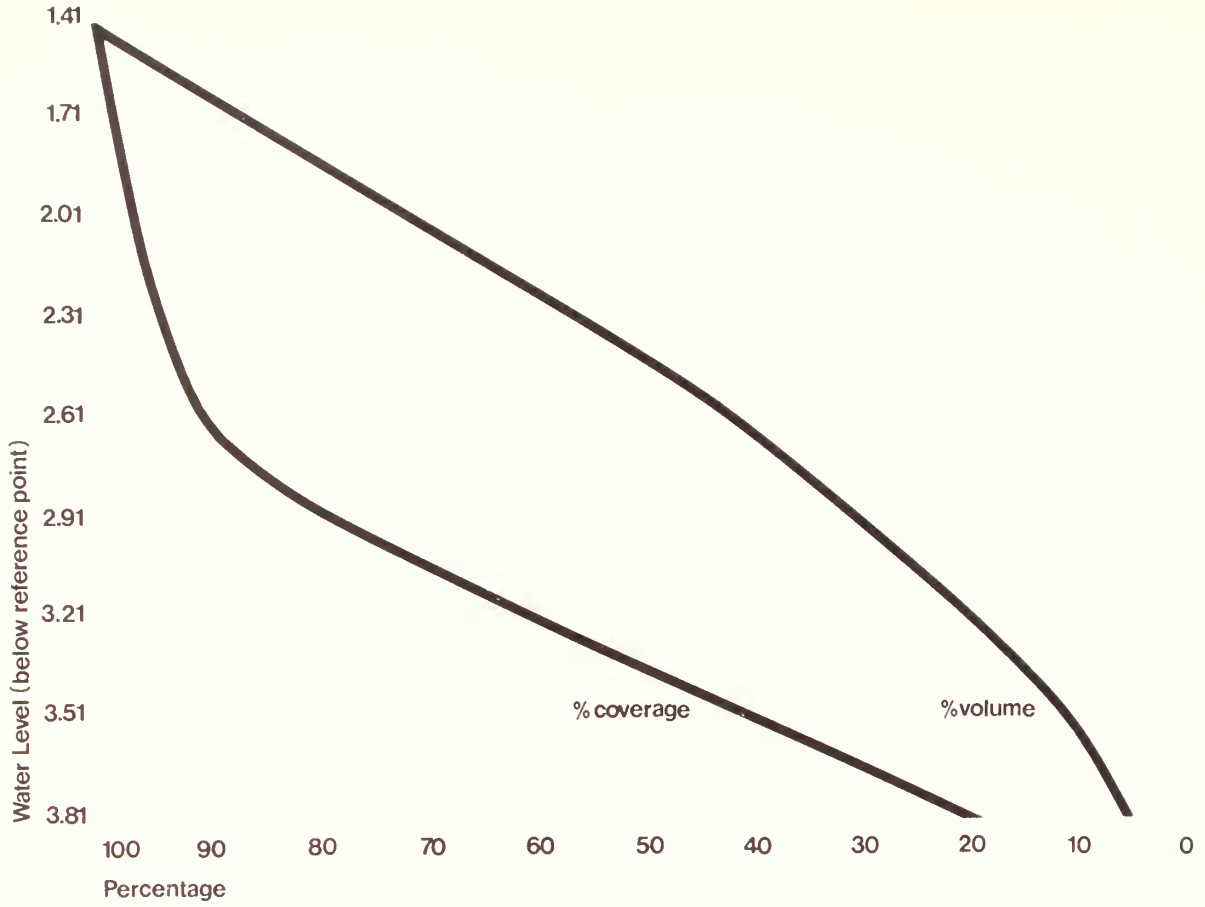



Figure 11 Percentage changes in surface area and volume of water over the natural shelf at Devils Hole as a function of water level.

An examination of the changes in surface area of Devils Hole as a function of water level (Figure 11) shows that if 0.43 m. below the copper washer is taken as 100%, .73 represents about 90% coverage, .82 represents about 85% coverage, .91 represents about 70% coverage, and 1.01 represents about 40% coverage. In estimated volumes these four levels represent 51%, 38%, 25%, and 16%, respectively. Since a fish lives in three dimensional space, the volumes represent more realistically the space available for the bulk of the important feeding and breeding activities of this species. Our data thus suggest that this species would probably fluctuate between about 200-400 individuals if water levels were maintained at about .82 m., thus providing about 38% of the volume and 85% of the surface area of the original, prepumping pool level.

As we alter our societal values, competition for use of water intensifies because one segment of society insists on retaining rights which another segment insists must shift to permit expression of other values. The importance of expressing societal values through legislation, resolution, publication, legal action, establishment of National Parks, and any other reasonable and legal manner, has been dramatically portrayed by Judge Foley's reference to such evidence as being of importance in reaching his landmark decision. Research in the National Parks is essential not alone for the intrinsic value of knowing, but also because that knowledge will frequently be essential to help guide decisions that give expression to society's values.

LITERATURE CITED

BRETT, J. R. 1956. Some principles in the thermal requirements of fishes. Quart. Rev. Biol. 31: 75-87.

BROWN, J. H. and C. R. FELDMUTH. 1971. Evolution in constant and fluctuating environments: thermal tolerances of desert pupfish *(Cyprinodon)*.

DEACON, J. E., ed. 1967. The ecology of Sarasota Springs, Death Valley National Monument. Report to National Park Service. mimeo. 104 pp.

DEACON, J. E., ed. 1968. Ecological studies of aquatic habitats in Death Valley National Monument, with special reference to Saratoga Springs. Report to National Park Service. mimeo. 82 pp.

DEACON, J. E. and B. L. WILSON. 1967. Daily activity cycles of *Crenichthys baileyi*, a fish endemic to Nevada. Southwest. Nat. 12(1):31-44.

DUDLEY, W. E. and J. D. LARSON. 1974. Effect of irrigation pumping on desert pupfish habitats in Ash Meadows, Nye Co., Nevada. U.S.G.S. open file report 74-188. Denver, Colo. 142 pp.

FRY, F. E. J. 1971. The effect of environmental factors on the physiology of fish. Chap. 1, pp. 1-99, *In:* Hoar, W. S. and D. J. Randall. Fish Physiol. Vol. 6. Academic Press, N.Y.

HOLDEN, P. B. and C. B. STALNAKER. 1975. Distribution and abundance of mainstream fishes of the middle and upper Colorado River basins, 1967-73. Trans. Am. Fish. Soc. 104(2):217-231.

HUBBS, O., R. C. BAIRD and J. W. GERALD. 1967. Effects of dissolved oxygen concentration and light on activity cycles of fishes inhabiting warm springs. Amer. Midl. Nat. 77:104-115.

HUBBS, C. and W. F. HETTLER. 1964. Observations on the toleration of high temperatures and low dissolved oxygen in natural waters by *Crenichthys baileyi*. S. W. Nat. 8:245-248.

JAMES, C. J. 1969. Aspects of the ecology of the Devils Hole pupfish, *Cyprinodon diabolis* Wales. M.S. Thesis. Univ. Nev. Las Vegas, Las Vegas, Nev. 70 pp.

MEHRINGER, P. J., JR. and C. N. WARREN. Marsh, dune and archeological chronology, Ash Meadow, Amargosa Desert, Nevada. pp 120-151. *In:* Elson, R. (ed.). Holocene environmental change in the great basin. Nev. Arch. Sur. Research Paper No. 6, July 1976, Reno, Nevada.

MINCKLEY, C. O. and J. E. DEACON. 1973. Observations on the reproductive cycle of *Cyprinodon diabolis*. Copeia. 1973(3):610-613.

MINCKLEY, W. L. and J. E. DEACON. 1968. Southwestern fishes and the enigma of "Endangered Species." Science. 159:1424-1432.

OTTO, R. G. and S. D. GERKING. 1973. Heat tolerance of a Death Valley pupfish (Genus *Cyprinodon*). Physiol. Zool. 46(1):43-49.

SHRODE, J. 1974. Genetic and temperature effects on development of the Amargosa pupfish. Ph.D. Thesis. Arizona State Univ., Tempe, Ariz. 61 pp.

VANICEK, C. D. 1967. Ecological studies of native Green River fishes below Flaming Gorge Dam, 1964-1966. Ph.D. Thesis. Utah State Univ., Logan, Utah. 124 pp.

VANICEK, C. D. and R. H. KRAMER. 1969. Life history of the Colorado squawfish, *Ptychocheilus lucius*, and the Colorado chub, *Gila robusta*, in the Green River in Dinosaur National Monument, 1964-1966. Trans. Am. Fish. Soc. 98(2):193-208.

VANICEK, C. D., R. H. KRAMER and D. R. FRANKLIN. 1970. Distribution of Green River fishes in Utah and Colorado following closure of Flaming Gorge Dam. Southwest Nat. 14(3):297-315.

# THE NPS AND INFORMATION: A NEEDED PARTNERSHIP

Charles Douglas[1]

There is more information available than we know what to do with. Information scientists have seen the problem coming for many years, but they have not been able to forestall it. The problem is here and can only get worse. Before we look at the future, let's see what has been done and what is being done now.

The amount of literature related to managing and long-range planning for natural resources is no exception to the dilemma posed by the enormous amount of available information from all sources. Coping with the environment is an involved enterprise. Knowledge of the environment is initiated from many sources: biology, chemistry, the atmospheric sciences, health sciences, air pollution, water resources, civil, electrical, and mechanical engineering, energy, legislation, transportation, social, management, political, and economics, to name but a few.

Many indexing and abstracting services already exist in several areas that would be of interest to environmental scientists: Chemical Abstracts, Biological Abstracts, Nuclear Science Abstracts, Physics Abstracts, Water Pollution Abstracts, Engineering Index, Environmental Abstracts, the NASA Star, and the Government Research Abstracts. There are also other publications relating to topics that are of interest to environmentalists such as journal articles, congressional hearings, documents, theses translations, conference proceedings, and monographs.

With all of this information being generated, it is no wonder that the computer has been called upon to assist in its storage, manipulation, and retrieval. At the present time there are collections of machine-readable data produced by both the federal government and commercial organizations which can be searched for some aspects of the environmental literature.

For several years now, the concept of a total environmental information system has been postulated. In Stockholm in 1972 the United Nations Conference on the Human Environment recommended an information referral service. Participants in this conference suggested "a modest and practical tool to tell what information services exist, where they are, and how to gain access to them." In 1972, William Ruckelshaus, then head of the Environmental Protection Agency, commented on our uncoordinated or nonexistent information retrieval systems and stated that environmental information is generated by at least 75 different sources within the federal government.

In 1973, the United States Congress passed a bill which allowed the U.S. to participate in the United National Environmental Program (UNEP). This program was devoted to the development and support of an international system for the exchange of information. In 1972, Congress proposed the establishment of a national environmental data system. This system was to serve as the central point "for the selection, storage, analysis, retrieval, and dissemination of environmental data made available to it by federal agencies, state and local governments, individuals and private institutions." This National Environmental Data System and Environmental Center Act was then vetoed by former President Nixon.

Congress, in 1973, again introduced the bill with an additional statement: "There is hereby established a National Environmental Data System. The Data System shall include an appropriate network of new and existing information processing or computer facilities both private and public in various areas of the United States, which, through a system of interconnections, are in communication with a central facility for input, access, and general management. It shall also include all of the ancillary software and support services usually required for effective information system operation." This bill was also vetoed.

It has been said many times by persons involved in federal policy making that a national environmental information system should be established. Dr. John W. Townsend, Jr., of the National Oceanographic and Atmospheric Administration, when speaking of a national system said as early as 1972 that this system should not be one big monolithic center but an interrelated system of centers to provide users "with the types of environmental data they need, when they need it, in the forms and formats they require."

In the meantime, many federal agencies have developed data systems which deal with environmental information. These systems are to be found in the Departments of Agriculture, Commerce, Defense, Health, Education, and Welfare, the Environmental Protection Agency, and the National Aeronautics and Space Administration.

Some of these systems are extremely active, providing information on a regular basis to many users: EPA has APTIC (Air Pollution Information Center), NERC (National Environmental Research Center), NEDS (National Emissions Data System), SAROAD (Storage and Retrieval of Aerometric Data), STORET (National Water Quality Information System), SWIRS (Solid Waste Information Retrieval System), ENVIRON (Environmental Retrieval On-Line), and NOISE (Noise Information System). The Environmental Information Systems Office (EISO) at the Energy Research and Development Administration's National Laboratory in Oak Ridge provides information appearing in the Water Resources, Energy, Toxic Materials, Heated Effluent, Mercury, and Nuclear Science data bases. NOAA has an Environmental Data Service, called ENDEX (Environmental Data Index). This service provides "a rapid referral service to existing national and global environmental science data files."

There are many activities being carried out by commercial firms in the area of environmental sciences. None of these activities, however, are as extensive as the existing federal systems.

It is now time to look at how the National

[1]The University of Georgia, Athens.

Park Service fits into the information handling picture. There is no doubt that the approximately 300 national park sites have been looked at over a long period of time; consequently, large files of information have been acquired. This information exists in individual parks, in many forms. One such form is internal files, usually with a classification schedule oriented toward administrative functions, rather than project or topic, with the result that reports related to a particular subject such as beach erosion are distributed throughout the files. Since the classification schedule is designed for servicewide use, hence is based on broad generic categories, large clusters of documents in a relatively few categories tend to occur at the local park level, making the potentially most important reports least retrievable. Information exists also in NPS Libraries in many of the parks, some with one classification scheme, some with another, and some with no classification system at all. Another very valuable form of information is in research collections belonging to NPS employees. These reports, data, and knowledge contained in heads that have been collected over the years and moved with the person. Other sources of information are inventories of resources done by state and local units of government, by major conservation groups, and by regional planning bodies. There are also extensive data in the files of NASA, EPA, USGS, and U.S. Bureau of Sport Fisheries and Wildlife. Much valuable information is produced by universities and should be incorporated into any information system developed by the Park Service.

There appears to be no overall policy within the NPS concerning the generation, distribution, organization, storage, and retrieval of all of the available information materials. Maps, for example, are scattered; some are catalogued but most are not; no central inventory exists, so it is usually not possible to determine if a particular map has been produced or if a later version is available; nor is it possible in most cases to determine the storage location of a map known to exist. Virtually the same situation exists for all other types of informational resources generated by or for the NPS.

With Congress declaring the 1970s as the environmental decade, resulting in increased interest in the environment, and with the ever increasing costs of managing natural resources, it became apparent that there was a need for a systematic procedure for collecting information to manage these resources. It was also apparent that it would be necessary to record this collected information in an organized manner so that it could be used not only for immediate management problems but also for long-range planning for the national park system. It was recognized that the historical record would also be important for determining trends and their impact on the parks, the management goals which had been established, and the long-term effects on the ecosystem which the parks represent. Being cognizant of these things, tne NPS commissioned a preliminary planning study for the design of an ecological and environmental management information system, a system that would be a part of its management and long-range planning for the natural resources under its jurisdiction.

The Ecological and Environmental Management Information System (EEMIS) has been conceived as a very broad and complex project, ranging from the handling of quantitative data, such as the number of various species of wildlife and their migration patterns, to sophisticated modelling and simulation techniques for projecting the effects of actions before they are taken.

The planning study suggests that EEMIS include information in four broad categories, the same four that NPS uses in some of its present inventories: (1) Physical Characteristics, (2) Biological Characteristics, (3) Cultural Characteristics, and (4) Socioeconomic Characteristics. The first, Physical Characteristics, would include such factors as the location and size of the area, topography, geology and soils, hydrology and climate. The Biological Characteristics would comprise principally the plants and animals of the area and their interactions with the environment. Cultural Characteristics would include past and present land use, existing facilities, and historical attributes. The Socioeconomic Characteristics of the region surrounding the immediate area should include such factors as visitor origins, rural-urban population distribution, economic and industrial bases, age, and racial composition which influence to a certain degree the kinds of recreational activities and types of facilities available. The relative importance of these characteristics may vary somewhat from region to region, but all need to be considered in the collection and evaluation of data for effective management. Together these categories represent an unparalleled effort to collect and relate information about the full range of variables which constitute the ecosystem. The large size of EEMIS, which will eventually handle information for the approximately 300 national park sites, makes a computer-based system a necessity in order to store, manipulate, and retrieve the large collection of data which will result.

The EEMIS planning study has now been completed, but much time, effort, and of course money will be required to make it operational. The system design will have to be compatible with the operational environment to be accepted by and useful to the NPS staff. That is, it must support decision-making at the level where it occurs--at the individual park for the large parks or at the regional offices for smaller parks managed from those locations. This may seem obvious, but it is exactly the reverse of the design concept used for most corporate management information systems. In most corporate systems, the design facilitates decision-making from the top down. If it is to be successful, the system implemented for the NPS must be compatible with and support the existing environment which is basically decision-making from the bottom up.

In arriving at a decision to recommend the building of a global system design to meet the NPS information needs, careful consideration was given to the enormous diversity of the parks and to their requirements or needs which were identified. Consideration was also given to the operational environment within which it must function, the existing information resources, the state-of-the-art in information processing systems of all kinds, and NPS expertise in and experience with formal and informal information systems.

It has been recommended that the information needs of the NPS would best be served through an integrated collection of subsystems, rather than one monolithic centralized system. There are a number of reasons for recommending this design concept. First, the wide diversity in the NPS data (graphics, bibliographic, narrative, quantitative) requires a correspondingly wide range of information processing techniques (*e.g.*, plotting or drawing, test processing, and statistical analysis, to mention only the more obvious). Also, there are a number of

significantly different functions to be served by the total system--management summary reporting, inventory control, maintenance scheduling, demand retrieval, publishing, archival recording, trend analysis, and many more. Given the current state-of-the-art in file structures and file processing techniques, it would be prohibitively expensive, if not technically impossible, to accomplish all these functions through one monolithic processing system operating from one logically organized data base. Even if it were technologically possible, such a system would probably be so complex that it would prove operationally cumbersome and conceptually difficult to understand and use.

The extremely large size of the data collections which will eventually result from an NPS-wide implementation would probably prove unmanageable in terms of administrative span of control, especially as there is little prior experience within the Park Service upon which to build. For this and other reasons, phased implementation of identifiable subsystems over a period of time would provide greater probability of success, allowing time for education of the NPS personnel both as operators and as users of the various components. The subsystem approach will also result in shorter development periods than would a single, monolithic system, at least so far as visible progress from the users' viewpoint is concerned. It also permits prior investments in existing computer-based processing systems (*e.g.*, the graphic display modules developed for the Great Smoky Mountains RBI) to be incorporated either on a temporary or a permanent basis.

Integration of the recommended subsystems would be achieved through a "star" configuration with a central subsystem serving a master coordinating function. All information between subsystems passes to and from this central subsystem; there is no direct interchange between other pairs of subsystems. A direct interchange between the non-central subsystems would result in a loss of data control and would make the entire system more technically difficult to operate. For the system to be successful, the central subsystem must be advised of changes in the status of the other subsystems; the likelihood of the central subsystem being notified of changes in the subsystems decreases substantially if other pairs of the subsystem are allowed to link directly.

Analysis of the information content, as well as the potential demand and usage modes, suggests that most, if not all, of the proposed subsystems should be combinations of manual and automated systems, where the automation may be either mechanical or electronic or both. There does not appear to be any justification, for example, for the extremely costly conversion of old drawings and maps to digital form; their value is primarily historical and the probability of use is relatively low for on-going park management purposes. However, they should be cataloged so they are accessible through the system for scientific study (and perhaps legal) purposes. Manual and/or microform storage would seem appropriate for these types of informational materials. A similar case can be made for the bibliographic materials. Little justification exists for digitizing the text of books, reports, etc.; they should reside in libraries. The rare, one-of-a-kind documents should be microfilmed, however, to provide security backup. Specific recommendations for the manual and automated components of the individual subsystems would be the subject of a more detailed design level of the study, assuming the proposed global design is adopted.

The question of exactly which components would comprise the NPS EEMIS is not one easily answered. Certainly it seems clear that the Resources Data System (RDS), which ideally fills the requirements for the central coordinating mode, is a proper subset of the EEMIS. It also seems desirable to include in the EEMIS those subsystems which process significant collections of data common to the RDS, regardless of whether it is preprocessing (*i.e.*, serves as input to the RDS) or postprocessing (*e.g.*, analysis). Inclusion of subsystems which serve primarily as input sources to the RDS for pointers, status items, or quantitative data (*e.g.*, document identifiers or visitor counts) is optional, but it would seem desirable to include those subsystems which have as their primary purpose support to the ecological and environmental missions of the parks. Based on these guidelines, EEMIS should include, as a minimum, five basic subsystems: the RDS, Bibliographic System, Planning Management System, Graphics System, and Archaeology and Specimen System. Other subsystems which would lie outside the scope of the EEMIS under these guidelines, but which provide input to the RDS, are shown to provide perspective on the relationship of the EEMIS to still other NPS information systems. These other subsystems: Inventory and Maintenance System, Visitor Reservation System, and Law Enforcement System do not necessarily constitute a complete set, however, as there will undoubtedly be others which should be included in both categories. Nor does the schematic representation attempt to show other existing NPS systems which have no direct input to or output from the central RDS system (*e.g.*, financial and administrative systems).

The names of the proposed subsystems have been deliberately generalized to avoid any implication that they correspond to existing manual or computer-based systems. Rather, they are intended to identify the major types of data which are processed.

The central subsystem, the hub of the EEMIS, called the Natural Resources Data System, would be basically an inventory of data belonging to the four major categories: Physical, Biological, Cultural, and Socioeconomic. Included also in this central subsystem would be other types of data called "pointers" which would lead the user to information located in other subsystems (*e.g.*, the numbers of drawings, maps, documents, etc.) Access to this data is required in terms of the operational units of the NPS (*e.g.*, parks, regions, and WASO) and also by the types of data in the inventory (*e.g.*, flora, fauna, trails, visitor use, etc.). In effect, every item of data in the master data base of this subsystem just serves as an access point.

The Bibliographic System provides the descriptive cataloging (*e.g.*, titles, authors, and reference), associated surrogate information (*e.g.*, index entries, catalog codes, and abstracts), physical location, media characteristics, and ownership information for documents of all types. These include but are not limited to books, technical reports, manuscripts and similar informational materials commonly found in libraries or personal reference collections. It will also include information recorded in non-print media (*e.g.*, sound recordings, slides, films, magnetic tapes, and microforms of various kinds.) If desired, it can also include references to resource people or facilities. Reports generated as products of

the planning functions (*e.g.*, environmental impact statements, wilderness studies, etc.) would be recorded in this system as they were completed and published. This subsystem consists of two equally important components: the computer-based component, which provides the *access* to the documents, and the collection of information resources itself, which will remain in their present media (*i.e.*, print or non-print) and locations.

The Archaeological and Specimen Subsystem provides the inventory and cataloging records for archaeological and historical items and specimens. The information contained in this system will include a description of the object, its characteristics (*e.g.*, size, date found, probable date of object, value, etc.), and its location (*e.g.*, site, county, state, etc.). Records may also be maintained for exhibition purposes.

The Graphics Subsystem is one of the largest and most complex of the proposed subsystems. First, it includes a component like that of the Bibliographic Subsystem for providing access to the various collections of graphics by such data as the name of the map or drawing, geographical coordinates, type (*e.g.*, vegetation, hydrology, etc.), and similar characterizing information. It will also include descriptive information, such as the scale, source, physical size (for the print medium), density and track if computer-readable, physical location, ownership and similar attributes. A second component of the Graphics Subsystem is, of course, the graphics materials themselves (*i.e.*, the maps, drawings, photographics, etc.). As in the case of the bibliographic resources, it is assumed these, too, will remain in their present media, both print and non-print, and locations. In the future it is expected that much of the graphics information will be obtained in computer-readable form from projects like ERTS and Skylab, where graphic information is normally stored in digital form on magnetic tape. The third major component, and the one which makes the Graphics Subsystem unique among those proposed, is the display component required for those graphics materials which are stored in machine-readable form. This component encompasses all of the processing required to accept as input digitized graphics data and to produce for use maps or overlays with the desired information at the appropriate scales. Thus, this component includes processing functions for integrating ground truth data, adjusting for such conditions as curvature and atmospheric conditions, and plotting results for human use.

The Planning Management Subsystem is primarily a task management system for control of planning projects. As such, it would contain information which follows a project from its inception to its completion, providing such management reporting assistance as schedules, task assignments, status reports, PERT or Gantt charts, and budgetary summarization. Its primary purposes are support for active planning projects and information for the "customers" (*i.e.*, park personnel) or subcontractors as to overall project status.

The Visitor Reservation Subsystem, which lies outside the scope of the EEMIS as defined, has as its primary function the scheduling or reservations for use of the various park facilities (*e.g.*, camp sites, trails, wilderness areas, etc.). Primary input to the RDS from this system is visitor usage data which is expected to be of use in modeling and simulation studies.

The Law Enforcement Subsystem is basically an administrative reporting system through which historical records of various law enforcement activities are maintained, with periodic summary reports produced for management use.

The Inventory and Maintenance Subsystem is intended as an inventory control system for all physical property and facilities, which includes buildings, trails, roads, signs, and similar facilities, regardless of cost. The principal function of this system is to provide support to the maintenance personnel of the NPS, including scheduled preventive maintenance, budgetary planning, and historical records on these types of activities. Input to the RDS consists primarily of updates to the physical facilities records when changes, additions, or dispositions are made, especially those related in any manner to the transportation system (including trails). It is also possible that boundary changes would be entered to the RDS via this subsystem.

The planning stage for the EEMIS is now completed. The move to make it operational is the next step. There are many exciting possibilities if we allow ourselves to think about what the future might hold.

A park superintendent with a computer terminal on his desk would have immediate access to a network of national technical information banks; he could consult a national environmental computerized library; and he could obtain data immediately for answering questions, for simulation and modeling, and for filing necessary reports. This superintendent would have at his fingertips selected maps, legislation, manuscripts, data compilations, technical reports, books, films, specimens, computer software, personal expertise of NPS staff--in short, a full range of NPS information concerning not only his park but also all of the other park sites in the Service.

It would be possible to determine the location of old maps, old drawings, and old reports that might be of use in decision-making. Information would also be immediately available concerning the location of non-print media such as sound recordings, slides, films, magnetic tapes, and microforms of various kinds. Generated reports such as environmental impact statements and wilderness studies as well as an inventory and cataloging record for archeological and historical items and specimens would be immediately accessible. A superintendent would be able to follow any project from its inception to its completion, using such management reporting assistance as schedules, task assignments, status reports, PERT or Gantt charts, and budgetary summarization. The superintendent and maintenance chief would have an inventory control system for all physical property and facilities, which would include buildings, trails, roads, signs and similar facilities. In fact, only human imagination limits the possibilities.

Certainly there are and will be problems, but the technology exists now. What is needed is time, money, and strong motivation. It would be prohibitively expensive, both in time and money as well as probably technically impossible to accomplish all that has been envisioned in a short period of time. It is more realistic, therefore, to consider phasing in the implementation of subsystems one at a time. This would allow several things: (1) time for education of the NPS personnel both as operators and as users of the various components, (2) an appearance of visible progress from the user's viewpoint, (3) prior investments in existing computer-based

processing systems such as the graphic display modules developed for the Great Smoky Mountains RBI to be incorporated either on a temporary or permanent basis. In addition to a phasing in of the subsystems, it would be feasible to set up a few parks as prototypes, profiting from each experience. The planning has been done and now the motivation has to come from the Park Service itself, not from the Washington people, but from the level of those who have to deal with the parks on a day-to-day basis, those who would benefit most.

# ECOLOGY OF YELLOWSTONE THERMAL EFFLUENTS:

# THE BLUE-GREEN ALGAE - BRINE FLY COMMUNITY

Richard G. Wiegert[1]

## INTRODUCTION

The National Parks of our country, because of their varied habitats and protection from exploitation and unnatural perturbation, are ideal for field research in ecology. Of them all, Yellowstone National Park (YNP) is one of the most rewarding, in part because of size and age, but mostly because of its unique and abundant thermal features. Varying greatly in physical, chemical and biological characteristics, these thermal communities share the common thread of elevated temperature, providing a unique experience and a great outdoor laboratory.

The most outstanding thermal features of YNP are its many geysers and boiling pools. However, the communities developing in the outflows of these thermal features tend, because of the high temperatures, to be very simple taxonomically, often consisting solely of bacteria, seldom sustaining an animal grazing community and its attendant predators and parasites. Features such as the "acid outflows" support organisms that produce sulfuric acid and the resultant low pH attracts unique communities of organisms. With both high temperature and low pH, these communities also comprise only a few species of microorganisms. At lower temperatures very interesting animal communities develop in these acid systems, but the pH is very difficult to maintain in the laboratory and ecological work with these systems is hampered.

In the so-called "alkaline" spring areas, principally in the band of thermal features called Upper, Midway, and Lower Geyser Basins, conditions of temperature and pH are found which are neither too high nor too low, but are, as Goldilocks found the porridge and the bed of Baby Bear, "just right", for the development of an extremely interesting community of algae, arthropods, and bacteria.

In a sense I was preadapted when,in the summer of 1967, Tom and Louise Brock invited me to visit their Yellowstone laboratory and spend a few days doing radio isotope studies of the grazing food chain in these alkaline thermal communities. I was just then interested in the budding discipline of systems ecology but was becoming discouraged by the difficulties of beginning with models of the usual complex communities of old field, lake, or forest. I had for the past two years been looking for a naturally occurring community that was 1) Simple in the sense of containing few species yet containing all the usual ecological interactions (grazing, decomposition, predation, etc.), 2) Easy to sample, 3) Amenable to manipulation in the field, 4) Subject to laboratory study, at least at the level of the individual populations and 5) Capable of rapid successional change and the attainment of climax or steady state in weeks or months rather than decades or centuries. In short, I wanted an ecosystem where a small group of individuals could, in a few years, study in considerable detail the biology of at least all major groups of organisms and in many cases examine them species by species. The objective would be to construct a computer model of the system that would not only reproduce the normal states of the community, but would have the capability of predicting the behavior of the systems under a variety of perturbations. This model could in turn provide some insight into the kind of procedures that might be employed for the construction of models of the more complex systems on which the economic and recreational well being of man depend.

In 1967, on my first visit to the Brock's study area, I realized that I had found what I was looking for. For the past 8 years the ecology of the thermal algae-brine fly communities of YNP has been a major interest of mine. In this paper I wish to discuss briefly the major interactions and, by so doing, to tell the story of the development of an ecosystem model, a story still unfinished, but whose end is now known, if not yet written down.

This has truly been a team research effort, and I am indebted to all of my colleagues, including the five Ph.D. students, eight postdoctoral associates and 14 technicians who have been directly involved with this research over the past 8 years. The research has been supported by NSF Grants GB 21255 and GB 76813.

## THERMAL COMMUNITY LIFE CYCLE

In broad outline the story of successional life and death in an alkaline thermal-spring community is simple and straightforward. Within a few weeks of beginning our studies in 1968 the following sequence was worked out. At temperatures between about 40-50°C a mat of filamentous blue-green algae begins to grow on any firm substrate. The growth of this algal mat eventually changes what was originally a smooth sheet of water into a series of channelled flows. With continued growth of the algae, parts of the mat eventually reach the surface and cool, thus producing a heterogeneous mosaic of temperatures. The algae in these cool areas of the mat are no longer actively growing, for the nutrients supplied by the flowing water are cut off, but the temperature of these areas is now low enough (<40°C) so that the grazing brine flies *(Ephydridae)* can survive and they quickly saturate the area with eggs. The larvae of these flies begin to feed on the algal-bacterial mat, in the process breaking down its structure and "solubilizing" it until at the end the larvae are moving about in a semiliquid medium of water and fecal pellets, the latter often containing many algal cells and parts of filaments, as shown by U.V. microscopy.

Eventually, the larvae (many of which pupated and left as adults) eat through some critical

[1]Department of Zoology, University of Georgia, Athens 30602.

algal "dam" and hot water pours into the cool patch killing the remaining larvae, washing out the remaining cellular debris and starting the process of algal growth all over again. Thus at any point in space the community is in a constant state of flux, but over any larger area of algal mat, the standing crops of both algae and flies may exhibit a steady state.

## ECOSYSTEM MODELS

Constructing a model of an ecosystem involves a number of preliminary steps of the sort required for any ecological study. First an inventory of the species or at least the major functional groups of organisms must be drawn up. Next, their trophic interactions (and their behavioral interactions) must be worked out. Next, and most difficult of all, the functional form of the factors controlling the rate at which each group processes material of energy must be elucidated. Initially this is verbalized, then transformed into a mathematical expression and finally into a computer program whence simulation of community dynamics is possible.

First working out the developmental sequence in the alkaline thermal community, our immediate task was to provide a species list and work out the food web. Naturally, all these steps are not in reality done in a nice tight sequence, but proceed as larger saltations, returning to clean up problems bypassed for the convenience of the moment. Nevertheless, eventually the task of censusing was completed, showing a species complement of approximately 8-10 species of algae, perhaps twice that many 'kinds' of bacterium, 3 species of ephydrid fly and several predators and parasites, most of which reproduce and spend much or most of their life outside of the thermal algal mat proper.

In the particular springs chosen for this work, the dominant producer species is the blue-green alga *Mastigocladus laminosus*. This is fed upon by the major grazer, a species of brine fly *(Paracoenia turbida;* Ephydridae*)*. The brine fly is in turn utilized by a long-legged predatory fly *(Tachytrechus angustipennis;* Dolichopodidae*)* and a parasitic mite *(Partnuniella thermalis;* Hydrachnellae*)*. Under certain conditions a pupal parasite, the wasp *Urolepis rufipes* (Pteromalidae) can be important in this community. A number of other predators remove flies, among these are the sandpiper, tiger beetle and wolf spider. These major trophic interactions form the basis for the modeling efforts. The next step was to study, in detail, the biology of each group with a view toward revealing how it interacted with the various factors regulating growth and thus determining levels of energy flow and mineral cycling. As examples, I will discuss briefly the studies on algae, brine fly, and on long-legged fly, groups regulated primarily by an inorganic resource, intra-specific competition for space and behavioral interactions respectively.

### *The Study Sites*

Study of naturally-occurring springs has serious limitations. For one thing, control of flow is difficult or impossible. Indeed, many natural springs may abruptly shift their outlets or fluctuate widely in rate of flow. Furthermore, large animals stepping into the channel constitute an ever present (and quite common) hazard. Furthermore, the soft bottom of many natural algal systems made sampling difficult; up to a foot or more of silt may accumulate over the hard silica or "sinter" that forms the base of the system.

Thus the decision was made early to conduct the studies on communities developed on wooden troughs (called Boards) with water piped onto the upper end. These are all located at Serendipity Meadow adjacent to Firehole Lake Drive, Lower Geyser Basin, and have been described in a number of publications and range in size from a few centimeters in width and length to 1.2 x 24 meters with flow rates of up to 50 liters/min.

A short paper cannot even summarize the results of 8 years of investigations by our team of researchers, therefore I have provided (in an appendix) a list of the publications that have resulted from the work by the University of Georgia group in YNP. The three studies that are summarized here, namely those on: 1) producers, (blue-green algae), 2) the grazer, *(Paracoenia turbida)* and the predator *(Tachytrechus angustipennis)* were selected both for their importance in the system and to illustrate the differences in emphasis and procedure that must be employed to derive model-relevant parameters for organisms that differ greatly in the mechanisms controlling their utilization of resources.

## PRODUCERS: BLUE-GREEN ALGAE

The filamentous blue-green algae characteristic of the thermal alkaline area waters in the temperature range 40-56°C are limited primarily by physical constraints plus intra and interspecific competition for a limited renewable material resource, free carbon dioxide. Briefly, the initial observations were that under a given regimen of light intensity, day length temperature and flow conditions, the rate of net productivity decreased with distance from the source. A considerably smaller downstream decrease in the steady state standing crop and a shift in species dominance were also noted. Studies of photosynthesis rate, biomass and chlorophyll concentration showed a strong nonlinear relationship between these three variables. Gross photosynthesis was related to the 0.29 power of ash-free dry weight. Light intensity (at all levels above approximately 10% of full sunlight) showed no relationship to rate of gross photosynthesis. Respiration was linearly related to biomass; thus net rate of photosynthesis also followed the 0.29 power of biomass relationship.

Because the photosynthesis measurements were carried out in bottles under identical conditions of nutrient availability (source water from the single spring was used in all experiments) we next looked for any factor on the experimental board troughs that could have been correlated with the downstream decrease in rate of net productivity (the distance and volume of flow were such that temperature decrease downstream averaged less than 2°C). The only factor of this kind that could be identified was the concentration of free $CO_2$. From a high of 95 ppm, $CO_2$ declined to 15 ppm on the last of four short (2m) wooden troughs. The hypothesis was that the high levels of $CO_2$ in the source water were stimulating the high productivity near the source because the thermal water contained very high quantities of available phosphorus and the algae themselves are nitrogen fixers. The only way the available $CO_2$ can reach the vicinity of the individual filament is by diffusion through the interstitial water of the mat, although studies with micro pH probes showed that the first 1-2 mm of mat may be supplied with nutrients by direct replacement of water through turbulent flow. Putting all this information into the form of a model of algal growth the predictions of the model provided an

acceptable explanation of the downstream decrease in rate of net production and an approximation of the measured steady state.

## GRAZER: BRINE FLY

The brine fly *Paracoenia turbida* is an animal approximately one half as large as a house fly with a surprisingly large egg production and growth rate, giving a potential for increase that is the equivalent of that of *Drosophila*.

$$\left[r_{max} = 0.25 \text{ flies X fly}^{-1} \text{ day}^{-1}\right].$$

From the modeling standpoint, this potential rate of increase is a vital parameter for, when corrected by dividing by the fraction of food that is assimilated, it becomes an estimate of the maximum specific rate at which a growing fly population could ingest food. This specific rate of ingestion has the dimensions time $^{-1}$ and, when multiplied by the standing crop of flies, gives the instantaneous rate of ingestion measure in units of food per unit time.

The life history of the brine fly *Paracoenia* is not complex. The adults feed from an oviposit on the algal mat. The eggs hatch in two or more days (optimum development temperature is 35°C). The larvae pass through 3 instars in the course of approximately 6 days, pupate, and emerge as adults some 6 days later. The total life cycle from egg to egg can occur in a minimum of 14 days.

Behavioral factors have little importance in controlling the numbers of flies. The adults feed on the surface of the algal mat and always have an abundance of food. Studies of oviposition showed no effect of crowding up to the point where the flies became so dense that some could not reach the surface of the algae. However, because the eggs and larvae are killed by temperatures only slightly greater than 40°C, the only available habitat for the immature forms is in temporary cool spots in the algal mat caused by the growth of the algal shifting of hot water. Dense masses of eggs are deposited in these temporary cooler areas and the larvae quickly eat up most of the mat and destroy the filamentous structure. As more and more larvae enter the area (by continued egg deposition) some of the oldest larvae pupate and leave as adults. The remaining larvae soon show the effects of crowding; the growth rate declines, time to pupation grows longer, pupation occurs at a smaller average age, and mortality of both larvae and pupae increases. Studies of the crowding effect on larvae showed a threshold effect, probably due to the buildup of toxic waste products in the presence of abundant food. Although under laboratory conditions, the larvae can consume all their algal food and subsequently starve, in the field the crowding effect invariably begins long before the algae are gone because the cool patches have little or no water flowing through them, thus allowing toxic wastes to accumulate. Alternatively, the larvae may break down the algal mat holding back the hot water, causing their death and the death of many of the pupae.

Field and laboratory research on this species was directed toward the measurement of the various rates of ingestion and loss as well as the threshold of standing crop of flies and algae that determine whether flies are in an optimum environment or not. The result was definition of a community in which three distinct conditions can be identified: 1) a hot-flowing condition from which flies are excluded and algal growth is occurring, 2) a hot-stagnant condition with no net algal growth and from which fly eggs and larvae only are excluded, 3) a cool-stagnant condition in which both adult and larval flies are decimating the algae. At a given point therefore, the system is never constant; it is either growing or being destroyed. Over several square meters, however, these communities do often show considerable constancy of algal biomass and fly density. Superimposed on this pattern of fly-algae interactions is predation (and parasitism) of the brine flies. Except for an occasional exceptional circumstance of extreme fly abundance and low algal standing crop, the predators and parasites in this system do not control the flies; instead they are often themselves controlled by the long term fluctuations in fly density.

## PREDATOR: DOLICHOPODID FLY

A prominent member of the predator community is the long-legged fly, (Dolichopodidae) *Tachytrechus angustipennis*. The adult is the only life history stage of this species on the algal mats. The female fly lays its eggs in the fall (near the end of its life) and the larvae and pupae exist in the mud at the edges of the thermal effluents.

The adult is an active predator which seeks out the eggs and small larvae of *Paracoenia*. In contrast to the latter fly, behavior is an important factor controlling the abundance and predatory impact of *Tachytrechus*. Thus, a large share of the time spent studying this predator was devoted to observation. *Tachytrechus* males establish many short-lived territories during a day, from which they attempt to exclude all other insects except females of their species. Although the primary function of this behavior may be reproductive, it does result in a limit placed on the number of dolichopodids that can search a given area at the same time.

These flies are vey inefficient at extracting eggs of *Paracoenia* from the algal mat because these eggs are covered with recurved hooks which hold the eggs firmly in place. Larvae are somewhat more available, but the predator has difficulty handling anything larger than about 2nd instar. The major increase in size of the larva takes place during the 3 instar (half the total estimated development time), thus under normal circumstances most of the larval standing crop is unavailable to the predator. This fact, together with the single annual generation and low biotic potential of the dolichopodid fly renders it incapable of making serious inroads on its prey population.

## THE ECOSYSTEM MODEL

Information from studies such as those just described was used to construct detailed predictive computer models of the ecological energetics of the thermal algae consumer-predator community. Model predictions were tested by performing experiments on the entire ecosystem in the field. For example, shutting down the flow of water to create larger areas of cool-stagnant mat, thus increasing, at least temporarily, the fly density.

Once the most detailed model was tested sufficiently to establish its validity under a limited range of conditions, the model itself was rearranged in different configurations, each simpler than the last. For example, instead of

keeping track of each separate life history stage of the brine fly, various condensations were made ranging from all larval stages in one compartment to all brine flies in one compartment. Instead of mimicking the normal time delays in passage from egg to larva to pupa, the time delays were only approximated or removed entirely, etc. These condensed versions of the model were used to simulate the behavior of the system under a range of perturbations. These simulations were then examined to determine the degree to which a particular type of condensation had affected the predictions of the most detailed model. Out of this work, hopefully, will come some rules for modeling ecosystems that will prove useful to those contemplating models of larger complex systems that are vital to the well-being of man. The early progress appears promising and the work on the Yellowstone thermal communities is continuing.

## BIBLIOGRAPHY


BROCK, M. L., R. G. WIEGERT and T. D. BROCK. 1969. Feedings by *Paracoenia* and *Ephydra* (Diptera: Ephydridae) on the micro-organisms of hot springs. Ecology 50:192-200. (Appendix II).

COLLINS, N. C. Mechanisms determining the relative abundance of three brine flies (Diptera: Ephydridae) in thermal spring effluents. (submitted to Canadian Entomologist).

COLLINS, N. C. 1975. Population biology of a brine fly (Diptera: Ephydridae) in the presence of abundant algal food. Ecology 56: 1139-1148.

COLLINS, N. C. 1975. Tactics of host exploitation by a thermophilic water mite. Misc. Publ. Entomol. Soc. Am. 9:250-254.

COLLINS, N. C., R. MITCHELL AND R. G. WIEGERT. Functional analysis of a thermal spring ecosystem, with an evaluation of the role of consumers. Ecology (in press).

FRALEIGH, P. C. and R. G. WIEGERT. 1975. A model explaining successional change in standing crop of thermal blue-green algae. Ecology 56:656-664.

GORDEN, R. W. and R. G. WIEGERT. Bacterial types and interactions in a thermal blue-green algae-ephydrid fly ecosystem. *In*: Aquatic Microbial Communities, John Cairns, (ed). (in press).

KUENZEL, W. J. and R. G. WIEGERT. 1973. Energetics of a Spotted Sandpiper feeding on brine fly larvae (*Paracoenia;* Diptera; Ephydridae) in a thermal spring community. Wilson Bull. December.

KUENZEL, W. J. and R. G. WIEGERT. Yellowstone thermal effluent systems: Life cycle population dynamics, territoriality and energetics of a major insect predator (Diptera, Dolichopodidae. Oikos (in press).

MITCHELL, R. 1974. The evolution of thermophily in hot springs. Quart. Rev. Biol. 49:229-242.

MITCHELL, R. and B. L. REDMOND. 1974. Fine structure and respiration of the eggs of two ephydrid flies (Diptera: Ephydridae). Trans. Am. Micros. Soc. 93(1):113-118.

OWEN, D. F. and R. G. WIEGERT. 1976. Do consumers maximize plant fitness? Oikos 27:3(1-5).

WIEGERT, R. G. and P. C. FRALEIGH. 1972. Ecology of Yellowstone thermal effluent systems: net primary production and species diversity of a successional blue-green algal mat. Lim. & Ocean. 17:215-228.

WIEGERT, R. G. and R. MITCHELL. 1973. Ecology of Yellowstone thermal effluent systems: Intersects of blue-green algae, grazing flies (*Paracoenia*, Ephydridae) and water mites (*Partnuniella*, Hydrachnellae) *Hydrobiologia* 41:251-271.

WIEGERT, R. G. 1974. A general ecological model and its use in simulating algal-fly energetics in a thermal spring community. *In*: P. W. Geier, L. R. Clark, D. J. Anderson and H. A. Nix (Eds.) Insects: Studies in population management, Vol 1, pp. 85-102. Occasional Papers. Ecol. Soc. Austr., Canberra.

WIEGERT, R. G. 1974 Competition, a theory based on realistic general equations of population growth. Science 185:539-542.

WIEGERT, R. G. 1974. A general mathematical representation of ecological flux processes: description and use in ecosystem models. Proc. 6th Ann. S. E. Systems Sypm., R. Kinney (Ed.) TF-2 15 p. Baton Rouge. La.

WIEGERT, R. G. 1975. Mathematical Representation of ecological interactions. *In*: Ecosystem Analysis and Prediction. Proc. SIAM-SIMS Conf., Alta, Utah, S. A. Levin, ed. Philadelphia Soc. Ind. and Appl. Math.

WIEGERT, R. G. 1975. Simulation modeling of the algal-fly components of a thermal ecosystem: Effects of spatial heterogeneity, time delays and model condensation. *In*: Systems Analyses and Simulations in Ecology. B. C. Patten Ed. Vol. 3, Academic Press, N. Y. pp. 157-181.

WIEGERT, R. G. 1975. Simulation models of ecosystems. Ann. Rev. Ecol. and Syst. 6:311-338.

WIEGERT, R. G. 1977. Population models: experimental tools for analysis of ecosystems. Proceedings of Colloquium on Analysis of Ecosystems. Ohio State University Press, Columbus. (In Press). B. J. Horn, R. Mitchell and G. R. Stairs, Eds.

WIEGERT, R. G. 1977. *In*: Models as Ecological Tools: Theory & Case Histories. (In Press). C. Hall and J. Day, Editors. J. Wiley and Sons.

# ENERGY ANALYSIS OF THE EVERGLADES NATIONAL PARK[1]

Edward DeBellevue, Howard T. Odum, Joan Browder and George Gardner[2]

## INTRODUCTION

The design of humanity and nature now developing over the American landscape consists of a mixture of farms, urban areas, and natural areas and parks set aside for their special values. These contribute to the total economy of man and nature in many ways, some well-known and some under-evaluated. In applying systems approaches to understand the larger system of humanity and nature, many questions arise about the interactions of the parks with the other components of the environment. How much park area is needed in ratio to developed areas? How much do economic use and interfacing development threaten park values? How do park values compare with traditional economic values of developed areas?

Energy models may provide a method to evaluate and portray a park in intermediate complexity with enough detail to show major interactions, but not in so much detail that one cannot visualize operation. After pathways are evaluated numerically, energy analysis suggests answers to questions about comparative values. In this paper an energy analysis is made of the Everglades National Park and suggestions are made about impact interactions.

A national park is a complex environmental system which includes many component ecosystems, a pattern of management and human visitation, and, externally, a set of energy flows and economic interactions between the park and the economy of the county, the state, and the nation. This is a first attempt to show a national park as an integral part of a larger system and to point out what may be the most important components and interactions with model diagrams.

This is a component of the South Florida Study, Phase II of the Department of the Interior. A summary report has just been printed (Browder, Littlejohn, and Young, 1976). The large technical report which has details on the other systems of region, county, and ecological communities is being revised for publication.

## METHODS

Ideas and concepts of Everglades National Park in terms of its main components and pathways of interaction and influence were sought from Staff of Everglades Park and other sources and used to develop a preliminary model, in diagram form, using energy circuit symbols (Fig. 1). Discussion of the energy circuit language and the energetics approach to systems analysis can be found in two books (Odum, 1971; and Odum and Odum, 1976).

Following the development of the Park model, stocks and pathways were evaluated with available data. Stocks and flows were converted to equivalent energy values in coal equivalents based on the energy cost of their replacement. These data sources and calculations are presented in tabular form and summary numbers have been placed on appropriate figures. Quantification of stocks and flows was aided by an unpublished technical report of the South Florida Study, Phase II, in which were presented subsystem models for systems found within the Park such as mangrove, saltwater marsh, sawgrass, and wet prairie ecosystems, etc. Major flows and storages were aggregated to show perspective on major areas of interest, such as total income, total environmental work done by the Park's natural systems, total energy, and energy based purchases related to the Park.

Due to lack of available information on money spent outside of the Park by visitors to the Park, an indirect calculation was made by multiplying the number of visitors to the Park by days in the Park and by the normal tourist expenditure per day in Dade County. For each day in the Park, it was assumed that the person extended his stay in Florida by a day and, in the process of entering and leaving, spent this amount. Unfortunately, it was not possible to separate tourists from local visitors in the information provided by the Park, so an estimate was made that 10 percent of the visitors were local. The resulting figure is probably an underestimate because the number of tourists other than fishermen entering the Park from Everglades City, Chokoloskee, and the Florida Keys could not be counted.

The economic value of the Park fishery in terms of both commercial and sports fishing was estimated, based on the reported kilograms per year commercial and sport fish catch at Flamingo. Both catches were multiplied by the retail price of the fish as an estimate of their total value to the economy. The annual retail value of the Dry Tortugas shrimp fishery also was counted.

Use of the energy symbol language in model diagrams carries with it implications as to the mathematical relationships and performance of

[1]We thank the following agencies and persons for their time and efforts helping us obtain data and understanding used in evaluating the Everglades National Pärk Model: National Park Service, Washington, D.C.: J. Matthews; Everglades National Park Office: Assistant Superintendent Claude McClain, E. Countreman, G. Davis, T. Schmidt, Larry Bancroft, Frank Nix, Jerry Hammond, Ralph Mealey, Roger Ronek, Glen Garrer, and numerous other Park staff; National Marine Fisheries, Miami: J. Cato; National Audubon Society, Inc., Corkscrew Swamp Sanctuary: M. Duever; Central and Southern Flood Control District, WEst Palm Beath: W. Brannon; Florida State Board of Health, Vero Beach: G Omear; U. S. Army Corps of Engineers, Jacksonville: G. Beque; and Homestead Chamber of Commerce: D. Cappisalo. This work was accomplished under contract with the Department of the Interior, National Park Service, #PX-0001-60080.

[2]Center for Wetlands, University of Florida, Gainesville 32611.

the system with time. Two recent publications from the South Florida Study illustrate and further describe the energy circuit diagramming, evaluations, and simulation results (Zuchetto, 1976; and Bayley and Odum, 1976).

### *Calculation of Ratio of Work of the Economy to Work of the Park's Natural Ecosystems*

The model was further aggregated by combining flows into economic and natural categories and a ratio was calculated between the work of the associated economy and the work of the Park ecosystems (both in units of coal equivalent kilocalories). This ratio of fossil fuel energy input to natural energy input is called the investment ratio. The Park systems' investment ratio was compared to that of the United States, 2.5, to give perspective about the impact of the park on the economic system and vice versa.

### *Expressing Data in Coal Equivalents*

Table 1 shows the conversion factors used to estimate the energetic value of the stocks and flows evaluated for the model. The common energy unit is the "coal equivalent kilocalorie" (CE kcal). Footnotes to the table give the basis for the conversion factors, determined by means of analyzing systems in which the conversion of one kind of energy to another, such as coal to electricity, has been evaluated, showing all energy inputs and subsidies. The kilocalorie/dollar conversion was obtained by dividing the sum of the annual U.S. fuel usage and annual solar radiation (in CE kcals) by the gross national product (GNP); this ratio represents the energy invested for every dollar circulating in the national economy. Values understood in terms of dollars, weight, speed, etc., can be expressed in coal equivalents by use of the appropriate conversion factors. In most cases, resultant values represent replacement cost (how much energy that would have to be expended to recreate). See the Appendix for further discussion of the conversion factors.

### *Application of Decision Making*

The use of energy conversion factors and the investment ratio to aid decision-making was demonstrated with an exercise quantifying the potential impact of an increased water supply for the Park on the Park's value to the regional system.

## RESULTS

Results include a land use map of ecosystems in the Park, an evaluated model of the greater Park system, and summary diagrams of exchanges.

### *Distribution of Ecosystems in the Park*

Given in Fig. 2 is the land use map of the Everglades National Park in 1973. From this map, areas of ecosystems were measured (Table 2). Percentages of major ecosystems are diagrammed in Fig. 3. The area of broad shallow marshland that gave the park its name represents only 9 percent of the Park's 1.4 million acres. An additional 16 percent in wet prairie combines to make one quarter of the Park a freshwater wetlands. Interspersed are subtropical hammocks and pinelands which, although important in increasing the diversity and beauty of the Park, represent less than 2 percent of the total area. About three quarters of the Park are estuarine ecosystems; one quarter mangrove, one quarter marine meadows, 7 percent salt marsh, and an additional 14 percent where plankton is the major primary producer. About 40 percent of the Park is in Florida Bay, which includes the marine meadows and planktonic systems. Thus, the Park is predominantly an estuarine park, although a visitor driving along its main access road (SR 20) would see about half wet prairie and half mangroves. Creation of the Park preserved only a small percent of the historic "river of grass."

The Park's natural systems can be grouped into three main categories: freshwater wetlands, saltwater wetlands, and open water. These systems are responsible for 27, 39, and 33 percent respectively of the Park's total annual gross primary productivity of approximately 9.07 trillion CE kcal. Mangroves represent 33 percent of the total. Wet prairies account for 15 percent, and the marine meadows of Florida Bay account for 29 percent of the natural energy budget. The estuarine systems, consisting of saltwater wetlands and open water, account for over two thirds of the gross primary productivity, primarily because of the large area they cover.

Gross primary productivity (GPP) of ecosystems can be used as a measure of the "work of natural ecosystems" of potential benefit to man. GPP in coal equivalent units (CE kcal) multiplied by the kcal/$ ratio of the total economy, $19,600 kcal/$, yields an estimate of $412 million/yr. for the energetic value of the Park to the region. Two important pathways by which this value is realized are the tourist industry and the commercial and sport fishing industries. Other pathways less tangible and more difficult to quantify may be of equal importance to the region's economic well-being.

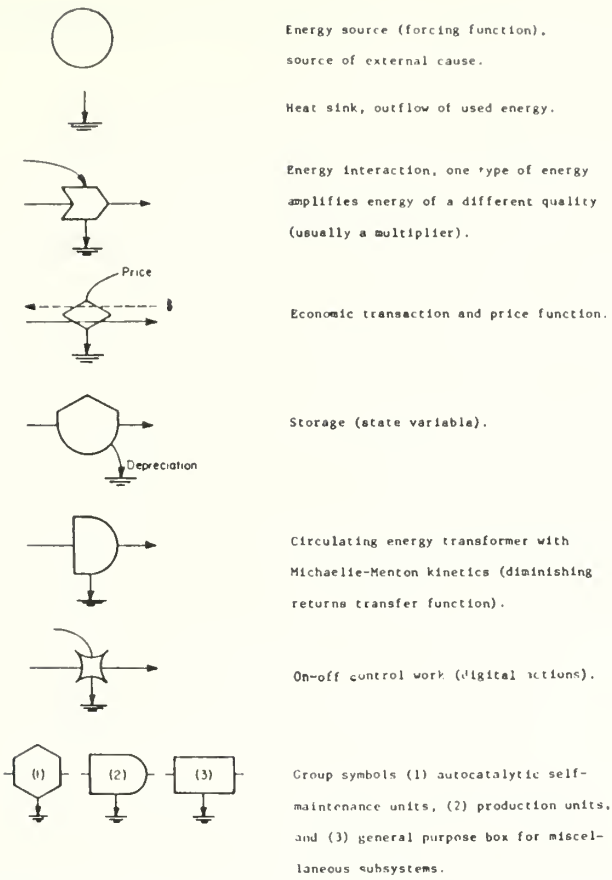
### *The Evaluated Model*

The model of Everglades National Park is shown in Fig. 4, and values are given in Table 3. The calculations and sources leading to the quantities in Table 3 are given in Appendix Table A1. On the left hand side of Fig. 4a and in greater detail in Fig. 4b are shown the interactions of sun, wind, rain, and tide; which produce the hammocks, and pinelands, sloughs and prairies, mangroves and salt marshes, and the plankton and submerged meadows of Florida Bay. From the energy flows, expressed as gross primary productivity, are generated the wilderness and wildlife values that attract visitors, produce food fish and shellfish, cause economic investments outside the Park, and even give esthetic value for people who never visit but appreciate it (right hand side of Fig. 4a).

Economic flows respond to the pumping action of this intangible quality termed "image." The Park's image may ultimately be dependant on the balance between production of value from all sources and loss of value with deaths, fading memory, and negative reputation factors, such as the abundance of summer mosquitoes or intrusions from adjacent urban or agricultural development. Water is an important input to the productivity and character of nature ecosystems and one which has greatly been changed by man's drainage works in the upper Everglades basin.

### *Inflows and Outflows*

Identified and evaluated in Fig. 5 are the major driving energy sources and flows in the form of matter, dollars and information, which flow between Everglades National Park and the region.




Energy source (forcing function), source of external cause.

Heat sink, outflow of used energy.

Energy interaction, one type of energy amplifies energy of a different quality (usually a multiplier).

Economic transaction and price function.

Storage (state variable).

Circulating energy transformer with Michaelis-Menton kinetics (diminishing returns transfer function).

On-off control work (digital actions).

Group symbols (1) autocatalytic self-maintenance units, (2) production units, and (3) general purpose box for miscellaneous subsystems.

FIGURE 1. Symbols used in energy analysis diagrams.

TABLE 1. Energy quality ratios used in this study.

| Energy Type | Fossil Fuel Equivalence Factor* (kcal FFe per kcal) | Source |
|---|---|---|
| Sunlight | $7 \times 10^{-4}$ | a |
| Sugar of gross production still distributed over land | 0.05 | a |
| Wood still distributed over land | 0.5 | a |
| Winds (10 mph) | 0.13 | a |
| Waves | 0.20 | a |
| Fossil Fuel (coal) | 1.0 | By definition |
| Tides | 1.6 | a |
| Water Elevation Potential | 1.7 | a |
| Water Chemical Potential | 0.1-10.0<br>3.1 | Appendix A<br>Kemp (1977) |
| Electricity | 3.6 | a |
| Dollar Flow, 1970 | 25,000 (kcal FFE/$) | a |

*Fossil fuel mined and stored at place of use

[a]From Odum and Brown (eds.) (1975); and Odum et al. (1976)

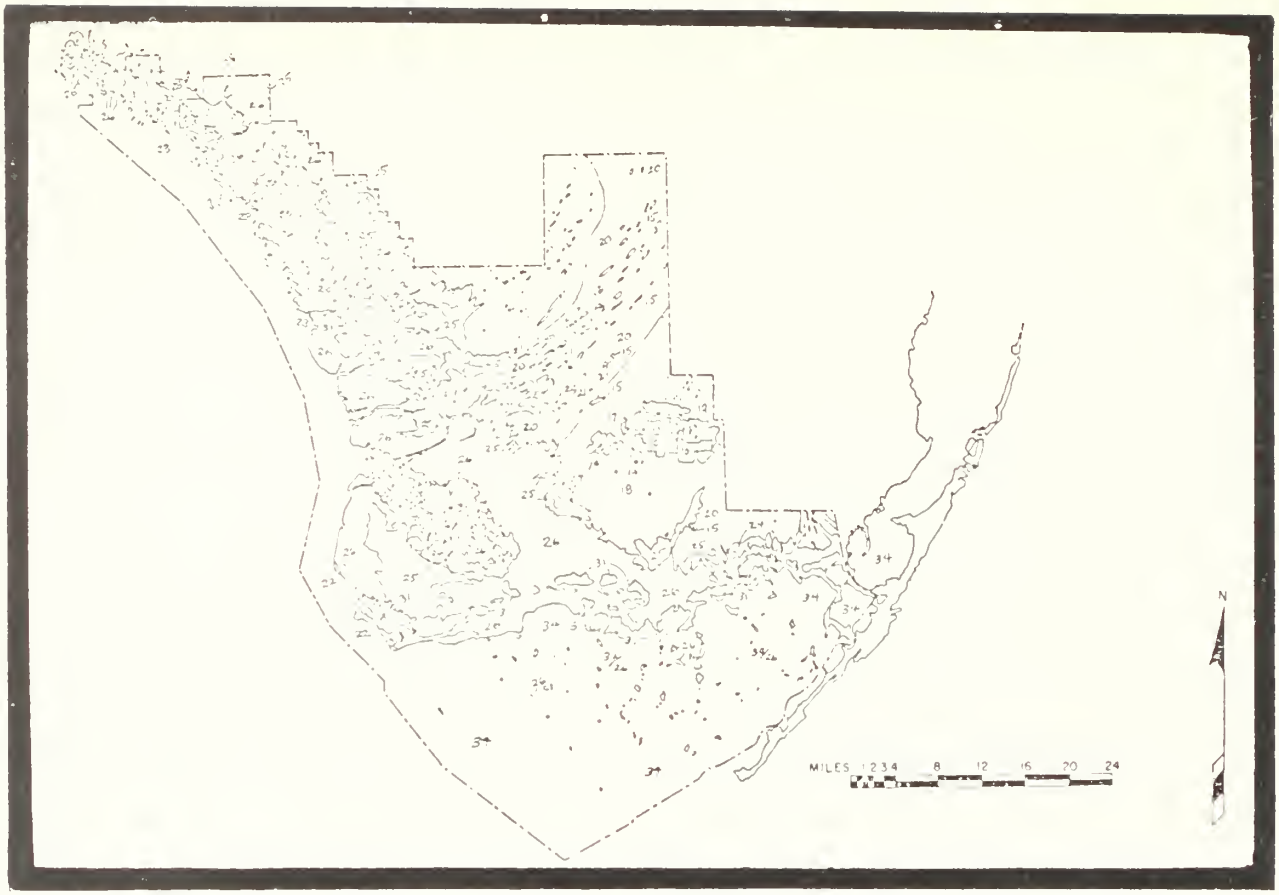



FIGURE 2. Ecosystems in Everglades National Park.

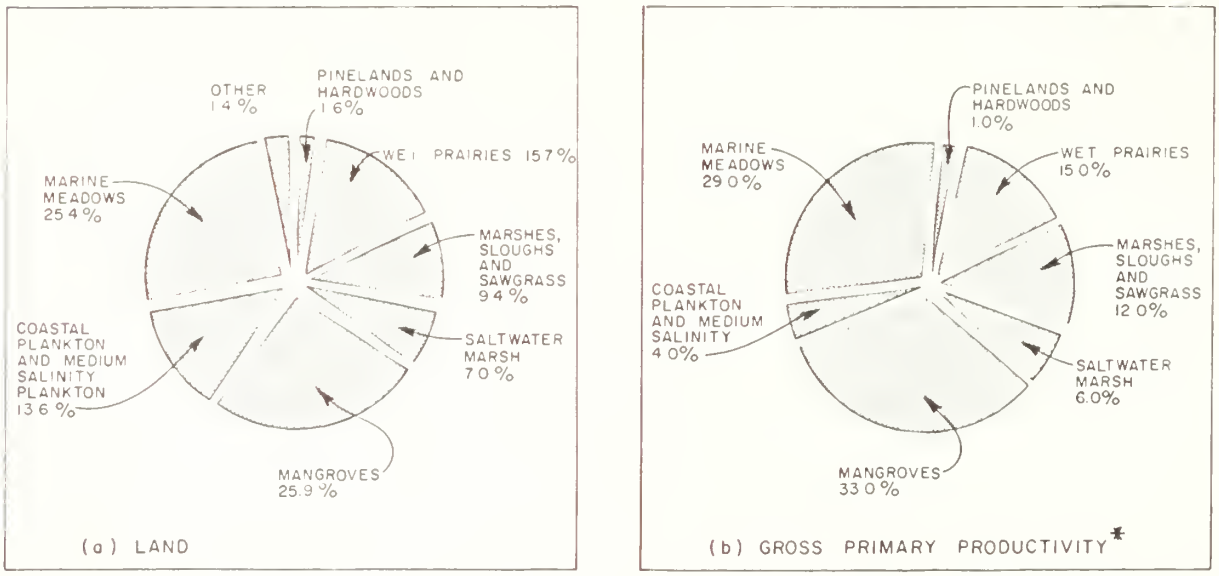



FIGURE 3. (a) Percent land areas of Everglades National Park by ecosystem type based on values from Table 2. (b) Percent gross primary production contribution by ecosystem type. Note: "Other" land use category not included.

TABLE 2. Area of energetic subsystems of Everglades National Park for 1973.

| Name | Map number | Proportion of area (%)[a] | Area (acres)[a] | (hectares)[a] |
|---|---|---|---|---|
| Residential (medium density) | 5 | <0.1 | 90 | 40 |
| Commercial & Industrial | 6 | <0.1 | 130 | 50 |
| Vegetable Crops | 10 | 0.4 | 5,060 | 2,050 |
| Pineland Sys. | 14 | 0.9 | 12,640 | 5,120 |
| Hardwood Sys. | 15 | 0.7 | 10,360 | 4,190 |
| Cypress (Domes & Strands) | 17 | <0.1 | 1,150 | 470 |
| Wet Prairie | 18 | 15.7 | 219,780 | 88,940 |
| Scrub Cypress | 19 | <0.1 | 930 | 380 |
| Marshes & Sloughs | 20 | 8.9 | 124,570 | 50,410 |
| Sawgrass Marsh | 21 | 0.5 | 7,290 | 2,950 |
| Beach & Dunes | 22 | <0.1 | 620 | 250 |
| Saline Transition | 23 | 0.1 | 1,560 | 630 |
| Scrub Mangrove | 24 | 0.3 | 4,880 | 1,970 |
| Saltwater Marsh | 25 | 7.0 | 97,920 | 39,630 |
| Mangroves | 26 | 25.9 | 362,510 | 146,710 |
| Coastal Plankton | 28 | 7.5 | 105,230 | 42,590 |
| Natural Embayments | 30 | 0.1 | 1,730 | 700 |
| Medium Salinity Plankton Estuary | 31 | 6.1 | 85,790 | 34,720 |
| Marine Meadows | 34 | 25.4 | 354,820 | 143,600 |
| | | 100.0 | 1,397,060 | 565,400 |

Source: measured from S. Fla. regional map by R. Costanza and T. Brown in Browder, Littlejohn, and Young, 1976.

[a] Rounded to nearest tenth percent, ten acres, ten hectares.

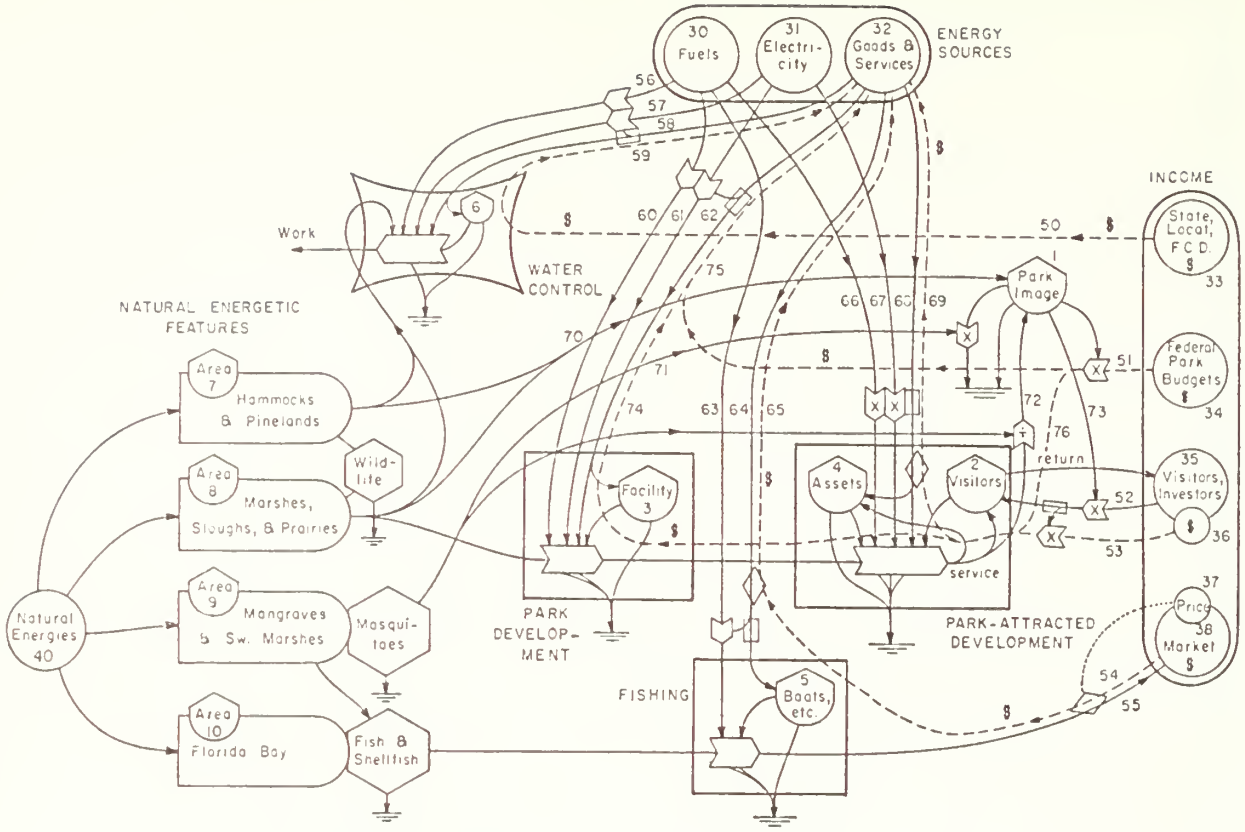



FIGURE 4a. Systems model, Everglades National Park.

TABLE 3. Values for model of the Everglades National Park and its external relationships (Fig. 4).*

| Footnote # | Name | Value |
|---|---|---|
| 1 | Image | |
| 2 | Visitors | 2787 Visotors |
| 3 | Park capital assets | $11,625,000 |
| 4 | Park related assets (outside park) | 125 million $ |
| 5 | Fishing related assets (boats, etc.) | $16.84x10$^6$ |
| 6 | Water control capital assets | $2.11x10$^6$ |
| 7 | Area of hardwoods & pinelands (incl tree islands) | 23,000 acres |
| 8 | Area of marshes, sloughs & wet prairies | 351,640 acres |
| 9 | Area of mangroves & s.w. marshes | 465,310 acres |
| 10 | Area of bay | 547,570 acres |
| 11 | Phosphorus in hammocks and pinelands | 0.369x10$^6$kg |
| 12 | Phosphorus in marshes, sloughs and wet prairies | 738x10$^6$kg |
| 13 | Phosphorus in mangroves | 346x10$^6$kg |
| 14 | Phosphorus in bay | 0.353x10$^6$kg |
| 15 | Groundwater | 1.85 million acre ft |
| 16 | Water in sloughs & wet prairies | 314x10$^3$acre ft |
| 17 | Water in mangroves | 502x10$^3$acre ft |
| 18 | Biomass of plants in hammocks & pinewoods | ** 8.4x10$^6$kg |
| 19 | Biomass of plants in slough and wet prairie | ** 980x1010$^6$kg |
| 20 | Fiomass of trees in mangroves | 1659x10$^6$kg |
| 21 | Biomass | 407x10$^6$kg |
| 22 | Organic matter in mangroves | 77,018x10$^6$ |
| 23 | Wildlife, crayfish, fish & wading birds | 0.003x10$^6$kg |
| 24 | Mosquitoes in mangroves only | 0.0081x10$^6$kg;39x10$^9$mos. |

| Footnote # | Name | Value |
|---|---|---|
| 25 | Invertebrates in bay | ** $28.4 \times 10^6$ kg |
| 26 | Fish in bay | $1.6 \times 10^6$ kg |
| 27 | Terrestrial Wildlife | no data available |
| 30 | Availability of fuel | $34.95 \times 10^{12}$ kcal/yr |
| 31 | Electric capacity | $38.68 \times 10^{12}$ kcal/yr |
| 32 | Availability of goods & services | $2.175 \times 10^9$ $/yr<br>$54.4 \times 10^{12}$ kcal/yr |
| 33 | Availability of FCD monies | $10,964,000 |
| 34 | Availability of Federal money | 403,900,000 $/yr |
| 35 | Population available for visiting | $211.4 \times 10^6$ |
| 36 | Dollar availability to visiting population | $977.3 \times 10^9$ $/yr |
| 37 | Price of fish | $4.30/kg (1.95/lb) |
| 38 | Money supply in market for fish | $187.5 \times 10^6$ |
| 39 | Water supply to north which is released to the park | 266,000 ac-ft/yr |
| 40 | Tidal energies | $0.1 \times 10^{12}$ FFE kcal/yr |
| 41 | Fish stocks outside the bay | ** $89.36 \times 10^6$ kg/yr |
| 42 | Solar and wind energy | $8.88 \times 10^{12}$ FFE kcal/yr |
| 43 | Source of rain to hammocks and pinelands | 98.2 inches/yr<br>190,620 ac ft/yr |
| 44 | Source of rain to slough marshes & wet prairies | 98.2 inches/yr<br>2,915,800 ac ft/yr |
| 45 | Source of rain to mangroves & s.w. marshes | 98.2 inches/yr<br>3,852,770 ac ft/yr |
| 50 | Money from state, local and flood control dist. due to park | $6,400/yr |
| 51 | Federal allocation to park | 2,455,000 $/yr |
| 52 | Visitors | 1,017,393 visitors/yr |
| 53 | Money spent in park attracted dev. by tourist | ** $45.5 \times 10^6$ $/yr |
| 54 | Retail value of fish | $23.48 \times 10^6$/yr |
| 55 | Fish and shellfish yield | $2.85 \times 10^6$ kg/yr |
| 56 | Fuels by FCD on park | $1.90/yr; $13.6 \times 10^6$ kcal/yr |
| 57 | Electricity used by FCD | $120/yr; $2.06 \times 10^6$ kcal/yr |
| 58 | Goods & services used by FCD | $6090/yr; $64.8 \times 10^6$ kcal/yr |
| 59 | Dollars for FCD for park | $6,400 |
| 60 | Fuels used in park | $3.94 \times 10^9$ kcal/yr |
| 61 | Electricity to park | $3. \times 10^9$ kcal/yr |
| 62 | Goods & services to park from external economy | $16 \times 10^9$ kcal/yr |
| 63 | Fuels to fishing | $1.135 \times 10^6$/yr or<br>$79.45 \times 10^9$ kcal/yr |
| 64 | Goods & services to boats | $12.35 \times 10^6$/yr or<br>$185.11 \times 10^9$ kcal/yr |
| 65 | Money spent on boat operations | $12.26 \times 10^6$/yr |
| 66 | Fuels used by park attracted development | ** $460 \times 10^9$ ffe kcal/yr |
| 67 | Electricity used by park attracted development | ** $284 \times 10^9$ ffe kcal/yr |
| 68 | Goods & services to park attracted development | ** $750 \times 10^9$ ffe kcal/yr |
| 69 | Money spent by park attracted development | ** $45.5 \times 10^6$ $/yr |
| 70 | Image and information from parks productivity and diversity | $8070 \times 10^9$ ffe/yr<br>$412 \times 10^6$ $/yr |
| 71 | Mosquito impact on image | ** $\approx 351.2 \times 10^6$ $/yr |

| Footnote # | Name | Value |
|---|---|---|
| 72 | Contributions of park attracted dev. to park image | |
| 73 | Contribution of image to attract visitors | |
| 74 | Income from park fees, etc. | |
| 75 | Cost of goods & services, Fuels, etc. | 820,000 $/yr |
| 76 | Park money to park attracted development | 2,071,000 $/yr |

*Calculations and sources in Appendix Table A-1.
**Values based on particularly sparse data.

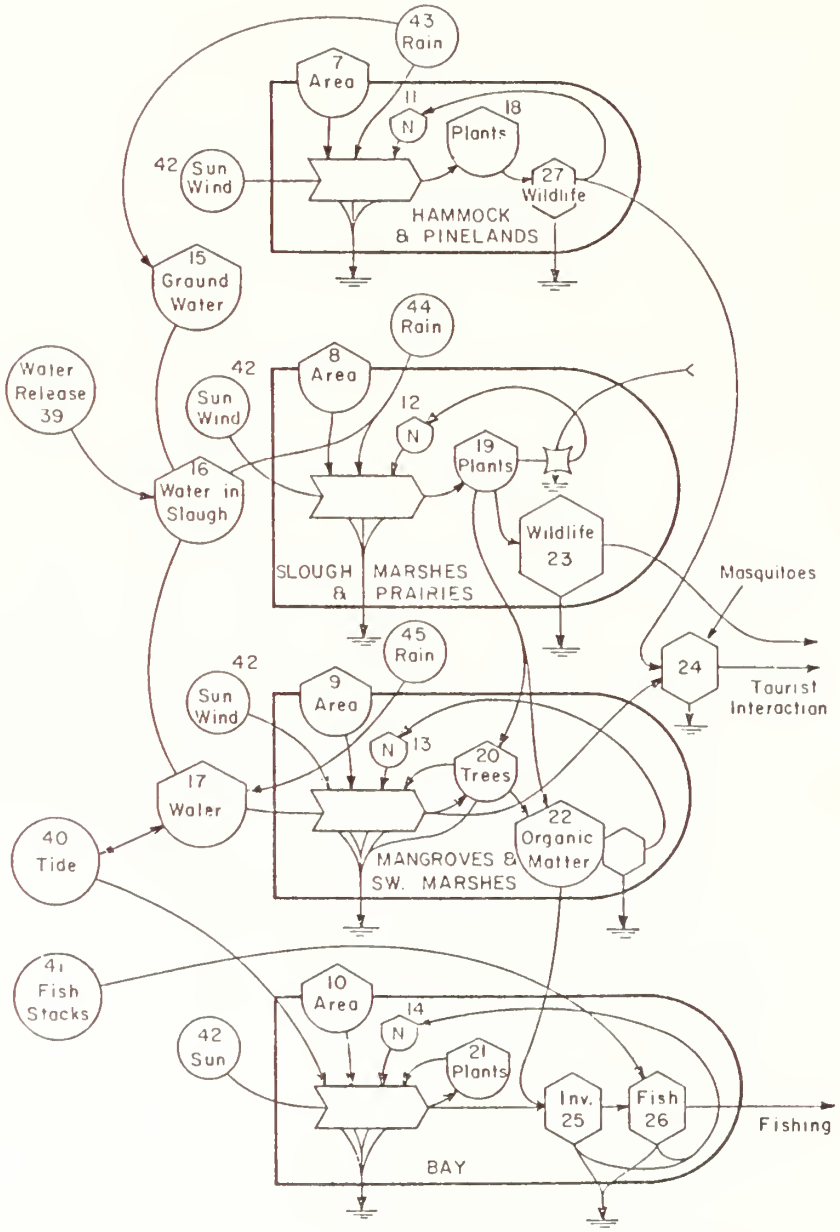



FIGURE 4b. Natural systems, Everglades National Park.

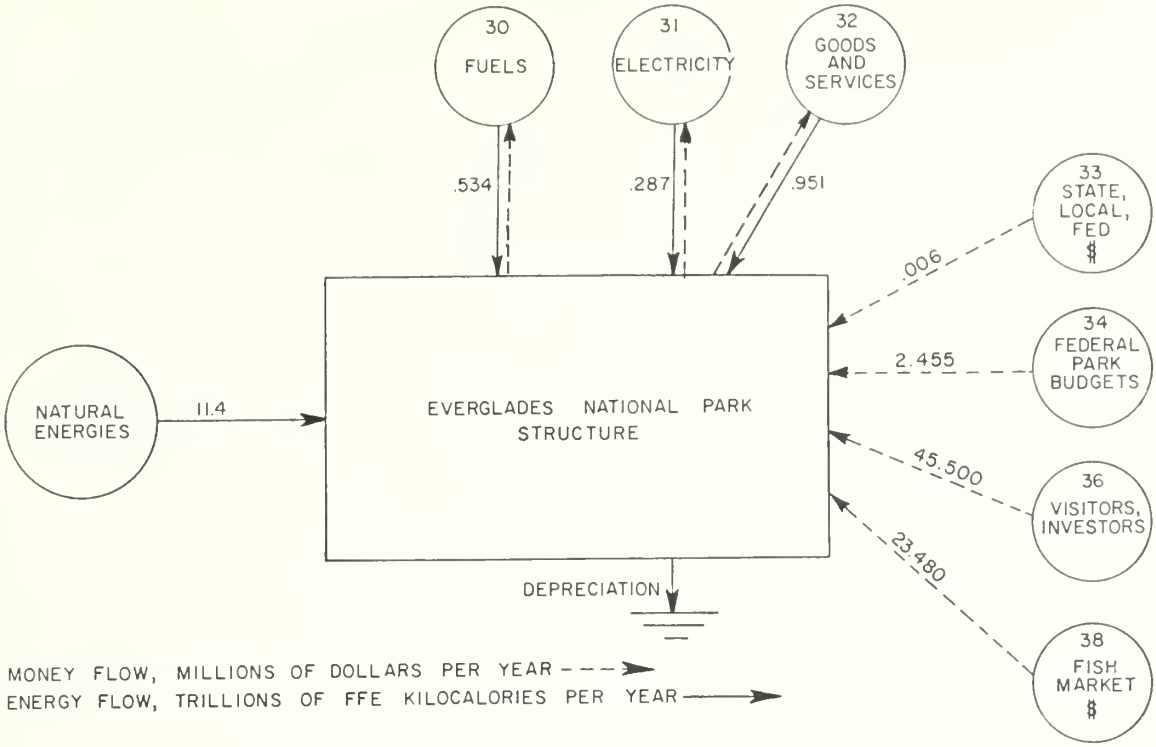
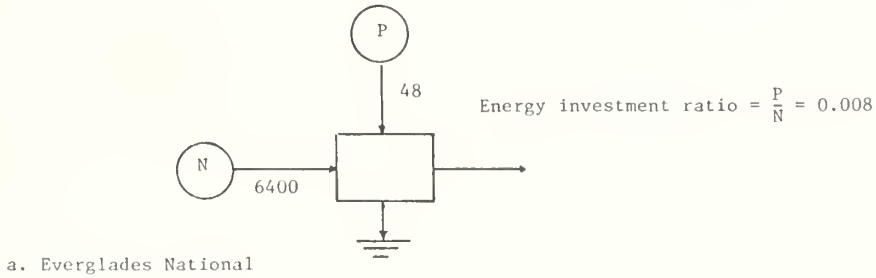
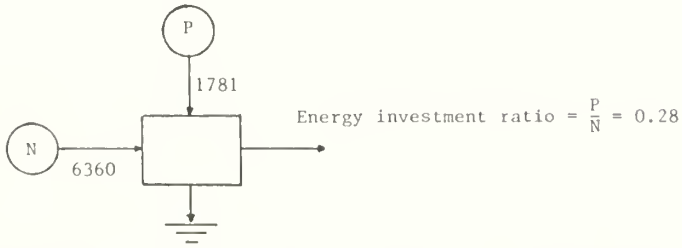



FIGURE 5. Details of Everglades National Park related dollar and energy flows, 1975.




a. Everglades National Park only.




b. Everglades National Park, park attracted development and related fishing industry.

x $10^9$ CE kcal/yr

P = Purchased energies for external economy

N = Natural energy (solar energy) incident on park.

FIGURE 6. Investment ratio of Everglades National Park and attracted development including related fishing industry. Based on land use data 1973, economic data 1974-1975 years. Natural energy was estimated as 4.56 X $10^6$ CE ac/yr X 1,397,000 acres; purchased energies in a. were estimated as sum of values for input energies #'s 60, 61, 62b. Fig. 1. Purchased energies in b. were sum of energy flow #'s 56, 57, 60, 61, 63, 64, 66, 67. in Fig. 1.

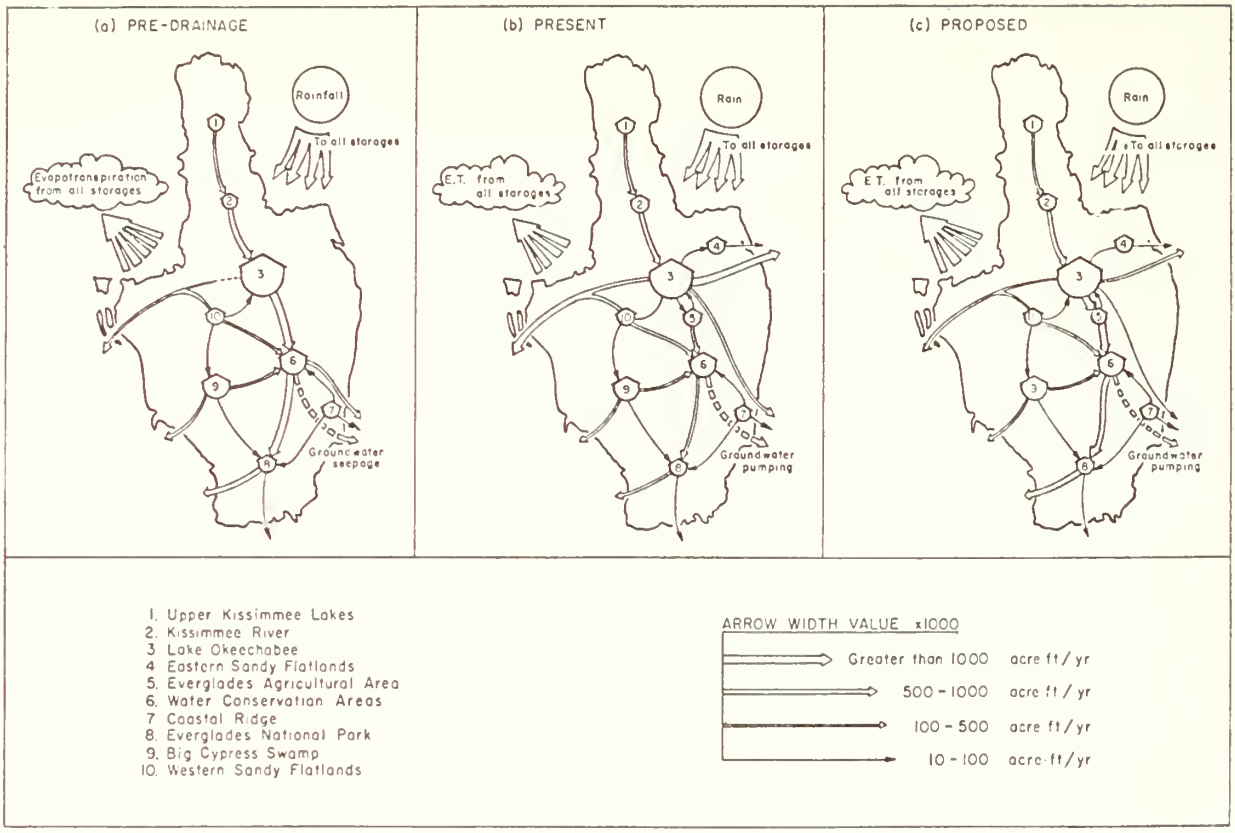



FIGURE 7. Hydrologic diagrams of the Kissimmee Everglade regions (data from Gayle et al. *in* Odum et al., 1975; and Carter et al.).

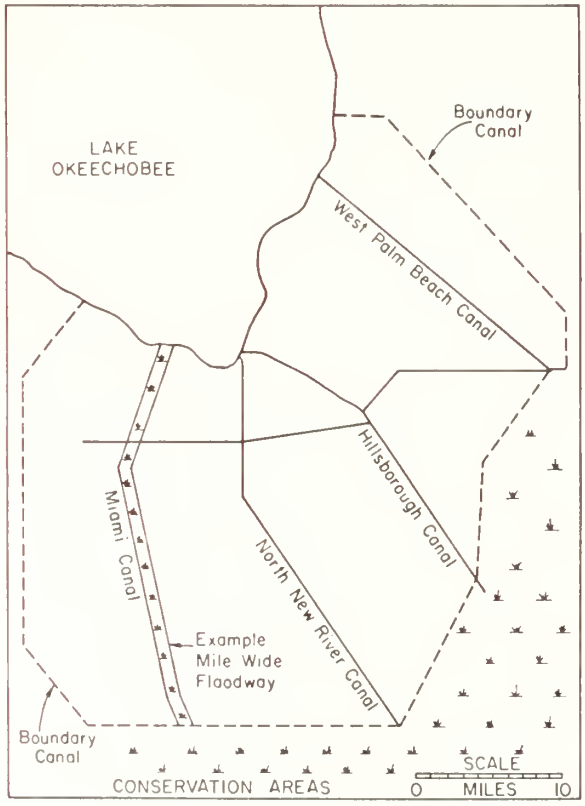



FIGURE 8. Everglades agriculture area showing an example of mile wide floodway to convey water from Lake Okeechobee to water conservation areas and Everglades National Park.

The natural system energy inputs are $6.4 \times 10^{12}$ CE kcal/yr of sunlight, $2.51 \times 10^{12}$ CE kcal/yr of wind and $2.5 \times 10^{12}$ CE kcal/yr of rain (as chemical potential to ocean salinity) totaling 11.4 trillion (CE kcal) annually. This amounts to 8.2% of the natural energy input to the Kissimmee-Okeechobee basin (Browder, Littlejohn, and Young, 1976).

In 1975 about 1,017,393 visitors came to Everglades National Park bringing an estimated $45.5 million dollars to the area around the Park (flows 52 and 53 in Fig. 2a). This represents 1% of the total regional tourist dollar income, and about 10% of the tourist dollars of Dade County (Miami-Metro. Dept. of Publicity & Tourism, 1976). An additional 23.6 million dollars are generated as retail sales of fish and shellfish. Values of sport and commercial fish and shellfish include wholesale shrimp value at the Dry Tortugas shrimp grounds, which are dependent on the Park. However, if the Park nurseries were not there, it is estimated, that 75% of the shrimp catch worth $37.6 million would be lost to the region's economy. (See footnote 54, Table A-1). The national park system contributed an additional $2.5 million in 1975 for park operations, mostly salaries for people working at the Park. Money provided by tourists, fishing, and the government contribute to the economy of the area surrounding the Park, providing funds for the purchase of goods and services for the urban system from outside the region.

Until June 1975, vegetable crops, primarily tomatoes, were grown within the Park boundary. The 1973-74 farm crop values were estimated at $7.7 million. The value of the tomatoes to the adjacent agribusiness (packing and marketing) was estimated to be $20 million (Cornwell and Atkins, 1975). Closing the "hole in the donut" to agricultural activity resulted in loss of 24% of Park related economy. However, the possible gain in water quality, protection of wildlife, and Park "image" by the action have not yet been quantified.

*Inputs From National Fossil Fueled Economy*

Fuel consumption for the Park facility, fishing industry and Park attracted development (#60, 63, 66, Fig. 3) was estimated at 534 billion CE kcal/yr. This plus 287 billion CE kcal/yr of electricity totaled 840 billion CE kcal/yr of energy consumed, representing 0.43% of regional energy consumption and about 1% of Dade County fuel consumption. The energetic value of goods and services used in the Park (#62, 64, 68, Fig. 3), 951 billion CE kcal/yr, represents 0.44% of the regional use of goods and services in energy terms. The total energy of fuels and goods and services used in the Park was estimated at 1.78 trillion CE kcal/yr.

*Energy Investment Ratio*

Flows of energy in coal equivalents are further aggregated in Fig. 6. An energy investment ratio (purchased energy/energy) was calculated for the Park alone (Fig. 6a) and for the Park and related Park development (Fig. 6b). The ratio for the Park alone was 0.008, while that for the Park and the Park influenced economy was 0.28. Each coal equivalent of solar energy captured by the Park's natural systems was associated with "attracting" or pumping 0.28 coal equivalents or fossil fuel generated goods and services into the region. This is much less than the 2.5 for the U.S. as a whole.

*The Value of Water as an Amplifier of the Flow of Energy in Everglades National Park*

In an energy system, each input can be considered to amplify the flow of another, i.e., act as a multiplier. It is common knowledge that water is a very sensitive factor in plant production, and this is particularly true for wetlands. A calculation was made for the value of water in plant production based on an empirical relation of net primary production in $g/m^2$-yr to precipitation in mm/yr (Leith and Whittaker, 1975).[3]

The energetic and economic value of 1 ac-ft of water in a region with an annual precipitation of 45-60 inches was estimated to be $0.666 \times 10^6$ CE/ac-ft or $34/ac-ft. This estimate is close to the $30/ac-ft for human use used by the U.S. Army Corps of Engineers in benefit-cost analysis. Control of the Park's surface water supply lies outside the Park's boundaries. South Florida's water management system and related problems are described in the South Florida report by Browder et al. (1976).

$$1000 \text{ mm/yr} = 1400 \text{ g/m}^2\text{/yr}$$

$$1500 \text{ mm/yr} = 1800 \text{ g/m}^2\text{/yr}$$

$$500 \text{ mm/yr} = 400 \text{ g/m}^2\text{/yr}$$

$$1 = 0.8 \text{ g/m}^2\cdot\text{mm}$$

$$\times 10 \text{ mm/cm} = 8 \text{ g/m}^2\cdot\text{cm}$$

$$\times 4.5 \text{ kcal/gm} = 36 \text{ kcal/m}^2\cdot\text{cm npp}$$

$$\times 3 \text{ gpp/npp} = 108 \text{ kcal/m}^2\cdot\text{cm gpp}$$

$$\times 0.05 \text{ CE/square} = 5.4 \text{ CE kcal/m}^2\cdot\text{cm gpp}$$

$$\times 4047 \text{ m}^2\text{/ac} = 21.8 \times 10^3 \text{ CE kcal/ac}\cdot\text{cm}$$

$$\times 2.54 \text{ cm/in} = 55.5 \times 10^3 \text{ CE kcal/ac in gpp}$$

$$\times 12 \text{ in/ft} = 0.666 \times 10^6 \times 10^6 \text{ CE kcal/ac-ft gpp}$$

$$\div 19{,}600 \text{ kcal/\$} = 34.00\text{\$/ac-ft value of water for gpp in the range of rainfall, for E.N. Park}$$

If the water supply to the park were increased by routing 500,000 additional acre feet of water south through the Everglades, then the amplifying effect of water could cause the productivity of the Park's ecosystems to increase by a value equivalent to $17 million/yr ($34/acre-ft x 500,000 acre ft/yr). This value should be realized in the increased availability of food for wildlife and in an increased ability of the park to attract visitors. It also should improve the fish production in central Florida Bay where present salt concentrations of 41 to 51 ppt are reflected in reduced standing crops of fish relative to other parts of the bay (T. Schmidt, 1976).

The ratio of fuel, goods and services to park related development, to the Park's GPP is 0.221; therefore, by the investment ratio hypothesis, an increase of $17 million/yr in natural production could generate $3.76 million/yr additional material from the external economy ($0.221 \times 17 \times 10^6$), an increase of 5.1%.

[3] Calculation of water amplifier values in primary production (values from Leith and Whittaker 1975).

## DISCUSSION

### *Assessment of Model and Evaluations*

This first attempt to estimate the flows of energy and money is likely to be underestimated. Among the pathways of interaction that we know about that are not yet estimated are:

1. Energy involvements of citizens who concern themselves with the park while using their energy-valuable time elsewhere.

2. Portions of the budgets of Federal, State, and Local institutions concerned with the Park beyond that spent directly and locally.

3. The total value of the sport fishery to the economy.

4. The value of the Park to sport and commercial fisheries of the Gulf as well as those of Florida Bay. Energy value of the Park as a source region affecting southwest wind to the metropolitan section of Miami in contributing to rainfall, air purity, and temperature.

5. Role of the Park in blocking overdevelopment and lowering energy effectiveness of suburban economy.

6. Role of the Park in providing food and habitat to migrating water fowl, wading birds, and Passerines whose perpetuation is important to recreational activities, forest insect control, and other aspects of natural ecosystems throughout the eastern seaboard.

### *Possible Meaning of Low Investment Ratio in Present Calculations*

A full discussion will await integration of these results with the rest of the South Florida Study in the forthcoming final version of the Technical Report.

The low ratio of purchased to natural energies may be interpreted by more than one hypothesis. As suggested in the previous paragraph the economy involved in the Park may be much underestimated. If, however, the true involvement of the economy of purchased attracted energy flow is less than the average in Florida, then one might expect to see more kinds of development involving the Park locally and at a distance.

It may be important to compare the investment ratio of the Everglades Park with those like Yellowstone that may be more heavily visited. The ultimate question is what is the carrying capacity of the Park in supporting economy. And vice versa, what is the economic involvement which will sufficiently impress the public decision process to maintain public support and backing for the parks in future periods when there may be declining available energy and real GNP?

### *A Suggestion to Restore a Corridor of "River of Grass"*

The timing and quantity of water released to Everglades National Park from the Everglades basin is thought to have changed significantly since the drainage of the Upper Everglades (Everglades Agricultural District) and the diking of the Central Everglades (Everglades Conservation Areas 1, 2, and 3). Wildlife depending on the aquatic system have decreased by an estimated 89 percent since 1947, suggesting that, on a long-term basis, the Park receives less water than it received historically (Kushlan and White, 1975), although 350,000 ac-ft annually was guaranteed when the present water control system north of the Park was implemented.

Presumably the decline in wildlife is due to fire death and stress in life cycles due to altered hydroperiods, such reduction in the primary productivity that is the base of many food chains.

Parker (1974) estimates that the outflow volume of the lower Everglades basin was roughly equal to the outflow of Kissimmee River into Lake Okeechobee (roughly one million ac-ft, Fig. 7a). The excess water from Lake Okeechobee normally drained by sheet flow over the Everglades and through the Caloosahatchee River. Drainage through the Caloosahatchee was intermittent and only when lake stages were high. Water in the Everglades was constrained from draining into the Atlantic by the Atlantic Coastal Ridge and the vegetation-clogged rivers in the transverse ridges. Thus, the predominant course of surface flow was down the length of the Everglades and into Florida Bay.

Over the last 100 years drainage works have reduced the flow of water out of the Everglades into Florida Bay by 1/5 to 1/2 (Fig. 7b). This was accomplished by dredging numerous large canals from levees from Lake Okeechobee and directing the water flow to sea before it could reach the Everglades. These works were constructed to regulate lake stages in Okeechobee, to irrigate and drain agricultural districts, and to maintain water levels in the water conservation areas. On the average over 1.5 million ac-ft of water leaves annually through canals.

The three major canals that are the only outlets leading from the lake to the Everglades Conservation Areas now are used to pump agricultural runoff north to the lake (Fig. 7b). This makes it impossible to release water from the lake south into the Everglades during most of the wet season. The water instead must be released to sea down the Caloosahatchee and St. Lucie canals to maintain "safe" levels in the lake. (See a more complete discussion of this problem in Browder et al., 1976).

Water "wasted" to sea by present drainage practices could be redistributed to the Everglades drainage basin to enhance natural productivity over much of South Florida by forming a shallow Everglades "floodway" between Lake Okeechobee and Conservation Area 3. The floodway could be diked to provide protection from high water in urban and agricultural areas. Based on Parker's (1974) estimates of the natural water supply to Florida Bay, around 500,000 ac-ft more water than the present average could be rerouted through the glades by such an outlet (Fig. 7c) approximating the natural situation (Fig. 7a).

A broad shallow floodway from the lake to Conservation Area 3 through the agricultural district could almost eliminate the loss of water through the Caloosahatchee and St. Lucie except in extremely wet years, and would increase the flow of water to Everglades National Park. The floodway would partially restore the natural pattern of water flow through the Everglades. Proper design to encourage the growth of emergent

vegetation might lead to the regeneration of rich organic soils to replace those which are being depleted through biochemical oxidation in the drained agricultural fields (Stephens, 1974). Users on either side could pump into and out of the swale. Agricultural nutrients would become a benefit rather than a liability when back-pumped into Lake Okeechobee.

An alternation of floodway and farmland over vertical (north-south) sections of the upper Everglades with reversal of roles of different vertical sections every 50 to 100 years, might greatly extend the productive life of the agricultural lands while at the same time restoring the natural north-south sheet flow through the Everglades.

Another possible design was proposed by the Army Corps of Engineers in 1955. They suggested a mile wide "floodway" from Lake Okeechobee to Conservation Area 3 (Alignments A or B, Plan 6 Floodway, Army Corps of Engineers, 1955), like the one pictured in Fig. 8. The Corps estimated that the mile-wide floodway would have the capacity to carry 16,800 $ft^3$/sec at the lake and 23,040 $ft^3$/sec at Conservation Area 3. At maximum flow for 100 days, the floodway could carry approximately 320,000 ac-ft of water from the lake to Conservation Area 3 at a lake stage of 17.6 ft. MSL. Emergent vegetation in the floodway would slow water flow considerably, and the floodway should be wider to carry this much water and serve its other roles.

## SUMMARY

The energy analysis of the Everglades Park suggests ways of measuring contributions of parks to the economy and their relative interaction. Comparing different parks may be useful, using models for comparative analysis. What is the range in investment ratios when heavily visited parks are included? Is the ratio a measure of economic impact on parks? The evaluation of energy quality of inputs suggests their relative importance. The very high energy cost and amplifier effect of fresh water in South Florida indicates why it was used on land in biological productivity and can be again if a small river of grass can be restored as a corridor serving agriculture, urban development, and the Park.

## APPENDICES

Appendices containing details of calculation, sources, and relevant literature will be published in the final technical report for the South Florida Project, Phase II, Center for Wetlands, University of Florida; or they will be available from the U.S. Dept. of the Interior, National Park Service, Contract report PX-0001-60080, Nov. 1976. Washington, D.C.

## LITERATURE CITED

ARMY CORPS OF ENGINEERS, JACKSONVILLE DISTRICT. March 28, 1955. Partial Definite Project Reports for Flood Control and Other Purposes, Part IV - Lake Okeechobee and Outlets, Supplement 2 Hydrology and Hydrologic Design. Section 5A - Design memorandum additional lake regulation facilities.

BAYLEY, S., and H. T. ODUM. 1976. Simulation of interrelations of the Everglades' marsh, peat, fire, water, and phosphorus. Ecological Modelling 1:169-188.

BROWDER, J., C. LITTLEJOHN, and D. YOUNG. 1976. South Florida: Seeking a Balance of Man and Nature. Bureau of Comprehensive Planning, Division of State Planning, Florida Dept. of Admin.; and National Park Service, Department of the Interior. Center for Wetlands, Univ. of Florida, Gainesville.

CORNWELL, G. W., and K. ATKINS. 1975. The impact of evicting farmers from Everglades National Park's hole-in-donut. Ecoimpact, Inc. Gainesville, Florida.

KEMP, M. 1977. Energy Analysis and Models of Power Plants in Coastal Zone. Ph.D. Dissertation. Dept. of Environmental Engineering Sciences, Univ. of Florida, Gainesville.

KUSHLAN, J. A., and D. A. WHITE. 1975. A survey of wading bird populations in southern Florida 1974-1975. Unpublished resource management report.

LEITH, H., and R. H. WHITTAKER. 1975. Primary Productivity of the Biosphere. Springer-Verlag, New York.

ODUM, H. T. 1971. Environment, Power, and Society. Wiley-Interscience, New York.

ODUM, H. T. et al. 1976. Net energy analysis of alternatives for the United States. Pages 254-304 *In:* U. S. Energy Policy: Trends and Goals. Part 5 - Middle and Long Term Energy Policies and Alternatives. 94th Congress, 2nd Session, Committee Print. Prepared for the Sub-committee on Energy and Power, of the Committee on Interstate and Foreign Commerce of the U.S. House of Representatives. 66-723. U. S. Govt. Printing Office, Washington, D.C.

ODUM, H. T., and M. T. BROWN (eds.). 1975. Carrying Capacity for Man and Nature in South Florida. Center for Wetlands, Univ. of Florida, Gainesville.

ODUM, H. T., and E. C. ODUM. 1976. Energy Basis for Man and Nature. McGraw-Hill, New York.

SCHMIDT, T. W. 1976. Florida Bay fisheries ecology. Interim report EVER-N-36-64.

ZUCHETTO, J. 1975. Energy-economic theory and mathematical models for combining the systems of man and nature, case study: the urban region of Miami, Florida. Ecological Modelling 1:241-268.

# MARINE BIOLOGICAL RESEARCH IN THE VIRGIN ISLANDS NATIONAL PARK

John E. Randall[1], Helen A. Randall[1], and Alan H. Robinson[2]

The Virgin Islands National Park on St. John was established in 1956. Though the island itself has much natural beauty, it is the sea around it that is the most captivating. Recognizing this, the National Park Service initiated a marine biological survey with the Marine Laboratory (now the Rosenstiel School of Marine and Atmospheric Science) of the University of Miami. This was supported by the U. S. Fish and Wildlife Service (Dingell-Johnson appropriation to the Virgin Islands), National Science Foundation, and the National Park Service.

The survey commenced in November 1958 and ended on June 30, 1961. The research was carried out at a combined residence-laboratory provided by the National Park Service at Lameshur Bay on the south shore of St. John. The Randalls were present during the entire survey period as was Gladston Matthias, an islander who assisted in fishing and other operations. The first year's diving assistant was Herman E. Kumpf, the second year's James R. Chess, and the third Robert E. Schroeder. Gilbert L. Voss, C. Richard Robins, and Lowell P. Thomas engaged in project activities at the University of Miami such as the curating of marine biological specimens.

Among the research projects undertaken during the survey were the preparation of a chart of the marine environments of St. John to the 10-fathom curve (Kumpf and H. Randall, 1961), a survey of commercial and sportfishing in the waters of the island (Idyll and J. Randall, 1959), the tagging of reef fishes for the study of growth and movements (J. Randall, 1962; 1963b), a study of the food habits of West Indian reef fishes (J. Randall, 1967; J. Randall and Hartman, 1968), the effect of grazing fishes on marine plants (J. Randall, 1961; 1965), analysis of fish populations on natural and artificial reefs in Lameshur Bay (J. Randall, 1963a), observations on the spawning and development of parrot-fishes (Randall and Randall, 1963), a study of the biology of the queen conch (J. Randall, 1964), a comparable study of the West Indian topshell (H. Randall, 1964), research on the biology of the sea urchin *Diadema antillarum* (J. Randall, Schroeder, and Starck, 1964), and observations of the predation by mongooses on the eggs of sea birds and the green turtle (Seaman and J. Randall, 1962).

Many systematic papers on fishes which were based wholly or in part on specimens from St. John have been published by J. Randall and associates, particularly C. Richard Robins and James E. Böhlke, culminating in the book *Caribbean Reef Fishes* (J. Randall, 1968). Systematic and ecological studies on marine invertebrates from St. John material have been completed by Lowell P. Thomas, Gilbert L. Voss, Raymond B. Manning, and Anthony J. Provenzano, Jr.

[1]Bernice P. Bishop Museum, Fish Division, P.O. Box 6037, Honolulu, HI 96818.

[2]National Park Service, Denver Service Center, P.O. Box 25287, Denver, CO 80225.

Lameshur Bay, St. John, was chosen for the scientists-in-the-sea programs -- Tektite I in 1969 and Tektite II in 1970. These were carried out with the support and cooperation of the U. S. Navy, National Aeronautics and Space Administration, Department of Health, Education, and Welfare, the Coast Guard, the National Science Foundation, the Smithsonian Institution, the Government of the Virgin Islands, the General Electric Company, and the Tai Ping Foundation. The Office of Naval Research was the principal supervising agency of Tektite I and the Department of Interior for Tektite II.

During Tektite I four aquanauts lived and conducted research underwater for 60 continuous days. This was the longest saturation dive that has been undertaken. Their base was a habitat of two cylinders 4 m in diameter and 6 m high joined by a flexible tunnel and seated on a rectangular base at a depth of 15 m. The men made excursions from the habitat up to 500 m or more, but remained within the depth range of 7 to 28 m. In addition to their own reseach, they served as subjects for comprehensive medical and behavioral studies.

Tektite II was a seven-month program consisting of ten different missions. Each mission which lasted from 10 to 20 days, involved four scientists and one engineer.

The Tektite programs were eminently successful, resulting in some fundamental marine biological research. Two Science Bulletins of the Natural History Museum, Los Angeles County, have been devoted to the results of these programs (Bulletin 14, 1972, edited by Bruce B. Collette and Sylvia A. Earle and Bulletin 20, 1975, edited by Sylvia A. Earle and Robert J. Lavenberg). Individual research papers within these bulletins are (from Bulletin 14): Sylvia A. Earle - The influence of herbivores on the marine plants of Grant Lameshur Bay, with an annotated list of plants; Thomas J. Bright - Bio-acoustic studies on reef organisms; Conrad Mahnken - Observations on cleaner shrimps on the genus *Periclimenes;* F. G. Hochberg, Jr. and Robert J. Ellis - Cymothoid isopods associated with reef fishes (abstract); William L. High and Alan J. Beardsley - The behavior of reef fishes in relation to fish pots (abstract); H. Edward Clifton and Ralph E. Hunter - the sand tilefish, *Malacanthus plumieri,* and the distribution of coarse debris near West Indian coral reefs; Ann C. Hartline, Peter H. Hartline, Alina M. Szmant and Arthur O. Flechsig - Escape response in a pomacentrid reef fish, *Chromis cyaneus;* Bruce B. Collette and Frank H. Talbot - Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover; C. Lavett Smith and James C. Tyler - Space resource sharing in a coral reef fish community; (from Bulletin 20): David A. Olsen, William F. Herrnkind and Richard A. Cooper - Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus,* of St. John, U.S. V.I. (I) Introduction and general population characteristics; David A. Olsen and Ian G. Koblic - Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus,* of St. John, U.S. V.I. (II) Growth and mortality; Richard A. Cooper, Robert Ellis and Steven Serfling - Population dynamics, ecology and behavior of spiny lobsters,

*Panulirus argus*, of St. John, U.S. V.I. (III) Population estimation and turnover; William F. Herrnkind, John A. VanDerwalker and Louis Barr - Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus*, of St. John, U.S. V.I. (IV) Habitation, patterns of movement and general behavior; Louis Barr - Biology and behavior of the arrow crab, *Stenorhynchus seticornis* (Herbst), in Lameshur Bay, St. John, Virgin Islands; Charles Birkeland and Brian Gregory - Foraging behavior and rates of feeding of the gastropod *Cyphoma gibbosum* (Linnaeus); C. C. Lee, E. L. Lee and J. S. Bunt - Distribution of biomass in a coral reef transect; Arthur C. Mathieson, Richard A. Fralick, Richard Burns and William Flahive - Phycological studies during Tektite II, at St. John, U.S. V.I.

Since 1966, the College of the Virgin Islands has operated the Virgin Islands Ecological Research Station at Lameshur Bay, St. John. In addition to playing host to the two Tektite projects, the station has provided support and facilities for projects investigating ciguatera (fish poisoning) and the development of commercial fisheries operations in the waters around the Virgin Islands. Results of these studies and other progress reports are available in a series of Contributions which may be obtained from the station's Director via Cruz Bay, St. John, U.S. V.I. 00830. The station, following a temporary closure in 1975-76, is available to student groups as well as long-term individual researchers.

Alan H. Robinson was in residence on St. John from 1970 through 1974 as the marine research biologist with the National Park Service. His efforts were divided between actual research, the identification of basic resource management problems, and the planning of specific inventory and research projects (National Park Service, 1975a; 1975b). Principal publications and activities included analysis of visitor damage along St. John and Buck Island's two underwater nature trails (Robinson, 1973), a two-year comprehensive analysis of coral-sand beach dynamics (Hoffman, Robinson and Dolan, 1974), an investigation of the development mechanisms and ecologic functions of saltponds on St. John (Robinson and Feazel, 1974), and an overview of research and resource management problems in the Virgin Islands National Park during the period 1970 through 1974 (Robinson, 1976a). The National Park Service, in cooperation with the College of the Virgin Islands' Ecological Research Station on St. John, provided major support for a variety of successful dissertation candidates from mainland institutions. A recent 2½-year study resulted in the most comprehensive quantitative analysis to date of fringing reef development on St. John (Feazel, 1975).

Several general publications and marine conservation initiatives, not strictly reporting research, but drawing substantially from combined research efforts from 1959 to 1975, have also appeared recently. These include a popular-style interpretive booklet "Virgin Islands National Park - The Story Behind the Scenery," with photography by Fritz Henle (Robinson, 1974). A summary paper in marine park planning is largely based upon observation and study of visitor activities and impacts in the Virgin Island park units (Robinson, 1976b). Substantial progress has been made, based also on surveys incidental to the research cited above, in establishing the first marine reserve within the park system of the Territory of the Virgin Islands - a coral reef reserve at Lagoon Point, St. John. On a broader scale, the research staff at the West Indies Laboratory of Fairleigh Dickinson University on St. Croix has recently completed an important natural area survey for the National Park Service's Natural Landmarks program (Adams, Gerhard, Ogden and Bowman, 1975). This natural region theme study has identified some 14 sites on the three U.S. Virgin Islands as potential natural landmarks, including terrestrial coastal valleys and shoreline, offshore bird islands, and classic coral-bounded bays. Although eventual official designation as landmarks would not automatically provide for public ownership or unqualified protection, the attention focused on these critical areas will go far to stimulate local government as well as private conservation/preservation initiatives.

The West Indies Laboratory of Fairleigh Dickinson University is currently undertaking a study of natural and man-induced changes in the ecosystem of Buck Island Reef National Monument with the support of the National Park Service. The principal investigators are W. B. and E. H. Gladfelter, R. K. Monahan, J. C. Ogden, and R. F. Dill. Buck Island is visited by approximately 50,000 persons each year, many of whom snorkel on the underwater trail of the island's barrier reef. The Laboratory scientists will inventory the marine resources and determine the rate of accrual and the rate of destruction and modification of these resources. This will involve mapping the area, a census of fish populations, study of the zonation of invertebrate and plant life, and the impact of human visitors.

Since the early 1970s, a Bureau of Fish and Wildlife has been operating with the Territorial Government's Department of Conservation and Cultural Affairs. The Bureau's prime marine responsibilities, under the leadership of long-time resident biologist Arthur E. Dammann, emphasize the concern to monitor and potentially improve the fisheries harvest of the Virgin Islands. This has included survey and analysis of extremely critical nursery grounds in the islands' remaining mangrove lagoons, artificial reef placement, and location of previously unexploited fish stocks at the edge of the islands' broad submarine shelf.

Although much progress has been made in recent years in our understanding of the classification, natural history and inter-relationships of the marine fauna and flora of the Virgin Islands and elsewhere in the Caribbean Sea, much remains to be learned. The Virgin Islands National Park and Buck Island Reef National Monument off St. Croix are the only marine preserves of the United States in the Caribbean Sea. Because of the protection provided for marine life at these islands, a unique opportunity exists for research. It is, for example, far easier to make observations or take underwater photographs of fishes in areas where man's usual predatory activities are curtailed. It is hoped that the National Park Service will continue to encourage and sponsor marine biological research in the Virgin Islands.

## LITERATURE CITED


ADAMS, J. B., L. C. GERHARD, J. C. OGDEN, and J. BOWMAN. 1975. Potential national natural landmarks U.S. Virgin Islands. Virgin Islands Natural Region Theme Study prepared for the National Park Service by West Indies Laboratory, St. Croix. 82 pp.

COLLETTE, B. B., and S. A. EARLE. 1972. Results of the Tektite Program: Ecology of coral reef fishes. Natural History Museum of Los Angeles County, Science Bulletin 14:1-180, chart.

EARLE, S. A., and R. J. LAVENBERG. 1975. Results of the Tektite Program: Coral reef invertebrates and plants. Natural History Museum of Los Angeles County, Science Bulletin 20:1-103.

FEAZEL, C. C. 1975. Ecozonation and sediment distribution of three reef areas on St. John, Virgin Islands. Ph.D. Thesis, Johns Hopkins University, Baltimore, Md. 224 pp.

HOFFMAN, S., A. H. ROBINSON, and R. DOLAN. 1974. Virgin Islands Beach Processes Investigation, St. John, Virgin Islands. Natl. Park Serv., Office of Natural Science Studies, Occ. Pap. No. 1:vii + 1-74.

IDYLL, C. P., and J. E. RANDALL. 1959. Sport and commercial fisheries potential of St. John, Virgin Islands. Fourth Internatl. Gamefish Conf. (1959), 9 pp. + addendum (1960), 2 pp.

KUMPF, H. E., and H. A. RANDALL. 1961. Charting the marine environments of St. John, U.S. Virgin Islands. Bull. Mar. Sci. Gulf and Carib. 11(4):543-551, 4 figs.

NATIONAL PARK SERVICE. 1975a. Resource Management Plan for Virgin Islands National Park. Virgin Islands Natl. Park, St. Thomas, U.S. V.I. 101 pp., with projects in appendix.

NATIONAL PARK SERVICE. 1975b. Resource Management Plan for Buck Island Reef National Monument. Virgin Islands Natl. Park, St. Thomas, U.S. V.I. 36 pp., with project status sheet.

RANDALL, H. A. 1964. A study of the growth and other aspects of the biology of the West Indian topshell, *Cittarium pica* (Linnaeus). Bull. Mar. Sci. Gulf and Carib. 14(3):424-443, 10 figs.

RANDALL, J. E. 1961. Overgrazing of algae by herbivorous marine fishes. Ecology 42(4):812.

RANDALL, J. E. 1962. Tagging reef fishes in the Virgin Islands. Proc. Gulf and Carib. Fish. Inst. (14th Ann. Session, 1961):201-241, 8 figs.

RANDALL, J. E. 1963a. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Carib. Jour. Sci. 3(1): 31-47.

RANDALL, J. E. 1963b. Additional recoveries of tagged reef fishes from the Virgin Islands. Proc. Gulf and Carib. Fish. Inst. (15th Ann. Session, 1962):155-157.

RANDALL, J. E. 1964. Contributions to the biology of the queen conch, *Strombus gigas*. Bull. Mar. Sci. Gulf and Carib. 14(2):246-295, 13 figs.

RANDALL, J. E. 1965. Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. Ecology 46(3):255-260, 4 figs.

RANDALL, J. E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanog. Miami 5:665-847.

RANDALL, J. E. 1968. Caribbean Reef Fishes. 305 pp., 319 illustr., TFH Publication, New Jersey.

RANDALL, J. E., and W. D. HARTMAN. 1968. Sponge-feeiding fishes of the West Indies. Marine Biology 1:216-225.

RANDALL, J. E., and H. A. RANDALL. 1963. The spawning and early development of the Atlantic parrot fish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. Zoologica 48(2):49-59, 2 pls., 2 text figs.

RANDALL, J. E., R. E. SCHROEDER, and W. A. STARCK, II. 1964. Notes on the biology of the echinoid *Diadema antillarum*. Carib. Jour. Sci. 4(2 & 3):421-433, 3 figs.

ROBINSON, A. H. 1973. Natural versus visitor related damage to coral reefs in Virgin Islands National Park and Buck Island Reef National Monument, with recommendations on underwater nature trails. Private printing. 24 pp., illustrated.

ROBINSON, A. H. 1974. Virgin Island National Park--The Story Behind the Scenery. 48 pp., with 102 color photos by Fritz Henle and Clarendon Bowman. K. C. Publications, Las Vegas, Nevada.

ROBINSON, A. H. 1976a. Marine research and resource management in Virgin Islands National Park. Trans. Natl. Park Centennial Symposium: Research in the parks, at AAAS meeting 28-29 December, 1971. USDOI/NPS Symposium Ser. No. 1:131-138.

ROBINSON, A. H. 1976b. Recreation, interpretation and environmental education in marine parks. Proc., I.U.C.N. Internatl. Conf. Mar. Parks and Reserves, working pap. no. 4:99-121. I.U.C.N. Publ. New Series No. 37.

ROBINSON, A. H., and C. C. FEAZEL. 1974. Fringing reefs, enclosing bays and saltponds in St. John, Virgin Islands. Oceans 7(5):40-43.

SEAMAN, G. A., and J. E. RANDALL. 1962. The mongoose as a predator in the Virgin Islands. Jour. Mammalogy 43(4):544-546.

# CLIMATOLOGICAL STUDIES IN YELLOWSTONE AND GRAND TETON NATIONAL PARKS

Richard A. Dirks[1]

## INTRODUCTION

The climatology of a region is a critical component in the effective management of the natural environment for its utilization in recreation and tourism. Recognizing the importance of baseline climatic data to management and research, climatological studies of Yellowstone and Grand Teton National Parks were initiated in 1973. Our research in the Parks has been conducted in two parts: (1) the assembly, summary, and interpretation of existing data in the Parks region, and (2) the collection, reduction, and interpretation of data from a special network of meteorological stations. Overall, this study is attempting to produce a comprehensive description of the climate of the Parks based on an evaluation of all available climatic records. The only previous attempt at a climatic summary was made for Yellowstone Park by Fletcher in 1927. In addition, individual station summaries have been published for several of the regular long term stations.

Fragmentary records of meteorological measurements date back to some of the early exploration chronicles and Park Superintendent reports at Yellowstone Park. Fairly complete records were kept at the Park Headquarters at Mammoth during the period 1879-1881. Superintendent Norris summarized his impressions of the Yellowstone Park climate in his 1879 and 1880 annual reports, in which he represented the climate as somewhat of a local anomaly resulting from the heat and moisture emitted by the hot springs and geysers. Continuous climatological records began at Mammoth in 1887 and represent the second longest continuous record of climatic data in the State of Wyoming. Continuous records in the Grand Teton Park date back to 1911 at Moran.

The region comprising Yellowstone National Park and Grand Teton National Park lies in the northwest corner of Wyoming with portions of the northern and western boundaries of Yellowstone Park extending into Montana and Idaho. Yellowstone Park is primarily a heavily forested volcanic plateau with an average elevation around 8,000 feet. The plateau is generally surrounded by high mountains except for the Snake River High Plains on the southwest which are about 1,000 feet lower in elevation than the volcanic plateau. The Continental Divide traverses the Park from the southeast corner in a west-northwesterly route so that approximately the southwest quarter of the Park represents headwaters of the Snake River drainage. Drainage to the north and east flows into the Yellowstone, Madison, and Gallatin Rivers. Some of the larger rivers, particularly the Yellowstone, have cut deep canyons into the lava plateau, in some places producing spectacular high waterfalls. At their lower reaches, both the Yellowstone River and the Madison River flow through relatively broad valleys at elevations below 7,500 feet, dropping below 5,200 feet near Gardiner, the lowest point in the Park. The highest elevation in the Park occurs on Electric Peak (11,155 feet), about six miles west of Gardiner.

[1]Department of Atmospheric Science, University of Wyoming, Laramie.

The physiography of Grand Teton National Park is characterized by the steep slopes of the Teton Mountains on the western boundary with several peaks exceeding 12,000 feet in elevation. This range extends south-southwestward from the Yellowstone Plateau and varies in width from 10 to 15 miles. The eastern slopes of the Teton Range fall abruptly down to Jackson Hole, a narrow intermontane basin about 48 miles long and 6 to 12 miles wide. The Snake River meanders through the basin floor which varies in altitude from 6,000 to 7,000 feet. To the east of Grand Teton National Park lie the Absaroka Mountains and to the southeast lies the Gros Ventre Range.

Due to the complexity of the region's mountain-valley topography and the frequent location of climate stations in locales of moderate climatic conditions (such as mountain valleys), a complete description of the Parks' diverse climates is not possible. In particular, the mountainous terrain of the Parks is not adequately represented by existing data.

### *Climate Description*

The following discussion of climatic elements is not intended as a complete description of the climate but rather to give an indication of its various features and, more importantly, to give examples of the types of climatic information which can be provided for applied needs.

In general, the climate of the Parks is characterized by short, cool summers, usually pleasant open fall, and long, rigorous winters, which tend to linger late into spring. The severity of winter is the result of persistent, rather low temperatures and much cloudy, unsettled weather with frequent light snows.

### *Temperature*

Temperature conditions in the Parks are typical of high altitude interior mountainous regions. Since the entire Parks region lies at high elevations leeward of major mountain ranges, the air is relatively dry, with a large diurnal temperature range. Daytime maxima of 70-80°F are commonly replaced by nighttime minima below 40°F during summer. Subfreezing temperatures occur during all summer months throughout the Park region except at elevations below 6,000 feet.

Daytime maximum temperatures during summer are closely aligned to elevation as seen in Figure 1. Below 7,000 feet July maxima often reach 80°F, but temperatures in excess of 90°F are rare. Daytime maxima rarely reach 80°F at high plateau and mountain stations (el. >7,500 feet).

Winters are cold with daily maxima often remaining below freezing. January is the coldest month with temperatures typically ranging from near zero at night to the middle twenties in the early afternoon at nonmountain locations.

Midwinter extremes can be very cold. The record low is -66°F at Riverside RS (West Yellowstone) on February 9, 1933, followed by -63°F on the same date at Moran. All areas of the Parks except Gardiner have recorded at least 40°F below zero. The occasional severe cold waves usually do not continue for more than two or three days; however, in December 1924, the minimum temperature at Mammoth Hot Springs did not rise above 26° below zero for five consecutive days and above 12° below zero for ten days.

The cold winter conditions are primarily of local origin produced by the combined effects of nocturnal radiation from a persistent winter snowpack through a clear, dry atmosphere. The drainage of radiationally cooled air into the basins and valleys may result in quite cold temperatures continuing for several days until this air is mixed out by strong winds or winter storm conditions. Extreme cold conditions occur when Arctic air invades the sheltered intermountain basins and valleys, stagnates there, and is further cooled by radiation and slope drainage. Since gravitational effects cause the cold air to drain into lower elevation valleys and basins, and cold air masses are often quite shallow, temperatures on the high plateaus and lower mountain slopes are often considerably warmer than temperatures at lower elevations during extreme cold situations. Figure 2 illustrates this situation from January daily minimum temperatures for three stations located along a valley slope near Gardiner: Stevens Creek at the valley floor (el. 5,450 feet), Hayes Ranch (el. 6,160 feet), and Parker Point (el. 7,830 feet). Under neutral lapse conditions, the temperature at Hayes Ranch should be about 4°F colder and at Parker Point 13°F colder than at the valley floor. Note the occasional deep isothermal or inversion conditions. Similar differences in mean climatic conditions are evident between Gardiner (el. 5,300 feet) and Yellowstone Park Headquarters (el. 6,341 feet), which lies well up the valley slope. Valley stations at Lamar RS (el. 6,470 feet) and Tower (el. 6,266 feet) are at about the same altitude as Yellowstone Park Headquarters but winter minimum temperatures are on the average 8-10°F colder.

West Yellowstone Basin has the dubious honor of recording the record minimum temperature for the Parks region, -66°F on February 9, 1933, at Riverside RS located just east of West Yellowstone. Average minimum temperatures during the winter are also among the lowest in the Parks region. Several factors seem to account for the occurrence of extremely low temperatures in this area. Cold air outbreaks which enter the valley are often stagnated because they must drain to the north. Secondly, being surrounded by high mountains on all sides, there is extensive down-slope drainage of cold air in the basin. Finally, the drainage flow out of the basin must pass through a narrow constriction near Hebgen Dam, which further retards cold air outflow. A similar situation exists in Jackson Hole and accounts for extreme cold conditions in that basin.

Lake Yellowstone temperature data should be quite typical of the plateau region if adjusted for minor lake influences during summer and fall, and if local adjustments are made for elevations.

### *Precipitation*

The normal annual precipitation at standard climatic stations in the Parks ranges from about 11 inches at Gardiner to 38 inches at Bechler River. Short term records suggest average values in excess of 50 inches over the southern Yellowstone Plateau and in the Snake River High Plains, the only area in the Park which does not lie in the rain shadow of a major mountain range. Even higher annual amounts undoubtedly occur in mountainous regions, since winter precipitation in particular is highly dependent upon elevation. Unfortunately, precipitation records do not exist for these areas.

Recently, Farnes (1971) has shown that mean annual precipitation for mountainous areas of Montana could be closely estimated from April 1 snow water equivalent measurements if corrections were applied for the canopy cover at each snow course. By plotting precipitation as a function of elevation for various terrain profiles and exposures, isohyetal maps could be constructed. Figure 3 shows the mean annual precipitation for Yellowstone National Park as determined by Farnes. Recent studies in Yellowstone National Park by Despain (1973) show that vegetation zones are well differentiated by mean annual precipitation and, furthermore, these zones are closely aligned to the precipitation analysis given by Farnes. Precipitation shows a large gradient from north to south in Jackson Hole. High values at Snake River exceed 30 inches annually, decreasing to 15 inches at Jackson.

The areas of high mean annual precipitation in the southern Yellowstone Plateau, the Snake River High Plains and mountains all show major increases in precipitation during mid-winter months. The remainder of the Parks region has a fairly uniform distribution of precipitation throughout the year with small peaks during June and mid-winter.

A wide range in annual snowfall occurs in the Parks due to the combination of elevation and "rain shadow" effects. Lowest values are estimated near 50 inches of Gardiner and 80-90 inches at Yellowstone Park HQ. Annual amounts increase southward across the Yellowstone Plateau to 150 inches at Lake Yellowstone, and in excess of 400 inches over the southwestern portion of Yellowstone National Park. The annual totals decrease to about 180 inches in the northern regions of Jackson Hole with further reduction to less than 100 inches at Jackson. At higher elevations annual snowfall is often in excess of 400 inches and locally may reach 600 inches. A recent analysis of average annual snowfall (1958-1972) by Farnes (1974) is reproduced in Figure 4.

Except for the southwestern portion of Yellowstone National Park and the higher mountains, heavy snowstorms are rare since upwind mountains protect most areas from immediate orographic upslope precipitation. Record daily snowfalls in these protected areas include 24 inches at West Yellowstone during January 1962, 21 inches at Moose during January 1962, and 14 inches at Yellowstone Park HQ on 24 October 1919. Although uncommon, significant amounts of snowfall have been measured during the summer months throughout the Parks except near Gardiner and in Jackson Hole.

Because of the persistent cold temperatures during winter throughout most of the Parks region, considerable accumulation of snow may occur. Lowest amounts occur in the Gardiner-Yellowstone Park HQ region where there is little accumulation until mid-winter or later. Average depths in this region are around 12 inches at the end of February with a record depth of 35.6 inches in March 1917 at Yellowstone Park HQ. Snow depths of 3-4 feet are not uncommon at West Yellowstone, Old Faithful and Moran, while at Jackson accumulations of 2-3 feet occur during

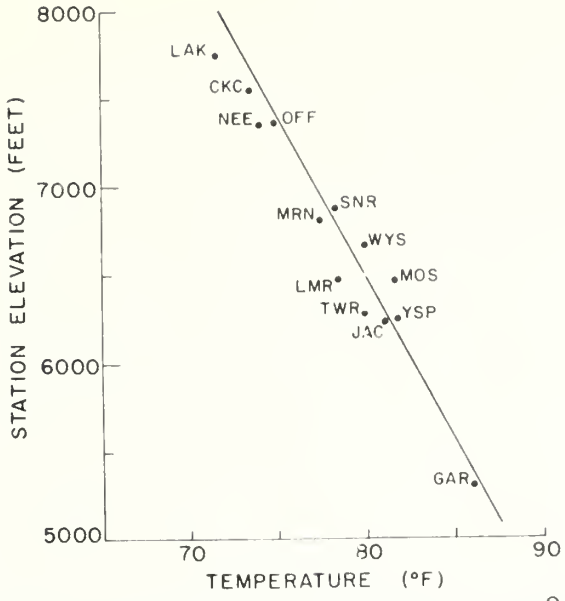



FIGURE 1. Mean maximum July temperatures ($^{O}$F) for Parks region stations plotted against station elevation (feet). Solid line is dry adiabatic lapse rate (-5.4$^{O}$F per 1,000 feet).

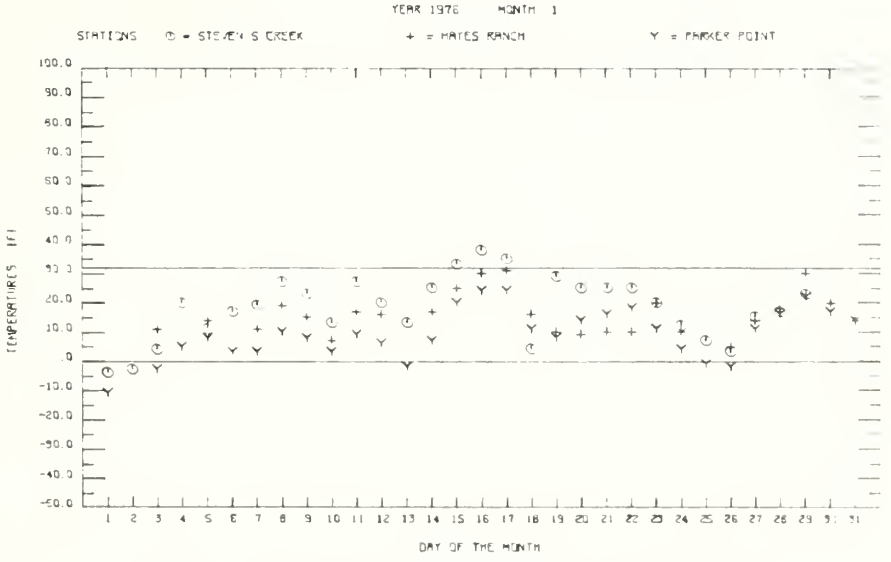



FIGURE 2. Daily minimum temperatires ($^{O}$F) at the 3-station transect near Gardiner, Montana.

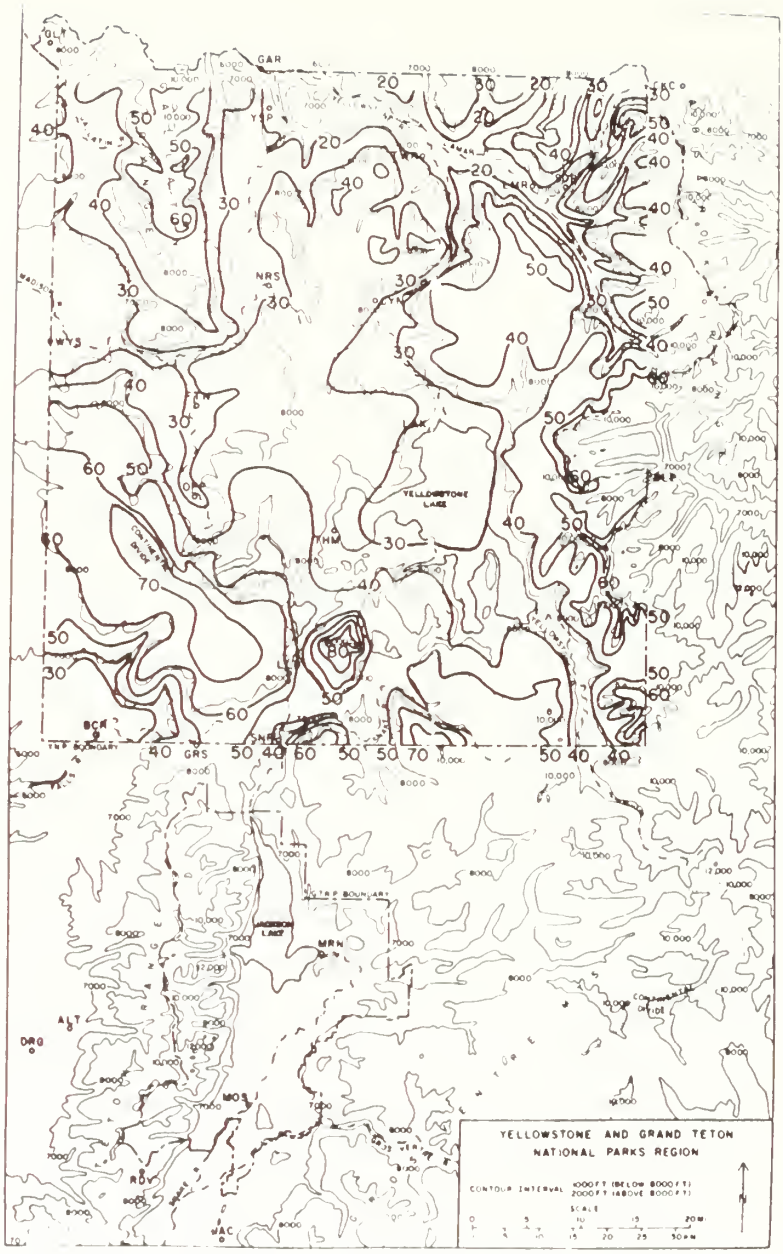



FIGURE 3. Mean annual precipitation (inches) for Yellowstone National Park (1953-67), by Farnes (1973).

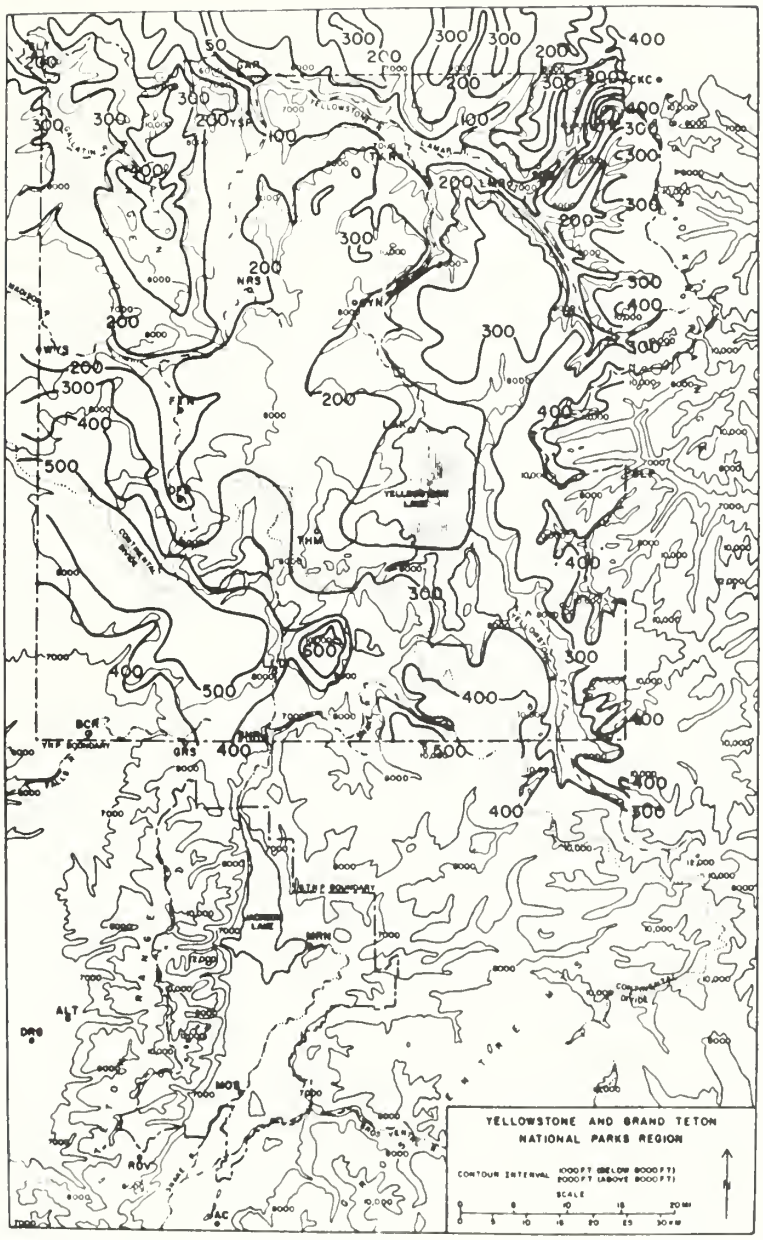



FIGURE 4. Mean annual snowfall (inches) for Yellowstone National Park (1958-72), by Farnes (1971).

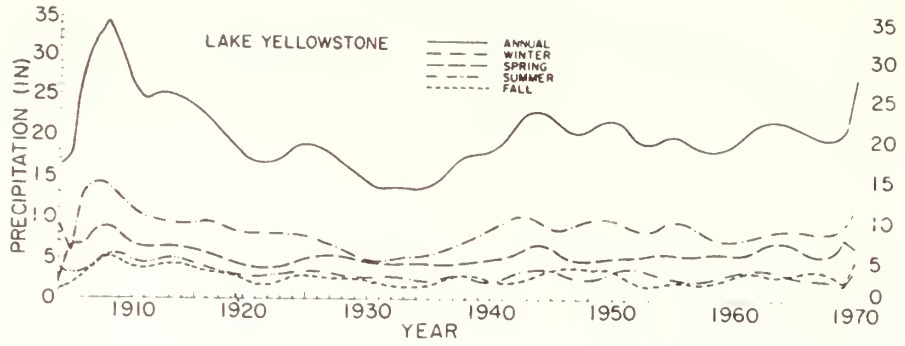



FIGURE 5. Seven-year seasonal and annual weighted mean precipitation at Lake Yellowstone (1904-70).

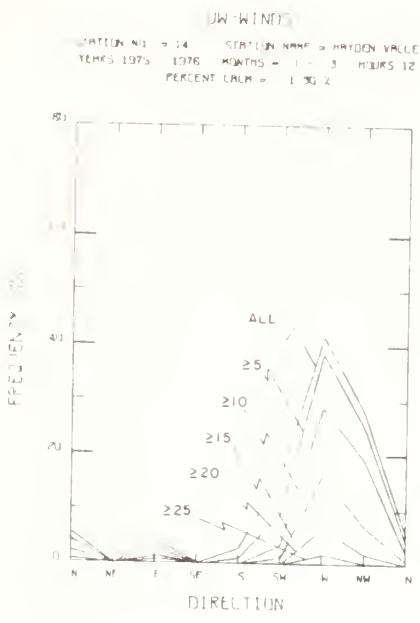



Figure 6

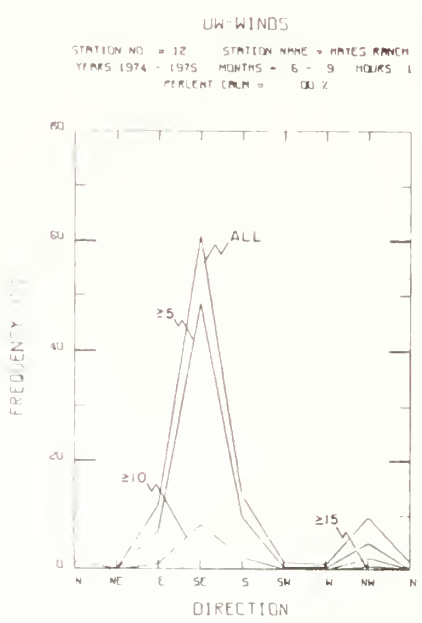



Figure 7

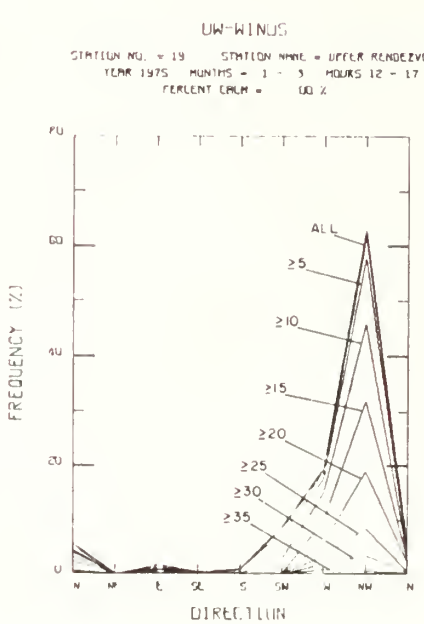



Figure 8

FIGURES 6-8. Frequency of occurrence of winds greater than or equal to the designated value (MPH) for each direction.

middle and late winter. High mountain snow courses frequently record depths in excess of 100 inches, and over 200 inches has been reported.

In an effort to determine long-term climatic trends in the Parks region, several analyses of the precipitation data were carried out. Data from several long-term station records were analyzed using a weighted running mean. The seasonal breakdown of data used was given by: Summer - July, August; Fall - September, October; Winter - November, December, January, February, March; Spring - April, May, June.

Lake Yellowstone annual precipitation (Figure 5) reached a maximum around 1908, then decreased gradually to its lowest point in 1930 remaining there until 1935; it again began increasing gradually until 1943, after which time the precipitation level has remained relatively constant except for a slight dip in the 1950's. Though winter precipitation contributes most of the total annual precipitation, long-term fluctuations in precipitation are reflected in all four seasons while short-term fluctuations generally are a function of changes in winter precipitation.

Further comparisons were made with frequency of drought occurrence -- that is, periods of no precipitation $\geq$ 15 days -- and the frequency of heavy precipitation events -- $\geq$ 0.5 inches per day. In general, all of these indicators showed a correlation in Parks precipitation with the 1930's drought. Other drought periods reported in the Great Plains and elsewhere are not generally reflected in the Parks data; and in some cases, well-defined local drought conditions and heavy precipitation conditions are evident only at individual stations.

No long-term trends are evident in the data from Yellowstone Park; however, there is some evidence of an increase in annual precipitation for Jackson Hole since the early 1950's from data at Moran and Jackson. This trend is due to increases in winter and spring precipitation.

### *Wind*

Wind is undoubtedly the most difficult of the standard meteorological parameters to measure and, furthermore, it has the greatest spatial and temporal variability near the surface. Local effects such as topographic channeling, slope winds, valley winds, mountain waves and obstructions produced by vegetation and terrain may frequently dominate the wind records at a particular site. Therefore, unless the exposure of a station is carefully examined, caution must be used in generalizing from its records.

Contemporary wind records in the Parks are sparse. Only fire weather stations, where observations are limited to one per day during summer months, have a reasonably complete network and many of these stations have been discontinued in recent years. Hourly winds are currently reported only at Jackson and West Yellowstone in the Parks region.

Reports of severe winds are infrequent. Wind speeds rarely exceed 40 mph at Yellowstone Park HQ. Maximum winds of 75 mph are reported for Jackson, occurring very infrequently. Moose, Moran, West Yellowstone and Lake Yellowstone have all reported occasional blow-down of timber due to damaging winds from intense thunderstorms. Strong winds from thunderstorms (60-80 mph) have also been reported occasionally at the fire lookouts on Mt. Washburn and Mt. Holmes during summer months. Regions of strong downslope chinook winds are not defined in the Parks although some of the late fall and springtime timber blow-down may be attributable to such phenomena. During winter persistent strong winds are common on upper mountain slopes.

In order to better define the wind climate of the Yellowstone-Grand Teton Parks region, field studies of climatic wind conditions were initiated during the summer of 1974. Three recording wind and temperature instruments were installed along a slope transect near Gardiner, Montana, on a southwest facing slope above the Yellowstone River, as described earlier. A second slope transect is situated at Teton Village, Wyoming, on the southeast facing slope of Rendezvous Peak in the Teton Range. Telemetered wind and temperature instruments are operated midway (el. 8,500 ft.) and near the top of the peak (el. 10,300 ft.). A recording wind instrument is also located on an exposed area of the central Yellowstone Plateau near Hayden Valley.

A preliminary analysis of data will be presented for several of these stations to illustrate the wide range of wind conditions and some of the characteristic conditions associated with certain topographic features.

During winter Hayden Valley is a rather harsh environment both day and night. Nocturnal wind conditions show a preference for southwesterly flow with speeds generally less than 10 mph, although, calm conditions occur only 15% of the time. Mid-winter days show a persistent strong northwesterly flow with the strongest winds from the west, sometimes having sustained velocities of 25 mph (Figure 6).

In a sheltered basin such as Jackson Hole, winds are generally light and calm conditions occur frequently during all seasons.

In contrast to Jackson, the wind data collected in the Yellowstone Valley near Gardiner show the classical characteristics of the mountain valley circulation. At night during summers (Figure 7) and both night and day in winter a weak downstream flow of cold air is commonly observed. During summer days a well-defined valley breeze is evident. Only occasionally is the local circulation over-powered by passing storm systems.

Characteristics of windflow in high mountain regions can be exemplified by the data at upper Rendezvous. During summer there is a dominant westerly and northwesterly flow both day and night, strong winds occur occasionally with average speeds 15 mph. During winter the wind speed increases somewhat with average speeds in excess of 20 mph and sustained speeds of 40-50 mph are observed (Figure 8). During winter the flow is generally northwesterly with some westerly and southwesterly components and a weak secondary peak from the east.

## CONCLUSIONS

There are many areas of environmental management in which climatological results can be applied to practical problems. A few examples include:

1. Environmental influences of weather on plant and animal life.

2. Research on the bioclimatology of insects and pests.

3. Research on the bioclimatology of plant diseases.

4. Meteorological influences on fire control, including controlled burning operations.

5. Location and design of structures, buildings and transportation routes.

6. Selection and layout of recreational areas-campsites, winter recreation sites, etc.

7. Water resource management for national park usage.

8. Meteorological aspects of air pollution related on tourism and nearby external sources such as lumber industry, mineral exploration and power plants.

These and other applied studies can be fruitfully pursued only if an adequate long-term base of climatological data is available on which local short term studies can be built. To provide and maintain such a data base requires a well-designed network of climatological stations located at carefully selected, representative sites, with regularly maintained and calibrated instruments. An accelerated effort is recommended in establishing such data backgrounds in large national parks. The pristine environment of remote areas of large national parks also provides an opportunity for collecting basic background data on many atmospheric parameters which are not subject to contamination by developing nearby sources. From such data long term natural trends can be more effectively assessed and natural responses of biological and geological processes to weather effects can be more readily determined. Such data collection is critical to both national parks management and national environmental management in general. Closely coordinated research between Parks scientists and managers and nearby university scientists would promote important opportunities and benefits for both groups.

As people and use pressures increase on many of our national parks' lands, increasing problems emerge in trying to maintain the quality of the natural environment. Maintenance of the environmental quality of our national parks requires that park administrators and scientific researchers cooperate to optimize environmental management procedures, both now and in the future.

## LITERATURE CITED


DESPAIN, D. G. 1973. Major vegetation zones of Yellowstone National Park. Unpublished, Information Paper No. 19, Yellowstone Park, National Park Service.

FARNES, P. E. 1971. Mountain precipitation and hydrology from snow surveys. Proceedings of the Western Snow Conference, Billings, Montana, April, 44-49.

_____. 1973. Preliminary analysis of mean annual precipitation for Yellowstone National Park. Unpublished, Soil Conservation Service, Bozeman, Montana.

_____. 1974. Preliminary analysis of mean annual snowfall for Yellowstone National Park. Unpublished, Soil Conservation Service, Bozeman, Montana.

# NATIONAL PARK SERVICE ARCHEOLOGICAL PROGRAMS: AN HISTORICAL OVERVIEW

Wilfred D. Logan[1] and F. A. Calabrese[2]

## PROGRAM DEVELOPMENT AND PAST PROBLEMS

I (Wilfred Logan) have been asked to present a brief, general history of the Service's concern with archeology. This history will have limitations in that it will be general. It will also be spotty, for I will use only a few areas and a few situations as examples. Some assertions I will make are based on intuition only, for, at this stage of my research into the history of our discipline in the Service, I cannot document everything. This history will be biased by my own experiences for I have played a part in much of what has transpired since World War II; sometimes unwittingly, sometimes with full knowledge as an enthusiastic activist. I give this warning of bias, for other interpretations of events are possible. On the whole I will try to review here how we got started, how we operated, and how effective we have been.

Federal concern with archeology pre-dates the National Park Service by many, many decades. The Smithsonian Institution has sponsored studies of antiquities since the 1840's. Other early studies and observations were made by a variety of individuals and groups--the Bureau of American Ethnology; both public and private institutions; private citizens, and concerned groups of interested laymen--who became increasingly alarmed over the fate of antiquities in the public domain. Some of these groups, both public and private, were engaged in research and the mitigation of impacts upon sites being destroyed or damaged by construction activities. Their concerns contributed to the stream of thought that brought about, ultimately, passage of the Antiquities Act of 1906. For those interested in details of this movement, Ronald F. Lee's (1970) presentation ably sets forth events leading to passage of this significant item of preservation legislation. The Antiquities Act is not only important for preservation of prehistoric sites but is also important because it adumbrated the National Parks Act of 1916. The creation of National Monuments under the terms of the 1906 Act, along with the existence of several National Parks prior to 1916, formed effective pre-conditions for an agency concerned with administration of lands set aside for educational and inspirational purposes.

Passage of the Antiquities Act resulted from alarm over the unscientific exploitation of ruins, primarily in the West. In effect, the Act prohibited "mining" of sites on the public domain by non-scientists. The Service, then, when it came into being, fell heir to a variety of areas preserving prehistoric remains. It is surprising in some respects, considering the number of prehistoric properties that came to the new Service, that prehistory has not had a more prominent position and a more profound role in Service administration.

As I view the Service's management of prehistory, both in care of sites and in research, I see several continuing threads of thought and action. Just as the Antiquities Act was brought into being by the efforts of scientists not necessarily employed by the Federal government, so was most early archeological work carried on by scientists from institutions not directly connected with the management of the sites. One such early example is the work of Jesse Walter Fewkes at Mesa Verde (Fewkes, 1909 and 1911). After the creation of the National Park Service, this pattern persisted, and the early policy was one in which research, by agencies and institutions other than the Service itself, was encouraged. This is largely true today. While such an approach may, in part, be desirable, I believe heavy reliance on this policy has helped develop an attitude of minimal concern, on the part of Service officials, for cultural resources which happen to exist on Service lands.

It is easy to see why such an approach should flourish. First, there is precedent, as there was no National Park Service when the early studies were carried on. Second, the tasks of the infant National Park Service were staggering with regard to organization; development of facilities; development of access; and development of an adequate budget. It would be natural to continue a pattern already set, rather than add to problems by trying to build an adequate research organization as well. Third, the other institutions and agencies by this time would have developed vested research interests, and would tend to encourage a situation in which they, not the Service, carried out the research required. A final reason would be economy. As many of the projects, especially in the early years were carried out by organizations with their own funding sources, the Service received the benefits of research gratis.

Whatever the reasons, the result, over the years, has been for administrations to emphasize construction, planning, concessions, visitor services, often at the expense of programs and organizations to study and serve the resources to be preserved.[3] With the influence of the large natural parks becoming, from the outset, the overwhelming concern of Service management, historic and prehistoric sites and research needs assumed at best a secondary status. The National Parks Act spoke of conserving "the natural and historic objects, and the wildlife therein . . ." Historically, however, the emphasis of Service programs has been on the natural objects and the wildlife, and even the former have not received the research support natural scientists believe is their due in preserving the Nation's irreplaceable treasures.

Although the effort has been too small in my opinion, archeological research, at one funding level or another, has been a continuing part of Service activity and significant contributions have been made to the body of knowledge husbanded by our Nation's anthropologists. The emphasis our

[1]National Park Service, Denver Service Center, Denver, Colorado.

[2]National Park Service, Midwest Archeological Center, Lincoln, Nebraska.

[3]This is not to say that maintenance of the resources has not been a concern. Very good ruins stabilization has been done almost from the beginning. I merely express the view that our efforts have suffered from too limited funding; less than fully trained personnel, and lack of enthusiasm for research, per se, where greater concern would have enhanced visitor experience and more enlightened resource management.

efforts have taken has reflected the intellectual biases of several generations of scholars in American prehistory. Early emphasis was on collection of objects--specimens for study and for exhibit purposes. Later, excavations in some Service areas contributed data to local cultural sequences. Today, studies focus on Man and his interaction with the natural environment, and currently, there is concern with "conservation archeology," i.e., the conservation of sites for the future, if alternatives exist, rather than excavation now.

Many of the earliest Service studies were brought about by the need to preserve southwestern ruins for exhibit to the public; to clear them and stabilize their walls for purposes of preservation and visitor safety. This was the intent of Fewkes' (1909, 1911) early work at Mesa Verde.

In the early years, particularly through the 1930's, major projects of large scope were a rarity. In part this reflected the state of the art of the time. It was really only after World War II that the Service sponsored any large archeological projects such as the Wetherill Mesa project. The Wetherill Mesa development was an outgrowth of the philosophy generated by the Service's Mission 66 program. Chapin Mesa and its ruin complex were suffering from excessive visitor impact. In keeping with the Mission 66 idea of promoting greater dispersal of visitors through parks in an effort to reduce impact, the Wetherill Mesa ruins were viewed as prime resources for development. It was thought such development would offer alternatives to the visitors. Although it fell somewhat short of its goals, the Wetherill Mesa project was a landmark in Service archeological work. It was administered and directed by Service personnel. Excellent physical facilities were provided, and it was adequately staffed on a multidisciplinary basis. Only the current Chaco research project is comparable in the field of prehistory. Directed by Douglas Osborne between the years 1958 and 1963, the Wetherwill Mesa project resulted in the preparation of several major manuscripts, some of which are yet to be printed.

Historical archeology in the Service has taken an evolutionary course somewhat separate from that of prehistory, although the personnel employed have shifted back and forth between the two fields. In the 1930's the Service performed, or sponsored, historical archeological projects (e.g., Ocmulgee Trading Post and Fort Sisseton, South Dakota). But the effort that dramatically brought the attention of scholars to the contributions archeology could make to the study of American history, and to planning and developing historic sites, was J. C. Harrington's excavation at Fort Necessity, Pennsylvania, in 1952 and 1953. Here Harrington fully demonstrated to historical scholars the validity of applying archeological field investigations to the solution of a historical problem. His work showed that previous assumptions concerning the location, size, and shape of George Washington's fort had been erroneous. He also extracted rather detailed information on the original fort structure, including the stockade and outer entrenchments, permitting an accurate reconstruction in place of the incorrect and conjectural development that preceded his work (Harrington 1957).

The Fort Necessity study was preceded and followed by several projects of lesser scope in a variety of areas: Theodore Roosevelt NMP, Fort Laramie, and Custer Battlefield, to name three. A second major effort in this period was conducted by John L. Cotter at Jamestown. Beginning in 1954, a team of investigators assembled by Cotter studied fully the Jamestown site, uncovering such eminently exhibitable features as the Glass Furnace. The Jamestown project served to establish historical archeology solidly as a form of research to be applied to the solution of historical problems, and Cotter's (1958) report is a classic in literature of this field. Jamestown was followed in rapid succession by work at Fort Frederica, Appomattox, Cumberland Gap, and Independence. Cotter supervised the Independence project, and here again applied the type of team effort that served him so well at Jamestown.

While historical archeological studies were burgeoning in the East, major historical studies were also initiated in some Western parks, including excavations at Tumacacori, Arizona; Fort Union, New Mexico; and Bent's Old Fort, Colorado. The work at Tumacacori was carried out by the late Paul Beaubien (1934 and 1935) and was probably the first historical excavation in a Western field area. One off-shoot of it was the later study, by Louis R. Caywood, of Spanish Majolica ceramics. Work at Fort Union was primarily a stabilization project, but excavation of various features in connection with the stabilization work furnished a rich body of information on life at the fort, and on the function of fort structures. Some minor historical archeological studies were done in the Midwest Region in the 1930's, but as at Fort Union, major work of this kind did not occur until after World War II. I believe that the post World War II salvage archeological program did much to advance the concept of archeological reseach as a contributor to historical programs. Many important historic sites were excavated in the course of reservoir salvage work, and this did have some influence on in-park work as well. The excavation of Bent's Old Fort, in the Midwest Region, was an interpretive necessity. When the area was authorized in 1960, no features of the fort survived above ground. It was evident that little could be done at the site without a full archeological study. In 1963, as Regional Archeologist for the Midwest Region, I participated in the Bent's Fort Master Plan effort. It was my express duty to develop plans for complete excavation of the fort. In the fall of 1963, Jackson W. Moore, Jr. was moved to the area to direct the excavations. He pursued this work between 1963 and 1966, and prepared a report, since published by the Colorado State Historical Society (Moore, 1973).

Service concern with archeological studies on lands other than those it administers also dates from the 1930's. However, major activity of this kind, again, followed World War II. The work of the 1930's resulted from Service involvement in Civilian Conservation Corps programs, and from projects funded by the Work Projects Administration. Following World War II, from 1946 until the present, the Service became involved in an archeological salvage effort of proportions unparalleled in the history of the science. Archeologists knew, beginning as early as 1944, that the Corps of Engineers and the Bureau of Reclamation had plans for extensive water control projects in thepost-war era. In that year, the President of the Society for American Archeology appointed a planning committee. The committee reviewed the plans of the major construction agencies as well as the previous Federal development related and archeological efforts, such as those of the Tennessee Valley Authority, Civilian Conservation Corps, and Work Projects Adminsitration. As a result of this committee's study, a Committee for the Recovery of Archeological Remains (CRAR) was established. CRAR was to advise the government on the emergency need, level of effort required, and trends that archeological work should take. The original Committee for the Recovery of Archeological Remains was composed of the following members: Williams D. Webb (Chairman), Frederick Johnson (Secretary), John Otis Brew and A. V. Kidder. William Duncan Strong was appointed as a liaison member for the National Research Council, and Frank H. H. Roberts, Jr. was liaison member for

the Smithsonian Institution. The Committee met annually in Washington with officials of the National Park Service; representatives of Federal construction agencies, the Smithsonian Institution, and the Secretary of the Interior. During the field seasons, individual members of the Committee made inspection trips to areas where fieldwork was in progress. They also met with key members of Congress concerning program needs.

Through the legal authority mandated under the Historic Sites Act of 1935, the Service and the Bureau of Reclamation became the agencies responsible for funding the salvage program. I was once told by the late John Corbett (then Chief Archeologist for the National Park Service), that consideration was given to requesting that the National Park Service accept full responsibility for administration and execution of the program. At the time, the Service Directorate had no interest in staffing for a major archeological research effort; hence, an arrangement was made whereby the Smithsonian Institution would carry out the actual fieldwork. This work began in 1946. Later, as the funding level and workload increased, the Service began to negotiate contracts and engage the assistance of universities. The effort grew to proportions unforeseen by anyone who contemplated the program at its outset.

The year 1946 saw, too, the appearance in the Washington Office of John M. Corbett, brought in from the field to administer the Service's part in the salvage program. Corbett, as Chief Archeologist, was to have a profound impact on the field of American archeology generally, as the scope of Federal involvement increased. The salvage program was administered by Corbett, who was also responsible for studies in National Park areas. Thus Corbett's influence on Federal archeology became immense. John was a man of vast energy and imposing appearance. From the beginning, he saw clearly the needs of the Service in archeology. He gave his career and his life, in effect, to seeing that these needs were filled. Few programs involving American archeology would be what they are today had it not been for the efforts of this man. The Service, and the field of American archeology owe John Maxwell Corbett a great debt, one that has been too little acknowledged.

As was pointed out above, the salvage program was administered by the Chief Archeologist, who was also responsible for studies in National Park areas. This had a profound impact on in-park studies in many ways. Obvious and first was the impact on funding. The salvage program demanded the lion's share of the monies involved--but it also had a positive impact, in that concepts, theories, and techniques developed in the emergency atmosphere of salvage came to be applied to problems in park areas or incorporated into park interpretive programs. Nevertheless, salvage was "where the action was," and I recall vividly my first years as Regional Archeologist, wherein I found it necessary to beg, borrow, and sometimes seemingly steal funds to launch sorely needed projects in the parks of the Midwest Region where there had been sad neglect of necessary surveys for archeological base map (i.e., Resource Basic data) purposes. We hardly knew, in those years, what our resources were in the parks, and we certainly were in no position to study, conserve, and protect them except as the need arose in an emergency. Usually, under such conditions, we were too late and badly underfunded to be effective.

As indicated in the introductory section of this paper, stabilization of ruins was a prime concern early in the Service's archeology program. Even before there was a National Park Service, there was a Ruins Stabilization program. The Division of Cultural Properties Conservation in the Western Archeological Center, is an outgrowth of the earlier Ruins Stabilization Team. In the early years, ruins stabilization was performed on a rather informal basis. In the 1930's Charlie Steen (later Regional Archeologist of the Southwest Region) and other archeologists moved about the Southwest stabilizing numerous ruins. The late R. Gordon Vivian was the preeminent figure in ruins stabilization, however. From the 1930's until his death in 1966, Gordon, with the standards he set, influenced the stabilization process throughout the National Park System. I will not go into the details of the development of Gordon's program here. The subject is well treated elsewhere by Pierson (1956:80-83). Gordon centered his activities at Chaco Canyon, but as the years progressed and the influence of his work spread to other Southwestern areas, pressure mounted for Gordon to move his headquarters from Chaco to Globe, Arizona, a move unpopular with Gordon because of his attachment to Chaco. Gordon resisted this effort successfully for some time, but eventually, when the Southwest Archeological Center was established it became necessary to move the Ruins Stabilization Unit into the new research-oriented organization. Even then, Gordon personally avoided Globe for a period of time.

For many years, from the time there were Regional Offices, responsibility for Park archeological studies was the duty of the Regional Archeologist. Of necessity, performance of the actual work was not centered in one single spot, and specific central physical facilities were not existent, unless one considers Vivian's headquarters at Chaco to have been such. There was constant talk of one area or another functioning as a center for archeological studies. I have not examined all of the legislation creating Service areas, where prehistory is a major theme, but it is my impression that the concept of such areas functioning as "centers" is repetitive. This is the case for Effigy Mounds and Ocmulgee National Monuments. In no case with which I am familiar, however, has the idea been successful. Effigy Mounds certainly does not function as a research center, and during the short period of time when Ocmulgee did, there was constant friction between the area staff and those attached to the Southeast Archeological Center.

The creation of the Southwest Archeological Center at Globe, Arizona, in 1954, was not an event with obvious portent for the future. At that time, when one thought of Service archeology, one still thought of the Southwest, forgetting the existence of the few scattered areas commemorating prehistory in the East. It seemed proper that there should be a research center serving this region, but no one would have thought of such for other parts of the United States. A good idea usually does not die, and other centers eventually were born. The Southwest Archeological Center at Globe occupied property which had an august history in the field of American archeology. The old Gila Pueblo had been headquarters of Harold Gladwin's research organization, and had therefore known the presence of figures impressive in the study of American prehistory. It was fit that the tradition should be carried on by the Service. The second Center, headquartered at Ocmulgee, was also appropriately located from the standpoint of continuing a proud tradition. Numerous people eminent in Southeastern prehistory had worked in the basement of the large Ocmulgee Visitor Center, and major projects had been directed from this base. Again, it was appropriate that the Southeast Archeological Center should occupy this space. In a different way, the same could be said of the Midwest Archeological Center when it came into being. The Midwest Center evolved from the earlier Smithsonian Institution, River Basin Surveys office, created in 1946 to

serve the archeological salvage program. The River Basin Surveys had performed prodigies in Plains research. It became the Midwest ARcheological Center as an artifact of shifting Federal agency philosophies and program emphases. There seems to have been a feeling within the Smithsonian Institution that River Basin Surveys was no longer compatible with the Smithsonian's mission. In 1968 the Secretary of the Smithsonian Institution appointed an ad hoc committee to study the River Basin Surveys program. The Committee recommended transfer of the organization to the National Park Service, since virtually all of its funding came from the Service, and the program it served was a Service responsibility. The shift to the Service was made, effective July 1, 1969, and John Corbett appointed me as the first Chief of the newly created archeological center. Ultimately, both the Southeast and Southwest Archeological Centers were moved to university campuses: the Southeast Center to Tallahassee, to an association with Florida State, and the Southwest Center to Tucson, associated there with the University of Arizona. Today the Midwest Center maintains an association with the University of Nebraska.

In 1969, also, still another Center was in stages of gestation. This was the Chaco Center, currently housed partly on the campus of the University of New Mexico and partly at Chaco Canyon. Discussions had been ongoing concerning the possibility of a major research effort at Chaco Canyon involving the Service and University of New Mexico. The University had a long history of involvement at Chaco Canyon.[4] Again, it was appropriate that the Chaco Center have an association with the University. In the fall of 1969, the writer and Zorro A. Bradley were sent by John Corbett to Albuquerque and Chaco to produce a prospectus for a Chaco Center, complete with a general research outline and multi-year budget for the research to be performed. Based on this and other documents, an agreement was reached and the Chaco Center was created with Robert W. Lister, formerly of the University of Colorado, as its Chief.

Although Chaco is the only Center created to serve a specialized function, it has contributed broadly to Service programs in prehistorical and historical archeology and through its energetic application of remote sensing research. Other Centers have developed one kind of specialization or another. The Southwest Archeological Center (now the Western Archeological Center) always led in Ruins Stabilization. For a period of time, due to the influence of the *Bertrand* project, the Midwest Center was a leader in the conservation of historical artifacts. Its research emphasis has always centered on the Plains, and currently it maintains a general field research orientation while it is developing specialized expertise in magnetometer surveys.

The Southeast Center traditionally has maintained a more generalized posture, but recently it has begun to focus on manipulation of computerized survey data to illuminate park needs. It is also placing heavy emphasis on littoral archeological studies--an emphasis that is natural and understandable considering the large number of coastal areas with which it is concerned.

The evolution of one additional phase of Service archeological endeavor must be briefly outlined. Archeological contributions to the planning process have always been a part of Service policy. For the most part, in earlier years, this contribution was sought only where prehistory was obviously involved, which meant, usually, that it was sought only for prehistoric areas. Time and the appearance of new legislation has modified this original simplistic approach. As we have obtained more detailed information on the location of archeological resources in Service areas, and as conformity to the newer legislation has improved, archeology has come to play a larger role. Once the offices of planning and construction within the Service drew upon the Regional Archeologists for review of their draft plans or completed plans. As the Service was being reorganized in 1971-72, archeologists were assigned to the staffs of the two Service Centers that then existed (i.e., Washington and San Francisco). Paul J. F. Schumacher held this position in San Francisco, and John L. Cotter functioned in this position for Washington, although he was located in Philadelphia. With the merging of these two offices into the single Denver Service Center, both of these men elected to retire, leaving a void in the area of archeological expertise and coordination. Late in 1972, I transferred from the Midwest Archeological Center to become the archeologist on the Historic Preservation Team of the Denver Service Center. Since that time, the Service Center has had considerable involvement in archeological work, reviewing programs, plans, and projects to provide adequate archeological contributions to the work underway. The archeological staff of the Service Center has also provided researchers to carry out limited projects in the field. On a scale somewhat more modest than that of the archeological centers, it has made significant contributions to research in the Parks. In one case its contribution was considerable, for virtually all of the archeological work connected with planning, development and restoration work for the Bicentennial of the American Revolution was carried cut by the Service Center archeological staff, with the research performed either through contracts, or, in some cases by Service Center archeologists.

The history presented on the preceding pages is, as I emphasized at the outset, general and spotty. I believe, though, that it reflects with some accuracy the trend and spirit of the activity within the Service. For many years the National Park Service led all agencies (federal, state, and local) in management of cultural resources. Whether this is still true today is difficult for me to judge. I am too close to the shifting policies and budget emphases to be an objective observer. I feel that, over all, given the limitations under which the program has functioned, the Service has done well. In fine, I think our situation is comparable to the story told of that day in the 1930's when Dizzy Dean, the late St. Louis Cardinal pitcher, was having a bad day on the mound. When the manager came out to ask Dean if they should put in a relief pitcher, old Diz shifted his quid of tobacco and replied with a question, "Who in the Hell have you got that's any better?"

## CURRENT PROBLEMS AND POTENTIAL SOLUTIONS

After a lengthy involvement as a researcher and administrator with Federal archeological programs, I (F. A. Calabrese) cannot help but agree with Logan's assertion that there is not another Federal agency better prepared to lead in the field of cultural resource management. However, the ability to maintain this lead is dependent somewhat upon a shift in current management attitudes toward the priority of consideration of cultural resources. Current Federal legislation, promoted by the professional archeological community and not the National Park Service, governing the protection of cultural resources is sufficient to protect that resource within National Park areas only if the

[4] Between the years 1929-47, the University was heavily involved in research at Chaco Canyon. For a period of years Chaco headquartered the University's field school in archeology.

intent of the legislation is followed. The legislation also outlines the Service and other Federal agency obligations with respect to management of cultural resources.

I wish now to point out some current resource management problems faced by the National Park Service (as well as other Federal agencies) and outline some alternatives for resolving some of these basic problems.

National Park Service archeological programs are in theory governed by both the legislation which was established to protect archeological sites and the Service's management guidelines for the preservation of historical and archeological resources. The Service still has a dual function with respect to cultural resource management. It is responsible for assisting other Federal agencies with adhering to legislation governing the protection of archeological resources on Federal lands and it is also responsible for protecting and preserving archeological sites within National Parks. Some people are familiar with the legislation which governs preservation and protection of the nation's archeological resources. For those who are not, the more important aspects of these are outlined below:

1. The Antiquities Act of 1906 (PL 59-209, 34 Stat 225); the first in a series of protective legislation for antiquities, requires individuals undertaking archeology on Federal lands to seek a permit through the Departmental consulting Archeologist, Office of Archeology and Historic Preservation before proceeding.

2. The Historic Sites Act of 1935 (PL 74-292, 49 Stat 666, 16 U.S.C. 461-467) and Historic Preservation Act of 1966 (PL 89-665, 80 Stat 915). The Historic Sites Act of 1935 establishes a national policy for the preservation of historic remains of national significance. The subsequent Historic Preservation Act of 1966 provides the legal backbone for protection of remains significant in American history, architecture, archeology, and culture. The 1966 Historic Preservation Act, through expansion of the Landmark program, establishes the National Register of Historic Places; defines the procedures which must be followed in evaluating cultural remains for inclusion on the National Register; establishes the Advisory Council for Historic Preservation as well as defines the required consideration (Section 106) for actions affecting Registered properties.

3. Executive Order 11593 (1971) tied the Historic Preservation Act of 1966 and the Historic Sites Act of 1935 making it policy for each Federal agency to inventory its land holdings, locate archeological sites, evaluate these sites for National Register significance and nominate those sites considered worthy of inclusion on the Register. Agencies are to administer and preserve their cultural properties in a spirit of trusteeship for future generations.

4. The Reservoir Salvage Act of 1960 (PL 86-523, 74 Stat 220) as amended by the Archeology and Historic Preservation Act of 1974 (PL 93-291, 88 Stat 174); are most important to current Federal archeological programs. The Reservoir Salvage Act provides for the preservation of historical and archeological data which might be lost as a result of dam construction. The amending 1974 legislation provides for the preservation of historic and archeological data which might otherwise be lost as the result of any alteration to the terrain caused by any agency of the United States or by any private person or corporation holding a license issued by a Federal agency.

Over the past 70 years it has been the responsibility of the National Park Service to interpret and administer this legislation and to guide and assist other Federal agencies with cultural resource management. It has only been in the past 5 years that other Federal agencies have taken cognizance of their own responsibility for these mandates. Up to this time the National Park Service assumed the responsibility for coordinating expenditure of Federal funds provided through the Department of the Interior for archeological salvage excavation prior to implementation of construction projects as well as the maintenance and consideration of the archeological resources within National Park areas. This was done with insufficient funds, usually with only a single professional archeologist per region. More importantly the energies of the Service's professional archeologists were more frequently diverted to assisting other Federal agencies and not toward resolving in-park archeological problems.

It was not until the enactment of the National Environmental Policy Act and Executive Order 11593, combined with the review procedure of the National Historic Preservation Act of 1966 and the President's Advisory Council that Service administrators began to take cognizance of the impact upon cultural resources in park areas. In effect now, the problems we face with respect to cultural resource preservation and management in our national parks are the result of an unplanned program of casual neglect.

The problems the Midwest Archeological Center encountered with respect to site preservation in both the Midwest and Rocky Mountain Regions' parks reflect the general problems that prevail in our parks through the country. Over the course of the past several years personnel from the Midwest Archeological Center have visited numerous park areas and witnessed considerable destruction of archeological sites, particularly in the southwestern cultural area. We presume the problem occurs in other parks--especially those lacking the staff and resources to protect their cultural remains. It is our belief that the problem is compounding. Unfortunately, we have neither the personnel, the resources nor the authority to combat this situation.

The problem of site destruction falls into several categories (1) destruction resulting from development and development-related activities planned by the Denver Service Center or Regional Offices (even though loss may be mitigated, sites are still gone forever); (2) destruction resulting from small construction and day-labor projects initiated by park areas and not coordinated with the Service archeologists; (3) destruction by uninformed park personnel, some of whom conceptualize the cultural resource as an expendable commodity unworthy of preservation; (4) unintentional vandalism, the general deterioration and destruction resulting from uneducated visitors climbing on standing walls, tramping across sites, carrying off artifactual materials, digging in mounds, picking at rock art, etc., out of curiosity; (5) intentional vandalism, the looting, digging and intentional destruction of walls, hearth areas, mounds, habitation and storage structures, etc., done out of malicious mischief or hope of monetary gain and (6) general deterioration as a result of wear by natural forces. The results and/or observations that have been made of these activities have been documented and the data are on file at the Midwest Archeological Center.

Two incidents of site destruction, one by day labor and a second by a contract/development operation, occurred recently in Grand Teton National Park. The first resulted in destruction of a major and what could have been highly significant archeological site at the outlet of Jenny Lake. The site was destroyed when heavy equipment was

utilized to move partially blown-down trees during the summer of 1974. The archeologist who first noted the site indicated that 18" of archeological materials had been removed. Clearly, the trees needed to be removed, however, this destruction without mitigation could have been avoided had the procedures established by NEPA and other protecting legislation, as well as the Service's historic preservation policies, been followed.

The second incident is the destruction of the archeological site on the north end of the Jackson Hole Airport runway. This occurred in clear violation of our policies, our stated objectives in the environmental impact statement and statements made to the Wyoming State Historic Preservation Officer and Advisory Council on Historic Preservation. Most frightening, however, is the precedent set by this action. In this case the environmental impact statment becomes a meaningless document, a paper exercise to soothe environmentalist concerns. It leaves the Service open to severe criticism.

The recent looting of archeological remains at Curecanti National Recreation Area by tourists who were shown sites by park personnel was noted earlier this spring by an archeological crew under the direction of Dr. David A. Breternitz. This we believe is carrying the purpose of recreation areas a bit too far. But it is indicative of the attitudes on the part of some park personnel for other park areas.

At Glen Canyon National Recreation Area we have documented vandalism of archeological remains by an employee of a concessionnaire. Further, it has been suggested on a national television program that Glen Canyon was an area to "search for arrowheads and Indian remains." This gives the impression that collection is an acceptable practice within our National Park Service areas.

In addition, at Glen Canyon the Davis Pool Pictograph Site, which is being used to test preservation techniques and materials, has been vandalized. Here, since methyl-methacrylate was applied to the site in April 1976, several fist-sized holes have been pecked into the sandstone panel. The white pictographs have also been outlined by charcoal. This particular site, though destined for inundation, is still a National Register property and approximately $25,000 is invested in preservation of this and similar sites. It is unmarked and unprotected by frequent patrol. It is easily accessible and subject to vandalism.

We have also witnessed pecking in an attempt to remove pictographs. We observed men urinating on rock art panels and have noted the use of standing walls for other excretory purposes. We have witnessed scratching, scraping and adding of contemporary symbols, names and other graffiti to rock wall faces.

The types of deterioration hardest to control are those occurring through the natural elements and/or human consumption by visitation. During a recent aerial reconnaissance of Mesa Verde we witnessed archeological sites covered by tin sheeting and metal which had collapsed. Other sites are partially exposed and partially protected.

The Service has initiated steps to resolve some of these problems. Specifically, attempts have been made to integrate archeological programming with developments from the initial phases of planning, design/development and ultimately, construction. However, because of the number of archeological sites and the rapidity at which development sometimes occurs as a result of add-on packages and politically sensitive projects (such as the Grand Teton airport), it is most difficult for us to provide adequate coverage given the size of our staff, funding and the time-frames generated.

The following steps must be taken if we are to resolve some of these major problems within the park areas.

1. Acquaint superintendent and park personnel with the kind and quality of cultural resources within their areas, the means of managing these resources and the problems they will encounter with the public in managing these resources. Few, if any parks now have developed Cultural Resource Management Policies and obviously, recreation areas have very different preservation problems from historic areas. This could be affected through an educational training course set up and/or monitored by Service archeologists. We have discussed this approach for some time, but do not have the personnel or funds to execute such a program.

2. A second major effort is needed in the programming of sufficient funds for signs, barriers and/or other means of protecting pictographs and/or standing structures and ruins. In the Horseshoe Canyon National Park where extremely significant and unique rock sites occur, the use of educational signs appears to help with the problem of tourist defacement of these National Register properties. Signs, obviously, will not deter the malicious vandal, but it can eliminate much of the vandalism done out of curiosity and ignorance.

3. Additional funds for inventory work are needed so that those sites most endangered can be listed and programmed for protection. I must stress that we are talking about large dollar amounts for the preservation of sites in this particular manner.

4. Funds must be programmed and projects implemented immediately to stabilize sites at Mesa Verde, Glen Canyon, Canyonlands and other southwestern and peripheral areas.

5. Additional funds and personnel must be made available for the coordination with the Regional Offices and the Denver Service Center to monitor upcoming development and construction-related programs in our national parks. Funds must be provided to maintain liaison, hire and maintain on-site archeologists and provide the necessary coordination between the regional offices and field areas.

6. Additional funds and personnel are needed to train preservation specialists for stabilization and maintenance of ruins and sites subject to deterioration by natural forces and heavy visitor use.

7. Large sums of money are needed for basic developmental research for preservation materials and innovative projects such as sub-surface site location and mapping utilizing remote and direct sensing techniques.

Over the course of the past three years, Service archeologists have asked for and stressed the need for economic and personnel support to meet the cultural resource preservation needs. Within the budgetary limitations available, we recognize that the Service has provided invaluable support. Administrators recognized our problems and needs, but faced with other problems feel unable to commit the resources necessary for the preservation of cultural remains. In other words, for some reason the priority of cultural resource protection and archeological research generally slips to the bottom of the priority list. We must caution now that the toll upon that resource is becoming greater by the year. With limited staff and funds we are unable to keep up with the pressure upon those resources, and it

is most painful to watch their deterioration.

It is realized that this is a solution to the problem of preservation; to an administrative, not a research problem. In addition to protection and preservation more and better planned research is needed.

Inventories to resolve research (as well as management) problems must be pursued within our National Parks. Some thorough archeological surveys, initiated in the early 1960's, at parks such as Dinosaur and Colorado National Monuments were well planned and executed. They now provide basic data for management as well as developing interpretive data and generating archeological information for these parks. These surveys were the forerunners to the complete inventories now required under Executive Order 11593.

It is incredible that we are only now just completing the archeological inventory at Mesa Verde National Park and that that inventory was done on a little over $10,000 a year for the past eight years. That those funds were inadequate to cover a park this size is apparent. Many major parks have not been inventoried in the Midwest and Rocky Mountain and other National Park Service Regions.

Recapitulating, we have outlined the development of archeological programs within and to the National Park Service since the enactment of the Antiquities Act of 1906. We have traced the Service's involvement in assisting other Federal agencies with cultural resource management problems, long before most agencies were aware of or willing to accept that they had problems.

The initiation of new research techniques and the development of innovative prehistoric and historic archeological research was stimulated by National Park Service funding and/or guidance through the salvage programs and work in National Parks. Considerably more would have been lost were it not for the Service archeologists assisting other Federal agencies during the rapid periods for development and construction following World War II.

While the Service continues to assist other Federal agencies, emphasis has shifted to the more pressing problem of the management of archeological resources within National Park areas. Despite existing legislation, policy and intent of the National Park Service, erosion of the cultural resources within the park areas continues. Various types of deterioration of the resources are considered. Steps to resolve some of these problems are provided.

In sum, we are suggesting that we (1) must develop a training program for initiating managers and park personnel into the sensible use, utilization and management of cultural resources; (2) must develop a program to continue our survey and inventory of park areas to allow proper management; (3) must provide money and personnel for basic developmental research projects for preservation and stabilization; and (4) should develop a sensible long-range goal for the use of cultural resources for interpretation and for providing basic information to the visitor.

BIBLIOGRAPHY


ANONYMOUS. n.d. National Park Service Southwest Archeological Center, Globe, Arizona. Unpublished document in the files of the Southwest Regional Office, Santa Fe, N. Mex.

COTTER, JOHN L. 1958. Archeological excavations at Jamestown, Virginia, Archeological Research Series No. 4. National Park Service, U.S. Department of the Interior, Washington, D.C.

FEWKES, JESSE WALTER. 1909. Antiquities of the Mesa Verde National Park--Spruce Tree House, Smithsonian Institution Bureau of American Ethnology, Bulletin 41. Washington. D.C.

FEWKES, JESSE WALTER. 1911. Antiquities of the Mesa Verde National PArk--Cliff Palace, Smithsonian Institution Bureau of American Ethnology, Bulletin 51. Washington, D.C.

HARRINGTON, J. C. 1957. New Light on Washington's Fort Necessity: a Report on the Archeological Explorations at Fort Necessity National Battlefield Site. Eastern National Park and Monument Association. Richmond, Va.

JOHNSON, FREDERICK. 1966. Archeology in an Emergency, Science, vol. 152, pp 1592-1597.

KING, DALE S. 1956. Some Historical Information Regarding Gila Pueblo. Unpublished memorandum in the files of the Southwest Regional Office, Santa Fe, N. Mex.

LEE, RONALD F. 1970. The Antiquities Act of 1906. Office of History and Historic Architecture, Eastern Service Center. Washington, D.C.

LEE, RONALD F. 1972. Family Tree of the National Park System: A Chart with Accompanying Text Designed to Illustrate the Growth of the National Park System, 1872-1972. Eastern National Park and Monument Association. Philadelphia.

LISTER, ROBERT H. 1968. Archeology for Laymen and Scientists at Mesa Verde, Science, vol. 169, pp 489-496.

MOORE, JACKSON W., JR. 1973. Bent's Old Fort: an Archeological Study. State Historical Society of Colorado. Denver, Colorado.

PIERSON, LLOYD M. 1956. A History of Chaco Canyon National Mounment. Unpublished ms. in the files of the National Park Service.

WEDEL, WALDO R. 1967. Salvage Archeology in the Missouri Basin, Science, vol. 156, pp 589-597.

# A RESOURCE BASIC INVENTORY TO SUPPORT LAND USE PLANNING FOR DELAWARE WATER GAP NATIONAL RECREATION AREA

J. Robert Stottlemyer[1]

## INTRODUCTION

The Delaware Water Gap National Recreation Area (DWGNRA) was established in 1965. It is located along the Delaware River between Stroundsburg, Pennsylvania, and Port Jervis, New York (Fig. 1). The Delaware River is one of the few remaining drainages within the northeastern United States not fully utilized. Over the last fifty years there has been considerable planning designed to regulate water flow within the basin. Congress authorized the Tocks Island Lake (TIL) project under the Flood Control Act of 1962. This project was to consist of an earth and rock fill dam and reservoir which was to provide for flood protection, water supply, power generation, and recreation. The TIL would raise the river water level 160 ft and would include relocation of U.S. 209 on much of the Pennsylvania side. The TIL was to have been an integral part of the DWGNRA, but its future now appears in doubt.

The recreation area has an authorized acreage of 72,000. Approximately one-half of this has been acquired. No major developments except for a combined headquarters-maintenance facility on the Pennsylvania side have been put in by Park Service, and none is presently planned.

The park lies within two major physiographic provinces. The entire area was glaciated during the Pleistocene Period. As a result, soil profiles are generally poorly developed and very shallow in many areas of the park. The park is within the oak-chestnut forest region with much of the area forested in hemlock-birch especially the poorer sites. Much of the river lowland is presently farmed under special use permit. The counties surrounding the park vary greatly as to their economic standing with the counties in New Jersey generally better off financially than those on the Pennsylvania side.

In gathering the data for DWGNRA, much time was spent in attempting to define specific objectives for application of the information. The recognition of data packages as a formal component of the planning process within the Park Service is relatively new. De facto, it is still experimental. The effort at DWGNRA was only the second undertaking involving the interfacing of automated data handling techniques with geographical and social-economic data. In no manner was this an attempt to develop a management information system if such can even be defined. The sole emphasis was on a planning data package. The reason for this is the planning component of the decision-making process within any agency is generally the simplest cycle to project, and decisions can be easily arrived at concerning appropriate data quality to synchronize with the planning cycle. In any experimental data acquisition and synthesis effort, one can ill-afford to initially expend energy on information not immediately applicable to the decision-making cycle.

Guidance as to the quality of data needed came from a variety of sources. The enabling legislation for DWGNRA obligates the Park Service to prepare a land management plan for those areas suitable for recreation, areas possessing outstanding natural and historical values, and any lands meeting multiple use needs such as hunting and possibly timbering. Additional ideas came from documents as the National Park System Plan (1971) which outlines what role individual park areas play in the National Park System. The criteria used in designating properties for the National Register of Historic Properties can also be of assistance.

The Park Service interprets its 1916 Organic Act and individual park area's enabling legislation through administrative policies which are published (1975). Since 1975 the emphasis is on the development and implementation of policies by land class as arrived at through the planning process. This requires as a first step consideration of the nature of the resource to be managed. The eventual land classification map is then further qualified by other factors such as social-economic conditions especially those of the coterminous counties and communities.

Policies related to resource management and visitor use are specifically implemented in a General Management Plan which consists of three major parts: A General Development Plan, a Visitor Use Plan, and a Resource Management Plan. It was the General Management Plan for which the data package for DWGNRA was designed.

In summary, the strategy was to review in detail the park's enabling legislation, the Park Service's administrative policies, and the park superintendent's management objectives in preparing a specific list of issues to be addressed in the near future with some indication of their priority. Then experts primarily from the academic world, were consulted to seek out what kinds of information were needed to answer such issues and where such information might be found. The decision to use automated data handling was based primarily on the amount of information to be gathered, its synthesis, and the need to evaluate a great number of possible contingencies in a relatively short time span.

## METHODOLOGY

Funding for this project was made available in the summer of 1974. A contract for the gathering and anlysis of regional social-economic data and a visitor use profile was let with the Department of Sociology, City University of New York. The gathering of resource data within and coterminous the park was by contract with the National Aeronautics and Space Administration at Bay St. Louis, Mississippi, which at the time had a unit established to prepare computer-based land use data packages. The decision to go with NASA was largely determined by the time constraints of the project.

For the social-economic analysis, the six counties surrounding the DWGNRA were intensively examined. Only existing regional information was examined in this phase of the analysis which included among others the following items: available public services; population income, movement, age trends; economic diversity; trends in county budgets and their appropriations; and primary industries.

[1]National Park Service, Mid-Atlantic Regional Office, Philadelphia.




FIGURE 1. Skylab photo of DWGNRA and coterminous lands.

A visitor use survey was also conducted. The objective was to determine present use patterns and trends within the park to get some indication of future recreation and facility demands. The survey was conducted on a busy late summer weekend. Six sites were selected at which 1000 questionnaires were distributed to one adult member of each traveling group. The questionnaires were returned by mail. The questionnaire was approved by the Office of Management and Budget. Three hundred and seventy-two were filled out and returned.

In evaluating resource characteristics within and coterminous the park, the objective was to determine resource suitability for a wide variety of possible park uses. The overall procedure consisted of the following steps: define the land use objectives, collect the basic data and process it, basic data digitization, generate base maps and overlays, convert polygon data to grid cell, derive further information from cell data, determine cell suitability for variety of potential land uses, set up environmental impact analysis, and develop land use plan alternatives with assessments.

The software program used in the land suitability analysis was the Harvard Grid (SYNMAP) significantly modified by the School of Forest Resources at Penn State University. To insure consideration of all applicable data, a matrix was generated showing the categories of data on the abscissa with geographical areas down to the county level or the ordinate. Data were collected primarily from the park and Federal, state, and local agencies. All information except topographic (elevation, slope, aspect) was obtained in the form of maps. Topographic information was purchased from the Defense Mapping Service on tapes in a grid format. Maps were digitized as polygons requiring that all map information be identified by alpha-numeric coding. A Numonics digitizer was used. The tapes containing the data from each source map were then plotted at the scale of the original source map to check accuracy. All maps digitized were then converted to the same scale (1:62,000). All data were then merged onto a single data file on tape.

Often source maps have errors such as distortion. Thus the previous steps can be time consuming and expensive. Considerable time was spent on this stage to ensure map accuracy so mismatch of information did not occur when the information from the varying sources was combined. With the correction of errors, the digital tape was ready for final overlay plotting at which time titles, legends and any other map information thought appropriate was combined on the overlay. Overlays were produced on a high-speed Xynetics plotter and the following information was displayed: maximum topography line, flood prone areas, drainage, TIL reservoir water line, DWGNRA boundary, land ownership, elevation, aspect, slope, vegetation, soil type, soil depth, geology, surface water, present land use, transportation, utilities, historic structures, archaeological sites, and critical areas.

This information was then converted to a one hectare grid cell format. The one hectare level of resolution was thought sufficient in this instance in view of the nature of the decisions to be made. The accuracy of the grid conversion was checked out by line printout display and more precisely by Ramtek (cathode) display. All of the above information was available for land within the park boundary. Soils and vegetation data were not initially obtained for the coterminous 250,000 acres.

In the determination of resource suitability or attractiveness for each grid cell, the following procedure was used. Data variables pertinent or relevant in evaluating the specific land use were selected. The relative weight or importance of the various levels within each variable were determined. Third, an overall multiplier to a particular data variable was assigned if it was felt one variable was quantifiably more important than another in the evaluation of resource suitability for a particular land use.

Examples of the types of land use evaluated at DWGNRA were trail hiking, intensive camping, swimming, high intensity recreation, access roads, fishing, hunting, farming, and boating.

An additional software procedure was tested to examine the importance of adjacent cell characteristics and their effect on the primary cell suitability for a particular use. The objective was to determine if overall suitability of park lands for a particular activity is significantly altered when the characteristics of coterminous cell layers are considered.

Several software programs were also tested in an attempt to utilize and evaluate the impact of planning contingencies. The three procedures sampled involved considerable differences in computer programming and computer time and none approached the ideal. The methods experimented with were the matrix approach, the inverse of cell suitability, and determining the mean suitability of all cells involved in a particular plan alternative. Space does not permit an elaboration of the specifics of these three procedures. However, the matrix approach is by far the most complex and most expensive.

## RESULTS AND THEIR APPLICATION

The project, with some exceptions, was completed on time. There were some procedural problems which are discussed in the following section. To indicate how the information results will be applied, highlights of the data analyses follow.

The results of the social-economic evaluations were the most revealing in terms of providing new information contrasting with popular belief. First, there is a great divergency in the ability of the coterminous counties to absorb the additional costs of services that will be required should visitor use of DWGNRA significantly increase. In general, counties on the Pennsylvania side are less equipped to handle any increased burden of additional public services. New Jersey counties have a younger and more diversified population with heavy reliance upon the New York City metropolitan area for a source of income. Recent changes in the quality of social services and present strengths regarding police, fire, transportation, and water services will allow these counties to absorb the costs of expanded social services more easily. Conversely, the provision of other types of services such as intensive camping is better provided relative to demand on the Pennsylvania side.

The type of present visitors and their demands on existing services also varied from popular belief (Robison 1976). Fifty-four percent had incomes in excess of $16,000/yr. Most come from the urban New York City area. Families with incomes under $10.000 or students make up a pronounced minority of present park visitation. Many visitors own second homes in the DWGNRA vicinity. Most visitor use consists of a one-day outing or weekend outing, and relatively little money is spent locally for meals or accommodations in view of the relative economic strength of present park visitors. Likewise, demands on park resources and services are mostly non-consumptive. Chief activities include hiking, photography, bird-watching, and antique shopping. Present visitors would rather

see little change in park-provided facilities requesting only a slight improvement in basic necessities and improved access to park information.

These results will be applied as overall planning qualifiers in the ongoing preparation of the park's general management plan. Primarily these results will serve to determine what goods and services the park will provide and what will be supplied by coterminous communities, and also to guide the sequencing of any eventual park developments so impacts to coterminous areas can be mitigated or at least minimized.

The final determinations of resource suitability also revealed some interesting results. Although the area is glaciated, a surprisingly large amount of park land (about 4500 hectares) meets average engineering criteria needed for locating development. If one examines present visitor use levels per developed acre in existing national parks (which reflect the average intensity of park development along with the willingness of Congress to appropriate funding for development), one finds a daily visitor use density of from 1-6 people per acre per day (Sudia et al. 1975). If one uses the mean visitor use density per developed acre of park land multiplied by the number of acres potentially suitable for development at DWGNRA, it is clear that suitability of the resource within DWGNRA will not be a limiting factor to park visitation.

There has been significant ground truthing done to confirm the results of the land suitability analyses. Areas indicated to have high suitability for development have been examined. Likewise, many areas shown to have very limited suitability have been examined to confirm the indicated limiting factor. One present visitor use demand which will probably be expanded is the use of trails. Many trails have been examined on the ground along with the suitability maps for locating trails to determine what difficulties might exist if present trails were expanded in use.

An interesting application of the suitability data came in locating a site for a septic tank for the Bushkill headquarters and maintenance area. The original contract anticipated such treatment but a site could not be located and an attempt was made to amend the contract upward for a $160,000 tertiary plant. Querying the suitability maps located four potential sites within reasonable distance and one was selected.

An initial draft of a land classification map is being prepared which will divide the park into those lands suitable for development, possessing outstanding natural value, historical value, and those remaining lands which might serve multiple uses. Within each of these land classes there will be subzones based upon resource suitability. In the final analysis, the planner will not be restricted to classify the land strictly according to resource suitability. Other factors as social-economic conditions will qualify the land classification imposed. But regardless of the eventual land classification scheme, the planners will know the relative constraints and attributes of the resource they may be using. The next step will be to integrate those quantifiable aspects of the social-economic survey with the geographical data in an attempt to assist planners developing a final land classification map.

Prior to completion of planning for DWGNRA, which will probably occur in the early summer of 1977, there will be further work done on developing a better model for the evaluation of the environmental impact of planning alternatives. Integrated with this will be an attempt to better quantify long-term maintenance costs associated with locating similar developments on sites of varying suitability. This may be the most important product resulting from the generation of sophisticated data packages for park planning. For in all probability it is the unanticipated maintenance contingency which creates the most havoc for a resource management agency. The inability to objectively quantify in the long-term the operational costs of a park and related maintenance emergencies is what uses up funding originally intended for long-term projects such as research and resource management.

Also to be completed and utilized in the ongoing planning effort will be a system approach in determining the capacity of the developed components within the park so visitor distribution and flow will take into account capacities for the developments leading into and away from a given point.

## DISCUSSION AND CONCLUSIONS

The preparation of data packages for the national parks has met only mild enthusiasm. There are many reasons for this but certainly three stand out. They are (1) the complexity of preparing such information bases, (2) the difficulty in application of the data to the decision-making process, and (3) the cost of such undertakings.

In the preparation of information bases, difficult decisions must be made very early in the process. The system employed must recognize the end use of the information gathered. If the information is to be used in resource management, who really controls this function in the organization and how will the information be used and what information is needed? Throughout the process is the danger of over-emphasis of technology in information handling. Hardware and software are much advanced compared to the realistic needs of most federal agencies. There is a real danger in expending funds just to gather information especially geographical information.

There are also complex questions related to standards for data acquisition. Our experience in the efforts at DWGNRA has shown the lack of adherence to standard procedures in mapping and listing of information is extremely expensive to correct when combining information from varying sources. This problem the information synthesizer has little control over. A decision then has to be made whether to take the time to correct source information or remove it from the list of desired data. Another early question to answer is whether to use automated data handling techniques. Ideally, the question could be answered by optimizing economic and time factors. However, such information is rarely available. The decision must then be based primarily on the amount of information to be handled and the time in which it must be available in a synthesized form.

But the item most likely to unduly complicate the preparation of information bases is the initial poor definition of problems to be resolved. The lack of specifically itemized objectives and the lack of clearly understood end-products increases the chance of taking an inordinate number of tangents in the synthesis of sophisticated information bases.

The second difficulty is perhaps the most crucial that being how to phase the information quantity and quality with the decision-making cycle. Early in the preparation of any information base a decision must be reached on whether to concentrate on general or specific information. That is whether to side in the favor of decision-

making qualifiers or information to quantify specific aspects of problems. At DWGNRA one of the early mistakes was not providing sufficient emphasis on social-economic qualifiers. Too much emphasis was placed upon traditional quantifiable geographic information.

The anatomy of the decision-making structure of an organization must be known by someone involved in the preparation of information bases. Park management is carried out in a cyclic manner. Decisions are made on weekly, annual, multi-year cycles and an information base must be so designed to provide the right types of information at the proper resolution synchronized with the decision-making cycle. The anatomy of the decision-making cycle also assists in making a decision on when to interface computers in data handling. If the information needed must be highly mobile, that is readily available for the analysis of a variety of contingencies, then it is probable automated data handling should be employed. Part of the decision-making cycle consists of the planning cycle which is perhaps the best place to start information bases since the types of decisions and their sequence are fairly easy to understand and project. The relative straightforward design of planning within Park Service was the reason the information base at DWGNRA initially concentrated on planning data.

But even a full and accurate comprehension of the decision-making cycle does not insure use of the information package generated. At present there appears very few instances in or outside the Park Service where the decision-maker directly interfaces with an information base. Rather he relies upon subordinates to interrogate whatever information system is available and provide results in terms the decision-maker can comprehend.

The third major difficulty in selling the value of information bases is their cost. The cost of information bases is up front. That is, it requires a reasonably large initial investment of funding early in planning. The Park Service, like many other land managing agencies, has not been used to spending large sums of money in planning especially in the early stages. The cost for such information packages can be expensive. The DWGNRA cost nearly $1.0 per acre for the intensive survey within the park boundaries, and $0.25 per acre for the extensive analysis of coterminous lands. The acquisition of geographical information only in a grid format can reduce these costs with figures quoted by the U.S. Forest Service as low as $0.10 an acre.

But in the end, it must be recognized the basic value of information bases has to be, in some manner, economic. Somebody has to make a decision on how much should be expended for additional information. In short, the cost of an information system is going to depend on what needs to be known and how well does it need to be known. Economic exchange values, that is cost-benefit alalysis, should probably not be applied to information bases. The reason for this is obvious. Many factors cannot be quantified in such terms. But most decision-makers, both within the federal government and private industry, do not seem to be using cost-benefit analyses as a justification for additional data acquisition, but rather the utility value of information bases. That is, top administration is willing to pay for information because it improves their confidence in making the correct decision.

## LITERATURE CITED


ANON. 1972. Part two of the National Park System Plan--Natural History. NPS, Washington, D.C. 140 p.

ANON. 1975. Administrative Policies. National Park Service, Washington, D.C. 130 p.

ROBISON, L. K. 1976. Delaware Water Gap National Recreation Area: A Visitor Use Survey. Unpub. Report submitted to Chief Scientist, Mid-Atlantic Region, NPS. 15 p.

SUDIA, T. W., and J. M. SIMPSON. 1973. Recreational carrying capacity of the national parks. NPS Guideline (3):25-34.

# THE SAGUARO GIANT CACTUS: AN ECOLOGICAL PERSPECTIVE

Warren F. Steenbergh and Charles H. Lowe[1]

## INTRODUCTION

As a direct result of the criteria used in the selection of natural features and phenomena for designation as national parks and national monuments, the National Park Service has inadvertently acquired unique problems with respect to maintaining the living natural resources assigned to its custody. This is especially true with regard to those National Park Service areas that were selected because of the unique qualities of specific plant populations.

The very qualities that made these plant populations attractive, unique or superlative examples of their kind, were the unrecognized expression of exceptional conditions, i.e., atypical environments within the overall species range in space or time. Thus the National Park Service has been entrusted with the care of plant populations that are the resulting relicts of past climatic conditions, such as redwoods, and sequoias, or populations that are situated near the critical geographic limits of the species distribution such as saguaros.

Instability is a primary characteristic of such populations responding - often in a dramatic manner - to a constantly changing climatic environment. Such is the prevailing condition and the "problem" of the saguaro population at Saguaro National Monument and elsewhere along the margins of its distribution in Arizona and northern Sonora.

The saguaro giant cactus is a drought-adapted, cold-tolerant, warm-desert species that occurs throughout the length and breadth of most of the Sonoran Desert (see Shreve 1951; Shreve and Wiggins 1964; Benson 1969; Hastings et al. 1972). Within that distribution it grows primarily on the coarse soils of south-facing rocky slopes and adjoining bajadas[2] and occurs sparsely or not at all on north-facing slopes or in the poorly aerated fine alluvial soil on the floor of the broad valleys that separate the characteristically discontinuous mountain ranges of the Basin-Range Province.

At the southern limits of its distribution in southern Sonora, small disjunct populations occur on the basalt outcrops of hills. Disjunct populations also occur on rocky south-facing slopes along the eastern and northern limits of its distribution in Sonora and Arizona. The Gulf of California marks the western limits of its distribution in Sonora. In southwestern Arizona and at the westernmost limits of its distribution in southeastern California within a few miles of the Colorado River near Blythe, sparse populations are directly associated with areas of concentrated runoff. The metropolis of the species population near the Arizona-Sonora border coincides more-or-less with the geographic center of its distribution. The saguaro population at Saguaro National Monument (east) occurs at the eastern, cold-limited margin of the species' distribution in Arizona.

With a maximum expected life-span twice our own, living saguaros have survived climatic events that long pre-date our recollection or knowledge. The species has survived through continuing environmental changes and has evolved during millions of years in environments that we have not experienced, and can but vaguely comprehend. However, examination of the question of what has happened, what is happening, and what will happen to the saguaro--at Saguaro National Monument and elsewhere throughout the range of its distribution in the Sonoran Desert--requires that perspective. It is within the framework and perspective of the evolutionary process that we explore the ecology of the saguaro.[3]

The National Park Service has long been concerned with the nature and cause of dramatic fluctuations that have grossly altered the structure of saguaro populations in certain portions of Saguaro National Monument.[4] In the Cactus Forest area of the original Saguaro National Monument, the once spectacular concentration of giant saguaros has dwindled in a few decades to an unimpressive population of sparsely scattered and dying old individuals.

More important to the present and future condition of this population, however, is the

[1]National Park Service, Cooperative National Park Resources Studies Unit, University of Arizona, Tucson 85721, and Department of Biological Sciences, University of Arizona, Tucson 85721, respectively.

[2]A bajada is the broad gently sloping alluvial plain extending from the base of the mountains to the valley floor.

[3]Investigations on the saguaro giant cactus (*Cereus giganteus*) Engelm., *Carnegiea* [Engelm.] Britt. and Rose) reported here and elsewhere were independently initiated in 1951 by Charles H. Lowe. Subsequently the work was continued with the support of the National Park Service (and others) in recognition of the need for basic knowledge of the biology of the species to provide information essential for ecologically sound management of the natural resources of Saguaro National Monument and other National Park System areas in southern Arizona. Vernacular and scientific names now most commonly used are saguaro and sahuaro, and *Cereus giganteus* or *Carnegiea gigantea*.

[4]Saguaro National Monument is comprised of two separate units situated on opposite sides of the Tucson basin. The original, Rincon Mountain Section (east unit) is located approximately 15 miles (24.2 km) east of the Tucson city center. The more recently established Tucson Mountain Section (west unit) is located about 15 miles (24.2 km) northwest of Tucson. Shelton (1972) provides a general description and account of the natural and human history of the Saguaro National Monument.

relative sparsity of younger plants. That condition--the lack of sufficient younger saguaros to replace dead and dying older saguaros--insures absolutely that the number of large saguaros in this population will continue to decline.

The problem long pre-dates the establishment of the original Saguaro National Monument in 1933. The predominance of older saguaros, and the lack of young individuals in photographs taken more than 40 years ago clearly reveal a population already many years in trouble. To a greater or lesser degree, other saguaro populations within Saguaro National Monument--and elsewhere--have undergone similar recent fluctuations.

In recognition of the needs of the National Park Service, continuing investigations on the ecology of the saguaro are designed to provide definitive knowledge of the problem and to develop information essential for interpretive and resource management programs. Experimental designs and the hypotheses that they test are directed specifically towards obtaining information on the operation of natural selection through climatic, and other physical and biotic factors that are critically limiting on saguaro populations. This report summarizes some of the more important results of these investigations contained in previous reports (Steenbergh and Lowe 1969; Steenbergh 1970, 1972; Steenbergh and Lowe 1976a, b) and discusses their relationship to the past, present and probable future status of these populations.

## LIFE HISTORY AND ENVIRONMENT

The saguaro has a life-span of 150-175 years (Shreve 1931) during which it produces on the order of 40 million viable seeds. For a population to maintain itself or to grow, one of those seeds must, within that period, germinate and survive approximately 30 years or more to the age when it becomes a reproductive member of the population. It is hardly surprising, therefore, to discover that only a minute percentage of the annual seed crop germinates and survives through the first year of life to become an established member of the population.

The saguaro blooms and produces an annual crop of succulent fruits during the driest period of the year. The peak of fruit-ripening and seedfall occurs in late June or early July, just prior to the arrival of germinating summer rains.

In the complete life cycle of the saguaro, the greatest mortality occurs during the pre-germination (seed) stage, the 1- to 5-week period between seedfall and germinating monsoon rains. During that period, the major portion of the annual seed crop is consumed by native animals--birds, mammals and insects. Seeds consumed by obligatory seed eaters are destroyed during digestion. However, other consumers, particularly omnivorous birds, which pass undamaged seeds through their digestive tracts, are important agents of seed dispersal.

The principal germination of saguaro seeds takes place in July and August from seeds of the current year's crop. Optimum conditions for natural germination coincide with the first full development of monsoon storms. Then, during the period from mid-July to mid-August, germination is normally associated with the occurrence of two or more rainstorms within a 2- to 5-day period.

The availability of moisture is the critical determinant in the germination process; temperature and light requirements are readily satisfied within all natural habitats of the saguaro. In continuous contact with free water, germination takes place in 48 to 72 hours. The summer climatic environment of the Tucson area is well within the range necessary for saguaro seed germination; it exceeds, in germination suitability, that of the drier, more westerly portions of the species' range. At Tucson, depending upon the overall intensity of monsoon development, the year-to-year suitability of conditions for natural germination ranges from poor to near optimum, but some natural germination occurs in all years.

Experimental evidence indicates that fewer than 1 in 200 seeds that reach a site where germination can occur survives to the seedling stage. We estimate that the net natural survival to the initial stage of seedling establishment is less than 1 per 1000 seeds produced.

For the saguaro, the greatest hazards to post-germination survival are associated with the pre-juvenile, seedling stage of life. Establishment is ordinarily reached at an age of 12-14 months.

The mean life expectancy of the newly emerged seedling is on the order of 2-6 weeks. Less than 1% of seedlings survive the first year of life to become established juvenile plants.

The tiny, succulent, weakly-rooted saguaro seedling is highly vulnerable to destruction by a broad variety of abiotic and biotic agents. These include freezing, drought, rodents, and insects. The relative importance of each factor varies with the habitat, the season, and from year-to-year.

Our data from Saguaro National Monument indicate that biotic factors account for the greatest number of saguaro deaths during the first few weeks of life. However, it is the extremes of the climatic environment--freezing and drought--that ultimately control the subsequent establishment and survival of young saguaro in the Tucson area and elsewhere along the northern and eastern limits of the plants' range in Arizona and Sonora.

The end of the establishment period and the beginning of the juvenile stage of life is marked by the advent of monsoon rains of the summer following germination. Rapidly increasing in size and root development during that second summer of growth, the young plant attains a substantially increased drought tolerance and an increased ability to survive insect attack.

The life expectancy of a juvenile saguaro increases rapidly with age--it outgrows its predators, and becomes increasingly able to survive the periodic hazards of the abiotic environment. In order of their relative importance, freezing, rodents and insects are the primary causes of death of established juvenile saguaros at Saguaro National Monument. With age and increase in size of the young plant during the second and succeeding years of life, the number and percentage of insect and rodent-caused deaths become progressively smaller. Healthy young plants greater than 5 cm (2 in) in height are relatively immune to destruction by these agents.

Freezing is the single most important cause of young saguaro mortality at Saguaro National Monument and elsewhere in the colder portions of the species' distribution. The resistance of

young saguaros to death from freezing increases with age-related changes in the size and form of the plants. Thus, freezing selectively removes the youngest members of the population--seedlings and juvenile plants less than 0.46 m (1.5 ft) tall.

There is little natural mortality of large juvenile and young unbranched adult saguaros with heights from 0.46 to 3.80 m (1.5-12.5 ft). Plants of that size range are relatively resistant to freezing, drought, or destruction by animals.

Vulnerability to climatic factors increases with age and height above 3.80 m. Deaths of large saguaros are almost entirely the result of the action of climatic factors--freezing, windthrow and lightning.

As with juvenile saguaros, freezing is the principal cause of death of large saguaros at Saguaro National Monument. In this northern portion of the geographic range of the saguaro, freezing selectively removes the youngest (smallest) and oldest (largest) members of the plant population, and favors the survival of intermediate age classes. Accordingly, the observed decline of saguaro populations at Saguaro National Monument, and the unbalanced age structure of these populations is primarily the result of recurring catastrophic freezes acting differentially upon 1) seedlings and small juvenile plants, 2) larger juvenile plants, and 3) large adult plants.

Topographic, edaphic, and plant community characteristics play a major role in germination, establishment and survival of young saguaros. Germination is dependent upon the existence of physically modified environments produced by trees, shrubs, rocks or other shade-producing objects. These shaded microhabitats provided moderated daytime temperatures that are within the upper range required for germination, and prolong periods of essential high moisture availability at the soil surface.

Establishment and survival of young saguaros are likewise dependent upon the physical protection provided by close association with other vegetation, detritus, and rocks. Acting singly or in combination, these moderate the limiting extremes of drought and winter cold, and in addition reduce the probability of discovery and destruction by animals.

Differential freeze-caused winter mortality of young saguaros associated with differences in the intensity and duration of subfreezing temperatures occurs in topographically different habitats. Differential survival of young saguaros occurs in rocky and non-rocky (flat) habitats, and on north and south-facing slopes. Seedling establishment is highest on south-facing slopes, lowest on north-facing slopes. In these habitats, higher soil moisture levels that favor pre-winter seedling survival in relatively arid environments are offset by subsequent freeze-caused winter mortality.

Growth of the saguaro is distinctly seasonal and takes place during coincident periods of relatively high temperatures and plant-available soil moisture. The principal growth of saguaros occurs during July, August and September, the period of warm summer rains, and ceases shortly after the end of those rains. In years when late winter rains provide adequate soil moisture and warm temperatures prevail, a secondary and minor period of apical growth occurs as early as February and March. The total summer growth of the saguaro is dependent upon the cumulative duration of periods of plant-available soil moisture. The annual increment of stem growth, therefore, is determined not only by the amount of precipitation, but in a large measure, by its temporal distribution. The annual height growth of young saguaros increases exponentially with age and increased size up to the age of first flowering. Then, with the onset of reproductive growth, a gradual reversal in the rate of annual height growth occurs as energy is increasingly diverted into the production of buds, flowers and fruits.

Apical growth rates provide a basis for determining saguaro height-age relationships, thus allowing estimates of population age structure. Regression analysis of data on the growth of seedling and juvenile saguaros in their natural habitats at Saguaro National Monument provides, for the first time, information on growth and age relationships of saguaros during the first critical years of life. The annual height growth increment for healthy young saguaros increases from a few millimeters per year during the earliest years of life to approximately 11.6 cm (4.5 in) per year during the 33rd year of life, the approximate age of first flower production.

Growth rates of the saguaro are highly variable. Two-fold or larger differences in annual height growth occur between individuals growing in the same immediate locality and topographic habitat. Similarly large variations in growth are associated with year-to-year variation in summer precipitation and winter temperatures. Significant differences in growth rates also occur in different topographic habitats under the same general climate.

The rate of saguaro growth differs widely from population to population in response to the broad range of climatic environments present within the extensive geographic range of the species. Generally, rates of saguaro growth decrease along a gradient of (1) decreasing summer precipitation from east to west, and (2) decreasing winter minimum temperatures from south to north latitudes, and from low to high elevations.

Freezing causes a significant reduction in saguaro growth which can continue for several years after such injury. In saguaro populations situated near the cold-limited northeastern boundary of their distribution, the growth-limiting effect of recurring catastrophic freezes offsets the advantage of relatively favorable moisture conditions. The average growth of large saguaros in these environments is less than in some more arid but warmer environments. Growth rates and, therefore, height-age relationships of saguaros growing in different portions of the species' range are not only determined by differences in precipitation and related availability of moisture but are also controlled by the frequency and intensity of sub-freezing temperatures. Established height-age relationships for saguaro populations growing in one locality, therefore, cannot be applied to populations growing in other locations without consideration of both of these controlling climatic variables.

Over a major portion of the saguaro species distribution, winter cold determines not only the growth rate, but also quantitative aspects of its reproductive success, local and absolute limits of distribution, population density and age-class structure, as well as the timing of the critical events in the life cycle of the saguaro.

## OVERVIEW AND OUTLOOK

Having established the nature and operation of the factors that control germination, establishment, and survival of saguaros in Saguaro National Monument and elsewhere in this more northerly portion of their range, it is possible to draw conclusions concerning the current status of these populations in relation to past conditions, events, and activities, and in some measure to predict their future course.

### Historical Factors

The condition of saguaro populations at Saguaro National Monument has been attributed in varying degrees to historic activities. These include removal of young saguaros by cactus merchants, woodcutting, grazing, fire control and predator control. These historical activities of humans and their domestic animals have been superimposed upon the natural environmental factors that limit the natural distribution of the saguaro and, within these limits, control its germination, establishment, and survival.

#### *Cactus Pirates*

During the early part of this century, large numbers of young saguaros in the vicinity of Tucson were removed for sale to cactus fanciers, and for landscaping purposes. There is no reliable basis for estimating the number of saguaros removed during these operations. That young saguaros were present at that time in numbers sufficient to support such operators, however, leaves no question that conditions were favorable for saguaro establishment, and for their survival to a size and age suitable for "harvest." It is likely that most of the saguaros sought and removed were the easily transplantable sizes of the 10- to 30-year-old age-group.

Plants of that age-class have a high natural life expectancy. They have grown beyond the age of high vulnerability to the principal agents of young saguaro mortality, and are entering a long period of growth when they are least vulnerable to the climatic factors that kill large adult plants. Thus, it is reasonable to assume that, in the absence of human intervention, a large proportion of those plants removed by cactus merchants would be alive today as intermediate-size adult saguaros--the age-group now largely missing in the Cactus Forest.

#### *Woodcutting*

Mesquite *(Prosopis juliflora)*, a preferred firewood species, was intensively cut within the Cactus Forest area of the monument. The durable cut stumps of this species are still abundant there, and most of the living mesquite trees are sprouted from old stumps. During the latter part of the last century the green wood of paloverde trees *(Cercidium microphyllum)* harvested in the Cactus Forest was used to fire limestone kilns located within the area. There is, however, no record of the number of paloverde trees removed for this use.

Activities of woodcutters affect the fate of young saguaros growing beneath the trees they remove. Not only are such saguaros liable to mechanical destruction by the woodcutters themselves, the survivors are fully exposed to trampling by cattle and to the full decimating impact of the biotic and abiotic environment. In addition to such direct destruction of established saguaros, woodcutting also reduced the number of favorable sites for subsequent saguaro establishment. Without the modifying influence of protective plant cover, the associated microhabitats were no longer suitable for the establishment of saguaros.

#### *Livestock Grazing*

Some portions of Saguaro National Monument have been subjected to intensive grazing by cattle for more than three-quarters of a century. In some localities, particularly the Cactus Forest area of the east monument, this has had an unquestionably detrimental effect on the germination, establishment and survival of young saguaros.

Direct destruction of young saguaros has resulted from trampling of cattle seeking shade and forage beneath the crowns of desert trees. Even more significant has been the impact of continued grazing pressure upon the physical structure of the plant community.

The primary role of historic livestock grazing has been to reduce the *density* of affected saguaro populations by decreasing the number and quality of sites suitable for germination, establishment and survival of young saguaros thereby increasing exposure to natural mortality-causing factors. Differential impact, i.e., differential mortality, has been associated with differences in the intensity and duration of grazing and the physical characteristics (rockiness) of the terrain. Mortality from natural factors is highest on intensively grazed, relatively flat non-rocky terrain, and lowest on less intensively grazed steep slopes with extensive rock outcrops. Natural regeneration of vegetation is occurring, and natural rates of germination, establishment, and survival of young plants are now occurring in habitats under National Park Service protection that were heavily grazed earlier in the century.

#### *Fire Control*

Fire is a natural cause of mortality of young saguaros near the upper elevational limits of their distribution. Our observations on natural fire-caused saguaro deaths in the Coronado and Tonto National forests in Arizona indicate that fire is a density-controlling factor in ungrazed habitats where grasses and other low-growing plant species provide a sufficiently continuous cover of combustible fuel to permit the spread of natural fire.

However, there is no known instance of fire-caused saguaro deaths within Saguaro National Monument. This is not only a result of a strict policy of controlling all fires, but even more directly a consequence of cattle grazing. Grasses that naturally would form a more-or-less continuous ground cover on the rocky footslopes have been closely cropped, and their density has been drastically reduced by long-continued cattle grazing. Fires can neither start nor spread in these denuded, grossly altered environments.

#### *Predator Control*

Predator control within and adjacent to both sections of Saguaro National Monument continued into the last decade cannot, with certainty, be related to the past and present condition of saguaro stands within the boundary. The whole question of the effect of predator control on

fluctuations in rodent populations seems inseparably related to a host of other factors ultimately of equal or greater importance in the dynamics of desert rodent populations. These include food and water supply, habitat modifications produced by livestock grazing, climatic cycles, and the resulting complex interactions including predation.

Ultimately, it seems that the most that can be said with regard to predator control is that to some degree it may have allowed populations of some prey species to increase until some other environmental factor became limiting on their numbers. There are no data that show that an increase in rodent predators on young saguaros actually resulted from predator control, that rodent populations were maintained at unnaturally high levels, or that the establishment of young saguaros was unnaturally limited by high populations of rodents resulting from the control of predators. Whatever the previous consequences of predator control on these saguaro populations, the present condition within the two sections of the monument appears to be that of an essentially natural relationship.

## Responses of an Abused Environment

The role of historical factors has been not to act as new and overriding controls; rather, historical factors have acted to intensify or mitigate the operation of natural regulating factors. Acting primarily in an indirect manner, the overall effect has been to decrease the number and suitability of sites for germination, establishment and survival of young saguaros. Within Saguaro National Monument, the saguaro has not been eliminated from any of its former habitats by these activities, but rather, in some habitats, the density of large juvenile and young adult plants is below the expected level for these habitats.

There is no cause to believe that historical factors have created irreversible deterioration of any of the primary habitats of the saguaro at Saguaro National Monument. Where elimination of adverse uses has been accomplished it has been followed by natural regeneration of the plant community, and by the establishment of large numbers of juvenile saguaros.

In contrast to the condition reported only a few years ago, and still presumed by many to be the situation, *there are today in each of the two sections of Saguaro National Monument thousands of young saguaros less than a half-meter (20 inches) tall.* These occur not only on the rocky footslopes of the Rincon and Tucson mountains--where the presence of substantial numbers of large juvenile and young adult saguaros indicates continued establishment and survival of young saguaros in these habitats--but notably in the non-rocky flat habitats of the Cactus Forest area, and the lower bajadas of the respective east and west sections of the monument.

## Hypotheses of Population Change

Some saguaro populations fluctuate markedly in density and age-structure. This is especially true *and even characteristically so* in the cold-limiting parts of the range of this subtropical species (see Harper 1967; Steenbergh and Lowe 1976a). Other investigators have offered, in various combinations, three basically differing hypotheses to explain observed fluctuation in saguaro populations in various localities including Saguaro National Monument. There are (1) over-grazing, (2) climatic change, and (3) "disease." However, as noted below, none of these hypotheses adequately accounts for the operation of the critically important climatic factors that ultimately limit the distribution and control the age-structure of those populations that are situated at the limits of the species' distribution.

The grazing-plus-rodents hypothesis suggests that in some habitats high rodent populations resulting from grazing-caused alterations of the plant community destroy young saguaros, causing a slow decline and disappearance of saguaro populations in these habitats. Obviously, overgrazing produces changes in the natural environment that are seriously detrimental to the establishment and survival of young saguaros. However, the hypothesis may overestimate the ultimate impact of rodents, and fails to accord sufficient importance to the *controlling* effect of recurring catastrophic freezes in these marginal habitats.

Climatic change, a shift toward slightly higher temperatures and lower rainfall (together with grazing) has also been proposed as a cause of the lack of young saguaros in the "valley" portions of Saguaro National Monument. However, the observed changes in the saguaro populations along the eastern and northern boundaries of its distribution--where the species is limited neither by lack of moisture nor high temperature--cannot be explained either by a decrease in mean winter or summer precipitation, or by a rise in mean winter temperatures.

"Bacterial necrosis disease" has also been proposed as a primary cause of saguaro population decline at Saguaro National Monument. The so-called "disease," however is a *result*--not a cause-- of saguaro death. Bacterial rot is the long-understood *subsequent* and ecologically important process of natural decomposition of soft tissues of saguaros that are killed outright or rendered physiologically dysfunctional by mechanical factors, primarily freezing and lightning (see Lowe 1964, 1966; Steenbergh 1972; Steenbergh and Lowe 1976a, b). Reported "epidemics of bacterial necrosis disease of the saguaro" are the inevitable response of the populations to recurring catastrophic freezes that are a normal characteristic of the regional climate.

## *Limiting Factors*

The saguaro giant cactus is not some rare exception to the fact that *environmental limiting factors* modify all terrestrial plant populations wherever located and, at the ultimate limits of the species distribution, such factors finally become 100% limiting. Our investigations and the work of others leave no doubt that natural environmental factors are the underlying cause of the dramatic changes that have occurred within the saguaro populations at Saguaro National Monument and elsewhere in the northern portion of its range.

Saguaro National Monument (east) is not only just near the saguaro's distribution limits, the saguaro species boundary line runs *through* the monument. The east monument population is a marginal one in every sense of the term. The particular populations in question are those which occupy marginal saguaro habitats--topographic situations where subfreezing temperatures are intensified by cold air drainage and accumulation.

Among the many physical and biotic factors acting upon these populations, it is climate--namely the extremes of winter cold--that is clearly the overriding factor in the regulation of these populations.

### *Populations in Response to Climatic Events*

Diverse records on saguaro populations (and other warm-desert plant populations) and on climatic events clearly tell the story of populations in trouble since the middle of the last century.

The presence of dense populations of saguaros near the base of the mountains east of Tucson during the latter part of the 19th century are indicated by the observations of Bigelow (1887) and Hubbard (1899). MacDougal (1908), however, commented generally on the difficulty of finding young saguaros. Shreve (1910) offered the first numerical data on saguaro populations at Tucson and concluded that the populations were not maintaining themselves.

The saguaro population in portions of Saguaro National Monument (east) was in a long-standing state of decadence at the time of the establishment of the monument in 1933. As seen in the photographs by Homer Shantz[5] (also see Hastings and Turner 1965) there is an abundance of large, old saguaros, and a conspicuous sparsity of juvenile and young adult saguaros. The very characteristic that inspired Shantz (1932) to say that "Nowhere in the world is there so fine a stand of giant sahuara (*Carnegia gigantia*) as in the University Cactus Forest" was the irrevocable condition that was to lead to the subsequent and inevitable dramatic decline of that same stand.

Analysis of saguaro populations at Saguaro National Monument carried out in 1941 by the USDA Bureau of Plant Industry (Gill and Lightle 1942, 1946; Gill 1951; Mielke 1944; also see Alcorn and May 1962; Steenbergh and Lowe 1976a) support earlier observations of Wilder and Wilder (1939) and Wilder (1940) that the number of young saguaros in the east monument flats stand had long been insufficient to maintain the stand, and that the highest densities of saguaros occurred on the rocky footslopes.

Investigations in 1962 and 1963 (Niering, Whittaker and Lowe 1963; Lowe 1964; Niering and Whittaker 1965) on saguaro populations in the vicinity of Tucson further confirm earlier observations that saguaro establishment and survival rates in rocky habitats are higher than in the finer soil of non-rocky habitats (also see Kramer 1962; Bingham 1963). More important, these studies further support the earlier observations by Thornber (1916) that massive die-off of saguaros is associated with catastrophic freezing, and explain the relationship of freezing weather to higher survival rates in rocky habitats. From the data in those reports, it can also be seen that freeze-caused saguaro mortality decreases from east to west along a gradient of increasingly warmer winter climate.

Further data on saguaro populations in Saguaro National Monument and the relationship of saguaro size and habitat to freeze-caused mortality, are reported by Steenbergh and Lowe (1976a). In that report, we conclude that catastrophic freezing selectively structures saguaro populations removing the smallest (youngest) and the largest (oldest) plants, leaving a high percentage of large juvenile and unbranched young adult saguaros with heights from 0.46 to 3.80 m (1.5-12.5 ft).

### *Catastrophic Freezes*

Daily weather observations provide a record of minimum temperatures in Tucson since 1895 (see Steenbergh and Lowe 1976a, Fig. 25). Other diverse records of these climatic events, and the response of saguaro populations and other cold sensitive plant populations are scattered throughout the literature (Thornber 1912, 1916; Wiggins 1937; Turnage and Hinckley 1938; Niering et al. 1963), and are, in fact, recorded in the responsive plant populations themselves.

Saguaro populations in the Tucson vicinity are an unexamined record of catastrophic freeze occurrence that long predates the oldest written weather records. The unbalanced size-class structure of these and other saguaro populations is an indication of past winter climate. In many northern saguaro populations constrictions near the base of the stem tell the story of previous catastrophic freezes. These constrictions result from freeze-caused crown-kill. In some habitats at Saguaro National Monument such scars, present on nearly every large juvenile and adult saguaro, provide a continuous record of recurring catastrophic freezes as old as the plants themselves. Based on the estimated age of larger saguaros in these habitats, recurring catastrophic freezes have been a *normal* part of these environments for more than 150 years.

Low temperature readings in Tucson recorded during the first decade of this century were followed by MacDougal's (1908) observation on the "...abundance of fallen skeletons...." The most noteworthy record of low temperature is the 6°F (-14.4°C) Tucson temperature recorded on January 13, 1913. As the first report on catastrophic freeze-kill of saguaros, Thornber's (1916) observations on the devastating effects of that freeze are particularly significant:

> *". . . during the very cold winter of 1912-13 thousands of small giant cactus plants growing near their greatest altitudinal limits were killed outright. Many other species also suffered great damage."*

The catastrophic freeze that occurred in January 1937, and the resulting severe damage to warm-desert plants, are the subject of a comprehensive report by Turnage and Hinckley (1938). Although damage to saguaros was not noted in that report, subsequent events leave no doubt that it was among the species most severely damaged by that freeze. The spectacular die-off of saguaros first noted in 1939 and continuing into the 1940's (Gill and Lightle 1942, 1946; Mielke 1944; Gill 1951) was the delayed response to the subfreezing temperatures of January 1937, the coldest period in 24 years (Turnage and Hinckley 1938).

It is well known that not all parts of a plant die at the same moment. This time scale of organ death is greatly exaggerated in the saguaro giant cactus. As many as nine years may elapse between lethal injury, and collapse of a freeze-damaged saguaro. Thus, the death of large saguaros lethally injured in 1937 escaped recognition until 1939 and later, when with their decay and collapse

[5] Homer L. Shantz photo collection, University of Arizona Herbarium.

death became obvious.

Saguaro die-off in response to catastrophic freeze followed by rapid thawing conditions in 1962 reported by Niering et al. (1963) and Lowe (1964) was followed by rapid collapse of many of the stricken individuals (see de Candolle 1852). However, as in the case of the 1937 freeze, the death of many plants did not become evident for one or more years after the freeze. The 1962 freeze also damaged saguaros and other plants at Organ Pipe Cactus National Monument where we observed resulting severe injury to senita (*Cereus schotti*) and organpipe cacti (*Cereus thurberi*), as well as to other cacti, elephant trees (*Bursera microphylla*) and other subtropical shrubs.

The initial response of saguaro populations to the freeze of January 1971 is described by Steenbergh and Lowe (1976a) and resulting collapse of saguaros has continued into 1976. We also observed, as a result of the 1971 freeze, damage to organpipe and senita cacti at Organ Pipe Cactus National Monument, and near Tucson, the death of other species of cacti, namely bisnaga (*Ferocactus wislizeni*) and the chainfruit cholla (*Opuntia fulgida*). In the Tucson vicinity, we also observed severe damage to desert ironwood (*Olneya tesota*), and foothill paloverde (*Cercidium microphyllum*) that in some localities resulted in the subsequent death of numerous individuals of both species.

It is evident from these diverse records that frequently recurring extremes of subfreezing temperatures are a long-standing normal characteristic of the climatic environment of the northern portions of the Sonoran Desert. Further, it is evident that these events exert a powerful influence not only on populations of the saguaro, but on populations of other cold-limited Sonoran Desert plant species as well. Acting in a catastrophic manner, such freezes are the primary control on the limits, local distribution and dynamics of saguaro populations at Saguaro National Monument and elsewhere in the colder portion of the species' distribution in Sonora and Arizona. Both the dramatic die-offs of large, old saguaros and the lack of younger replacements observed in these populations are the direct and inevitable response of these populations to the repeated occurrence of these devastating climatic events.

## THE OUTLOOK

The outlook for the future of saguaros at Saguaro National Monument is not an optimistic one. Neither, however, does it conform to the grim predictions of early extinction that some have offered. Barring unlikely sudden environmental changes in the habitats of its major occurrence within the monument, the saguaro will continue to survive long after our concern with the question is terminated.

There are today thousands of young saguaros at Saguaro National Monument, many of which will survive beyond a human lifetime. Many more of these, however, will perish during that time. Certainly, there will not be in our time--and perhaps never again--a return to the condition that inspired Homer Shantz (1932) to describe it as the finest stand of the giant saguaro in the world.

Generally, even in the absence of further adverse human influences, we can expect that the density of large saguaros in most, if not all, habitats within the monument will be lower than in the recent past. In some habitats, however, we can expect that with the complete elimination of livestock grazing an increase in the density of young saguaros will accompany a natural regeneration of the damaged plant communities.

Within the monument, continuing short term climatic variation can be expected to produce corresponding fluctuations of saguaro populations--but *not* to cause their early extirpation. Generally, this will effect changes in density, with unfavorable winter temperatures eliminating young plants from the least favorable microsites.

Saguaro populations, and other cold-limited Sonoran Desert plant species will continue to be controlled in the colder portions of their distributions by recurring catastrophic freezes. Any change in the frequency, intensity or duration of these recurring catastrophic freezes will result in a response by the affected populations. Any trend in these populations will follow the trend of those particular parameters of the winter climate that exert the greatest effect on the youngest members of the plant populations. Our lack of knowledge of long-term climatic trends and our inability to predict the occurrence of such critical climatic events, however, precludes long-range projections concerning the ultimate fate of these populations.

With its high reproductive potential and long life-span, the saguaro is well adapted to maintain itself in an environment in which occasional freezes that result in catastrophic die-off are followed by regeneration of the population during intervening periods of climatic remission. We have no information indicating that such climatic events have not similarly affected many past generations of saguaros in the same habitats where they presently occur. It is entirely possible that we have observed in these northern saguaro populations but one phase of the normal fluctuation of populations whose stability must be measured not in years, but in generations.

It may well be that the "problem" that we have observed--the "decline" of specific saguaro populations--is but a limitation imposed by our lifespan too brief to permit our recognition of an adaptive strategy of a longer lived species that by natural selection has evolved a near-perfect system for survival in an environment of recurring catastrophic climatic events. If that likely explanation is correct, then the real "problem" is neither in biology nor management, but in a limited perspective, and the only "solution" lies in the perspective offered by the time scale of evolution.

## LITERATURE CITED


ALCORN, S. M., and C. MAY. 1962. Attrition of a saguaro forest. Plant Dis. Rep. 46(3):156-158.

BENSON, L. 1969. The cacti of Arizona. 3rd ed. Univ. Arizona Press, Tucson. 218 pp.

BIGELOW, J., JR. 1887. After Geronimo. Installment XIII. Outing 9(6):522.

BINGHAM, S. B. 1963. Vegetation-soil relationships in two stands of the *Cercidium-Carnegiea* community of the Sonoran Desert. M.S. Thesis. Univ. of Arizona, Tucson. 84 pp.

CANDOLLE, M. A. DE. 1852. On the freezing of vegetables. Am. J. Sci. Arts II 14:445(Misc. Intell. #7).

GILL, L. S. 1951. Mortality of the giant cactus at Saguaro National Monument, 1941-1950. Saguaro National Monument Headquarters (Tucson, Arizona), Official Rep. 5 pp.; 2 tables; 1 fig.

GILL, L. S., and P. C. LIGHTLE. 1942. Cactus disease investigations. Saguaro National Monument Headquarters (Tucson, Arizona), Official Rep. 40 pp.; 9 tables; 15 figs.

GILL, L. S., and P. C. LIGHTLE. 1946. Analysis of mortality in saguaro cactus. Saguaro National Monument Headquarters (Tucson, Arizona), Official Rep. 4 pp.; 11 tables.

HARPER, J. L. 1967. A Darwinian approach to plant ecology. J. Anim. Ecol. 36(3):495-518.

HASTINGS, J. R., and R. M. TURNER. 1965. The changing mile: An ecological study of vegetation change with time in the lower mile of an arid and semiarid region. Univ. Arizona Press, Tucson. 317 pp.

HASTINGS, J. R., R. M. TURNER, and D. K. WARREN. 1972. *Carnegiea gigantea.* Page 63 *in* J. R. Hastings, R. M. Turner, and D. K. Warren, An atlas of some plant distributions in the Sonoran Desert. Univ. Ariz. Inst. Atmosph. Physics Tech. Rep. Meteorol. Climatol. Arid Regions No. 21.

HUBBARD, H. G. 1899. Insect fauna of the giant cactus of Arizona: Letters from the Southwest. Psyche 8(Suppl. 1):1-14.

KRAMER, R. J. 1962. The distribution of saguaro *(Cereus giganteus* Engelm.) in relation to certain soil characteristics. M.S. Thesis. Ariz. State Univ., Tempe. 120 pp.

LOWE, C. H. 1964. Arizona landscapes and habitats. Pages 1-132 *in* Charles H. Lowe (ed.), The vertebrates of Arizona. Univ. Arizona Press, Tucson.

LOWE, C. H. 1966. Life and death of the sahuaro in Arizona. Cactus Capital Chatter 1(8):2-3.

MACDOUGAL, D. T. 1908. Across Papagueria. Plant World 11(5):93-99; 11(6):123-131; (Also Am. Geogr. Soc. Bull. 40:1-21.)

MIELKE, J. L. 1944. Summary of results of control experiments on saguaro disease, Saguaro National Monument. Saguaro National Monument Headquarters (Tucson, Arizona), Official Rep. 4 pp.

NIERING, W. A., and R. H. WHITTAKER. 1965. The saguaro problem and grazing in southwestern National Monuments. Natl. Parks Mag. 39(213): 4-9; illus.

NEIRING, W. A., R. H. WHITTAKER, AND C. H. LOWE. 1963. The saguaro: A population in relation to environment. Science 142(3588):15-23.

SHANTZ, H. L. 1932. Description. *In* Roger W. Toll, Untitled report to the Director of National Park Service.

SHELTON, N. 1972. Saguaro National Monument, Arizona. U. S. Dept. Int., Natl. Park Serv. Nat. Hist. Ser. 98 pp.

SHREVE, F. 1910. The rate of establishment of the giant cactus. Plant World 13(10);235-240.

SHREVE, F. 1931. Fouquieriaceae, *Larrea tridentata, Carnegiea gigantea.* Die Pflanzenareale, Ser. 3(1):4-6; 3 maps.

SHREVE, F. 1951. Vegetation of the Sonoran Desert. Carnegie Inst. Wash. Publ. 591. 192 pp.; maps and photos.

SHREVE, F., and I. L. WIGGINS. 1964. Vegetation and flora of the Sonoran Desert. Stanford Univ. Press, Stanford, Calif. 2 vols. 1740 pp.

STEENBERGH, W. F. 1970. Rejection of bacterial rot by adult saguaro cacti *(Cereus giganteus).* J. Ariz. Acad. Sci. 6(1):78-91.

STEENBERGH, W. F. 1972. Lightning-caused destruction in a desert plant community. Southwest. Nat. 16(3/4):419-429.

STEENBERGH, W. F., and C. H. LOWE. 1969. Critical factors during the first years of life of the saguaro *(Cereus giganteus)* at Saguaro National Monument, Arizona. Ecology 50(5):825-834.

STEENBERGH, W. F., and C. H. LOWE. 1976a. Ecology of the saguaro. I. The role of freezing weather on a warm-desert plant population. Pages 49-92 *in* Research in the Parks. National Park Service symposium series no. 1. Government Printing Office, Washington, D.C. In Press.

STEENBERGH, W. F., and C. H. LOWE. 1976b. Ecology of the saguaro. II. Reproduction, germination, establishment, growth, and survival of the young plant. U.S. Dept. Int., Natl. Park Serv. Scientific Monogr. Series No. 8. In Press.

THORNBER, J. J. 1912. Resistance to frost of introduced trees and shrubs. Ariz. Agric. Exp. Stn. Timely Hints for Farmers No. 91.

THORNBER, J. J. 1916. Introduction. Pages 119-122 *in* J. C. T. Uphof, Cold-resistance in spineless cacti. Univ. Ariz. Agric. Exp. Bull. 79.

TURNAGE, W. V., and A. L. HINCKLEY. 1938. Freezing weather in relation to plant distribution in the Sonoran Desert. Ecol. Monogr. 8:529-550.

WIGGINS, I. L. 1937. Effects of the January freeze upon the pitahaya in Arizona. Cactus Succulent J. 8:171.

WILDER, C. S., and J. C. WILDER. 1939. Re-establishment of saguaros. Southwest. Mon. Spec. Rep. 26:153-160.

WILDER, J. C. 1940. Saguaros, old and young. Desert Plant Life 12(4):65-66.

# PREDICTING SPECIES CHANGES IN ISOLATED WILDLIFE PRESERVES

Ronald I. Miller and Larry D. Harris[1]

A relation between the size of an area and the total number of species in any taxon was documented for both plant and animal communities at the beginning of this century. Plant ecologists were the first to notice that a relative increase in species number correlates well with an increase in quadrat size (Arrhenius 1921, Gleason 1922). A concurrent study noted a similar relation between faunal species number and sample size (Willis 1922). This relation was later formalized with the introduction of the species-area curve (figure 1). This allometric formulation demonstrates that the incremental increase in the number of species recorded in an area declines for larger areas. In other words, an increase in a larger area involves a smaller species accrual than a similar increase in a smaller area.

Subsequent observations uncovered a unique relation between the observed number of species and the size of an island. Darlington (1957) was among the first to articulate this relation. He observed that the number of reptile species found on islands in the West Indies increased by 50% for every 10-fold increase in island (figure 2) size. This empirical relation was independently verified by Preston's (1962) model of finite species communities and thereafter generalized (MacArthur and Wilson 1967) as:

$$S = CA^z \qquad (1)$$

where S is the predicted number of species; C is a parameter primarily dependent upon the species diversity of the taxon being considered, the zoogeographic region and the underlying environmental heterogeneity; A is the area of the island and z represents the degree of relation between the species number and the size of the area. The validity of this equation for quantifying species numbers on both oceanic and continental islands has been empirically verified (Preston 1962, MacArthur and Wilson 1967, Vuilleumier 1970, Brown 1971, Terborgh 1974, 1975; Diamond 1975, Moore and Hooper 1975). The predictive power of this equation is based on both the geographic and ecological characteristics of an area.

The distinction between insular and sample communities is demonstrated by the empirical observation that isolated areas exhibit z-values [from equation (1)] between 0.20-0.35 while areas representing only samples of larger communities exhibit z-values ranging from 0.11-0.17 (Preston 1962). Differences in the number of species inhabiting island areas versus continental areas are explicable from this distinction.

The species contained by demarcated continental areas contiguous with surrounding habitat represent a sample from a larger community (figure 3). These groups of species will be greatly influenced by their interactions with surrounding species and thus they do not necessarily represent self-contained communities. On the other hand, species communities of insular areas represent communities characterized by an independence from contiguous environments. Thus insular communities have presumably developed an internal integrity lacking in sample areas. For this reason a greater species-area relation is observed in insular communities. Moreover, fewer species are found in insular areas than in sample areas of equal size, and therefore species communities on islands are comparatively depauperate.

It has recently been proposed that a species-area relation similar to the one found on islands may occur in continental areas separated from their surrounding gene pools (Diamond 1972, 1975; Hooper 1971, May 1975; Sullivan and Shaffer 1975, Terborgh 1974, 1975, Wilson and Willis 1975). This hypothesis is supported by a number of independent lines of observation. First, the number of species in naturally occurring isolated areas such as mountaintops (Brown 1971) and alpine grasslands (Vuilleumier 1970) is predicted by an insular species-area relation. Secondly, an island model explains a significant portion of the extinction rate recorded in the recently isolated avifaunal community of Barro Colorado Island (Willis 1974, Terborgh 1975). Finally, forest size is a significant predictor of the number of bird species in recently created "forest islands" in developed areas in both the United States (Galli et al. 1976) and in Great Britain (Moore and Hooper 1975).

As wildlife preserves and national parks become surrounded by "seas of civilization" they may begin to reach a condition similar to isolated continental areas (figure 4). As these protected areas transform from sample areas to islands one would expect the animal communities to change accordingly. Since sample continental areas generally contain more species per unit area than islands, newly demarcated preserves might be considered to be "supersaturated" with species. This implies that the transformation process is tantamount to species extirpation. As the preserve becomes progressively more isolated from the surrounding natural habitat the species ensemble will slowly be reduced and eventually achieve a lower number of species appropriate to the more insular condition.

The Theory of Island Biogeography asserts that the size and characteristics of island communities are determined by a dynamic equilibrium between species immigration and extinction rates (figure 5). The theory predicts that the variable processes of immigration and extinction on islands will produce a constant turnover of species. The relative effect of these processes will be based on the distance of the island from the nearest species pool and island size. This dynamic equilibrium will produce a characteristic number of resident species for each island. As yet, this model has not categorically been shown to occur on either island or isolated continental areas (Simberloff 1976).

We believe the applicability of the island concept to areas such as national parks and preserves, fast becoming isolates because of encroaching civilization, is solely predicated on the empirically based species-area phenomenon.

[1]School of Forest Resources and Conservation, University of Florida, Gainesville.

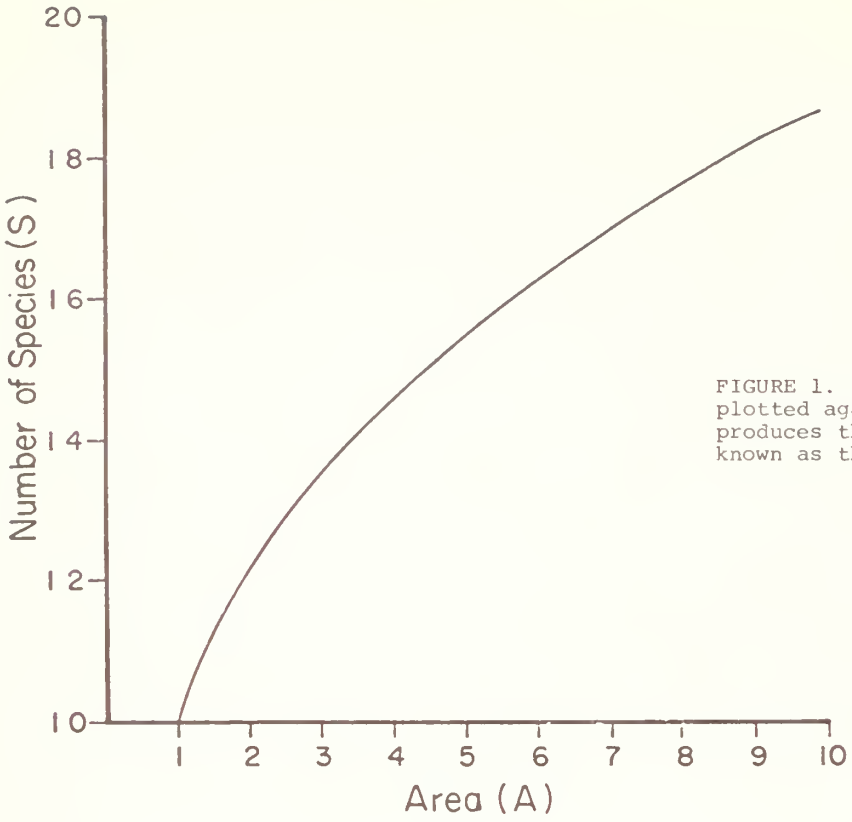



FIGURE 1. The number of recorded species (ordinate) plotted against areas of increasing size (abcissa) produces this characteristic allometric function known as the species area curve.

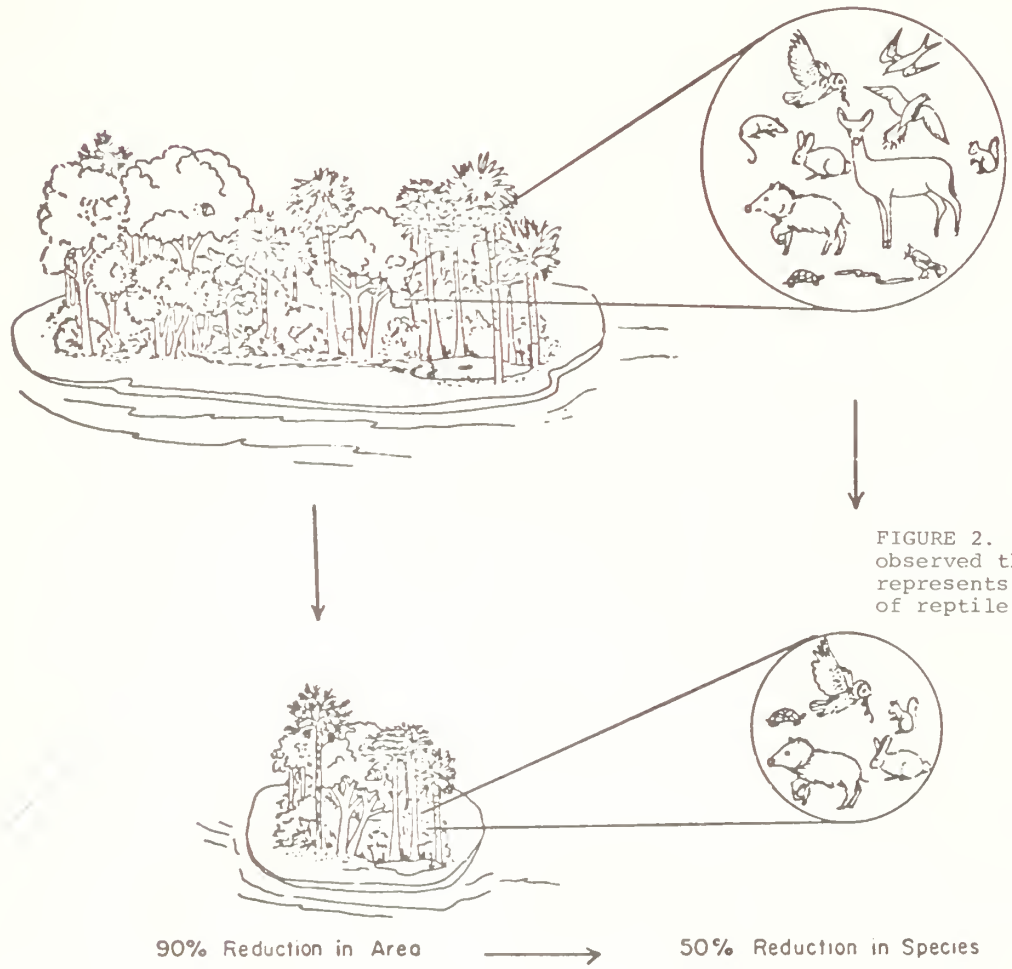



FIGURE 2. For islands, Darlington (1957) observed that a tenfold increase in area represents a 50% increase in the number of reptile species.

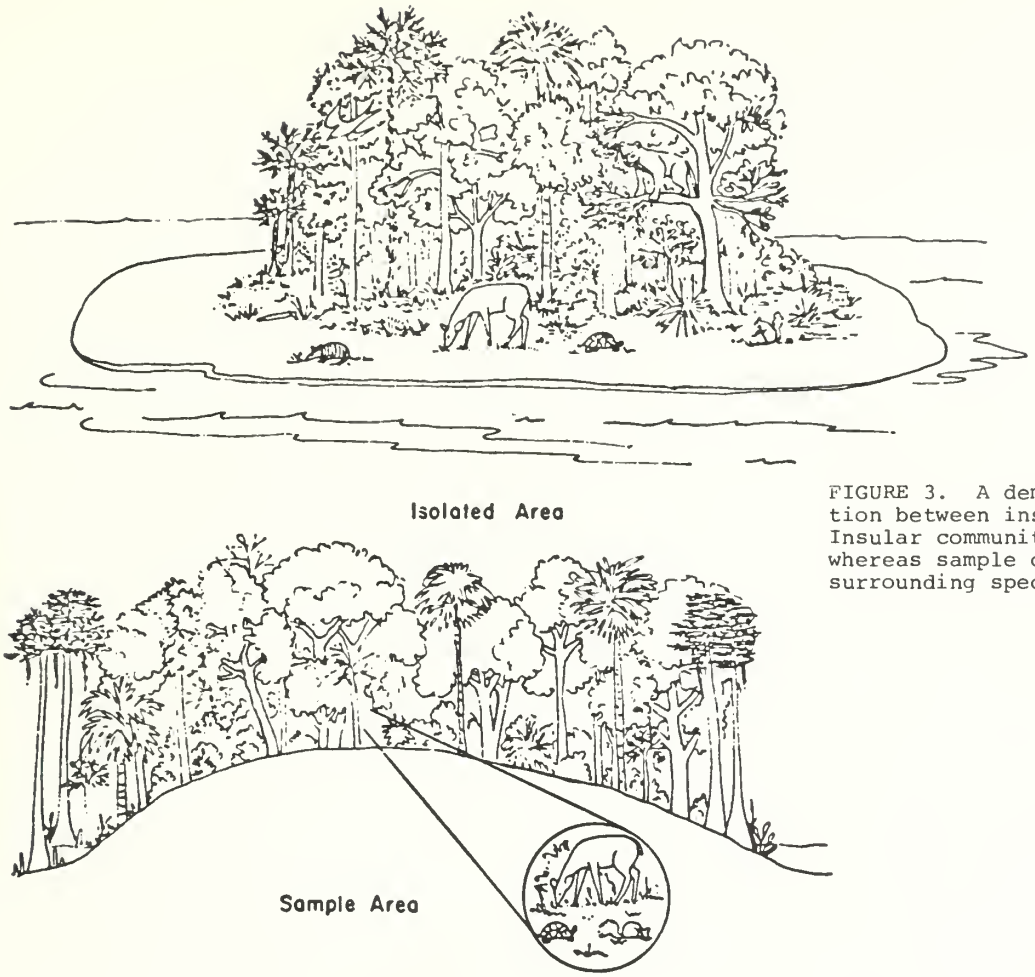



FIGURE 3. A demonstration of the distinction between insular and sample communities. Insular communities are self-contained, whereas sample communities interact with surrounding species.

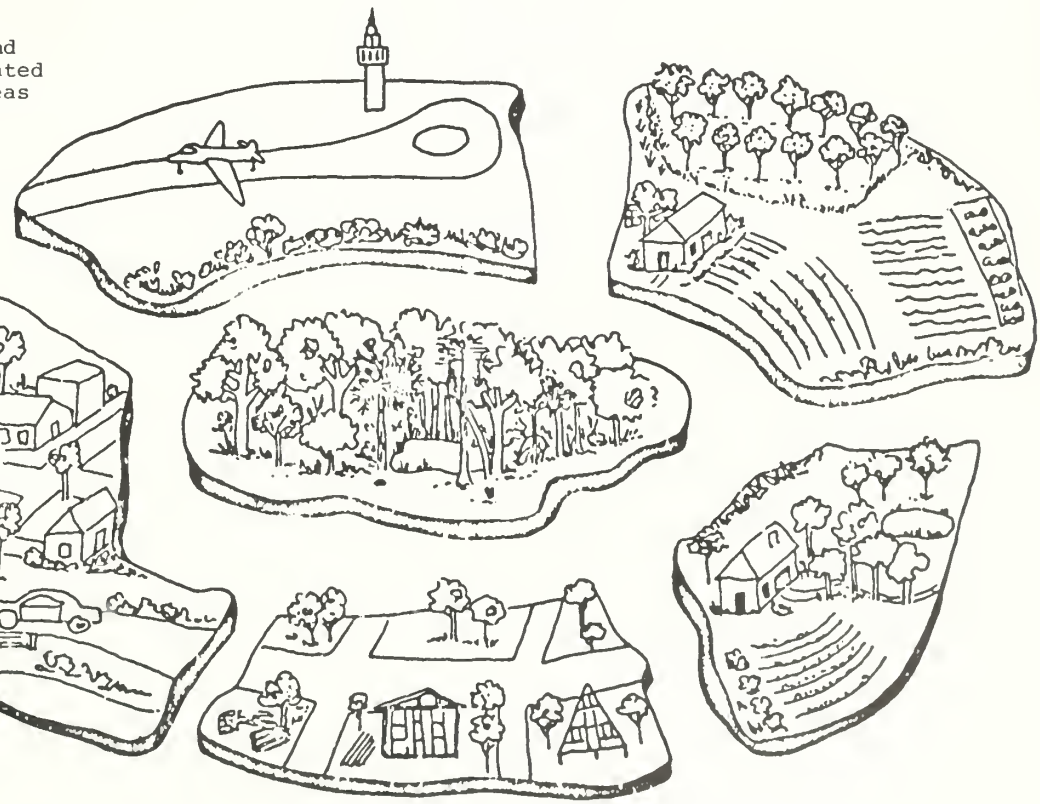


FIGURE 4. National parks and preserves are becoming isolated from surrounding natural areas by encroaching civilization.

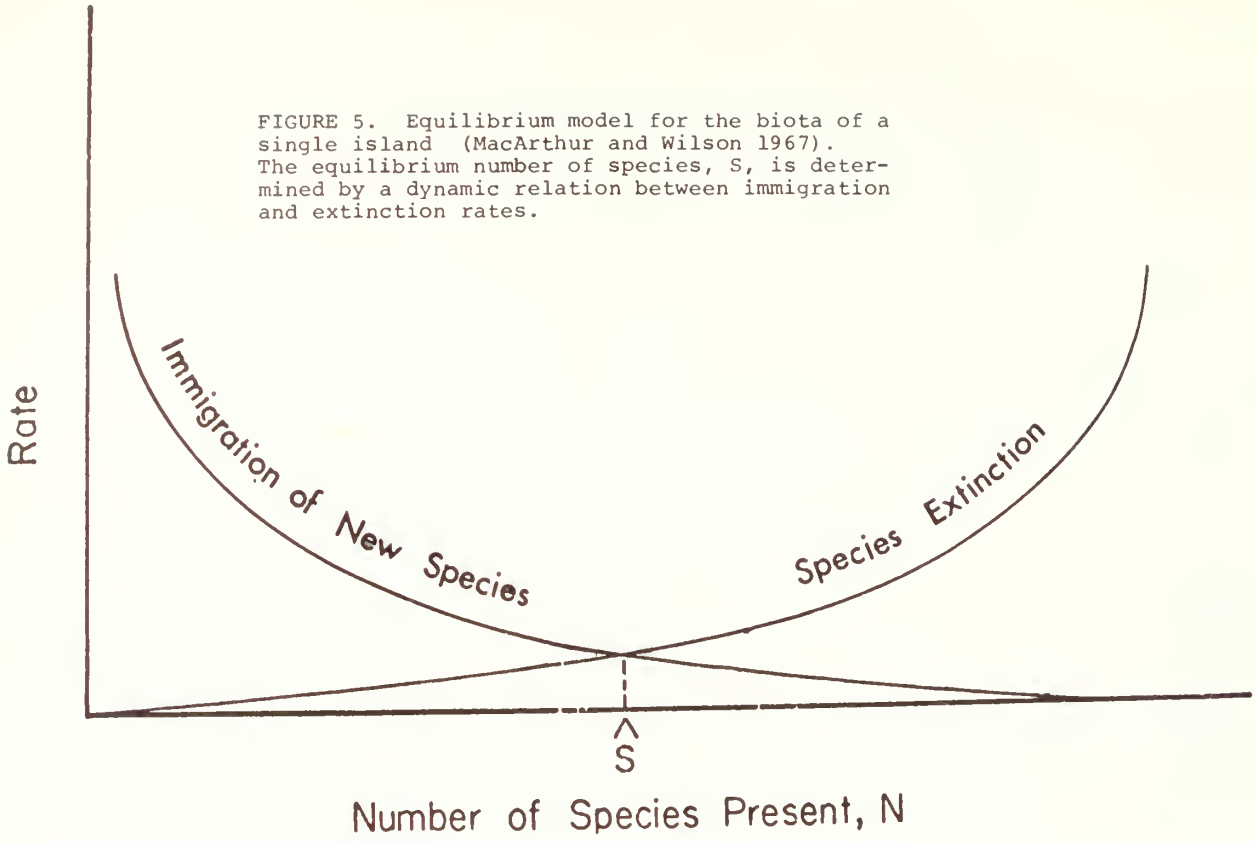



FIGURE 5. Equilibrium model for the biota of a single island (MacArthur and Wilson 1967). The equilibrium number of species, S, is determined by a dynamic relation between immigration and extinction rates.

Thus it is not necessary to invoke the unverified Theory of Island Biogeography to predict that a depauperization will probably occur in isolated parks and preserves. The dynamic equilibrium model only proposes a mechanism to explain the species-area phenomenon on islands.

Verification of the depauperization process in isolated preserves, predicated on the species-area relation, will most likely result from rigorous surveys of the species ensembles and populations within specific areas. In addition, research directed toward understanding the ecology in isolated communities will lead to predictions of species specific vulnerability to extirpation pressures within isolated preserves. Data for testing recent hypotheses (Diamond 1975, Wilson and Willis 1975) concerning the design and management of isolated communities are badly needed. Most importantly, understanding the possible effects of insularity in national parks and preserves will aid conservationists in their attempt to mitigate the extinction process in these areas.

## LITERATURE CITED

ARRHENIUS, O. 1921. Species and area. J. Ecol. 9:95-99.

BROWN, J. H. 1971. Mammals on mountaintops: non-equilibrium insular biogeography. Amer. Natur. 105(945):467-478.

DARLINGTON, P. 1957. Zoogeography. John Wiley and Sons, New York, 675 p.

DIAMOND, J. 1972. Biogeographic kinetics: Estimation of relaxation times for avifauna of Southwest Pacific islands. Proc. Nat. Acad. Sci. U.S.A. 69(11):3199-3203.

DIAMOND, J. 1975. The island dilemna: Lessons of modern geographical studies for the design of nature preserves. Bio. Conserv. 7:129-146.

GALLI, A. E., C. F. LECK, and R. T. FORMAN. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk 93:356-364.

GLEASON, H. A. 1922. On the relation between species and area. Ecology 3:158-162.

HOOPER, M. D. 1971. The size and surroundings of nature reserves, pp. 555-561. *In* The scientific management of animal and plant communities for conservation. E. Duffy and A. S. Watt (eds.). Blackwell, Oxford, England.

MACARTHUR, R. H. and E. O. WILSON. 1967. The theory of island biogeography, Princeton University Press, Princeton, 203 p.

MAY, R. M. 1975. Patterns of species abundance and diversity, pp. 81-120, *In* Ecology and evolution of communities. M. L. Cody and J. M. Diamond (eds.). Harvard Univ. Press, Cambridge.

MOORE, N. W. and M. D. HOOPER. 1975. On the number of bird species in British woods. Biol. Conserv. 8:239-250.

PRESTON, F. W. 1962. The canonical distribution of commonness and rarity. Ecology 43(2), p. 185-215, and p. 410-432.

SIMBERLOFF, D. S. 1976. Species turnover and equilibrium island biogeography. Science 194: 572-578.

SULLIVAN, A. F. and M. L. SHAFFER. 1975. Biogeography of the megazoo Science. 189:13-17.

TERBORGH, J. 1974. Preservation of natural diversity: The problem of extinction prone species. Bioscience 24(12):715-722.

VUILLEUMIER, F. 1970. Insular biogeography in continental regions. I. The Northern Andes of South America. Amer. Nat. 104(938):378-388.

WILLIS, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecol. Monogr. 44:153-169.

WILLIS, J. C. 1922. Age and area. Cambridge Univ. Press, Cambridge, 259 p.

WILSON, E. O. and E. O. WILLIS. 1975. Applied biogeography, pp. 522-536. *In* Ecology and evolution of communities. M. L. Cody and J. M. Diamond (eds.). Harvard Univ. Press. Cambridge.

# INSULARITY AND MAMMALS SPECIES NUMBER IN TWO NATIONAL PARKS

A. R. Weisbrod[1]

The broad stretches of life forms on the North American continent may appear to the casual observer as a monotonous superficially unbroken expanse of countryside. A more careful observer notes that each of the great biomes is in fact a complex mosaic of discrete areas, each separated from similar units by distinctly different habitats. The encroachment of modern civilization has reduced the original patterns to broken patches, isolated from one another by urban and agrarian activities and their connecting transportation routes. Some remnants of the original habitats have been set aside as parks, forests, refuges, and other similar natural areas held in common for public use by federal, state, and local governments, and by private individuals and organizations. Such preserved lands are effectively surrounded by a sea of civilization. The establishment, management, and use of such reserves must be accomplished with a firm knowledge and understanding of the ecological consequences of such isolation, if their biotas are to remain viable.

In the now famous book, The Theory of Island Biogeography, MacArthur and Wilson (1967) claimed that most areas are isolated to a greater or lesser extent from similar discrete areas. This property of insularity has various measurable influences on the structure of biotic communities within a given region. These influences include empirical relationships such as: the number of species present in the area is directly proportional to its size, the farther a given site is from a propagule source the fewer the species that may either reach or survive in the area, and the number of species a given area ultimately supports represents a dynamic equilibrium between immigration and extinction rates. These main points of their notions have been greatly reviewed, elaborated, and refined by a host of authors. For example, Gilroy (1975) suggested that immigration rates are affected proportionately by species not present in the area while extinction rates are proportional only to the species in the area. Diamond (1973) describes a phenomenon he terms "relaxation" in which previously settled areas which have become relatively isolated begin to lose marginal species as the equilibrium number adjusts downward. This adjustment is a response to either falling migration, rising extinctions, or both. As Wilson and Willis (1975) note, such relaxation first affects the large species or the specialized forms which by their nature often occur in low densities, and they require relatively large areas to survive. The effects of this truncation on these trophic relations concomitant with extreme isolation can result in the domination of relatively small areas by only a few generally opportunistic forms such as rats (*Rattus* spp.), rabbits (*Oryctolagus cuniculus*), and starlings (*Sturnus* spp.). These phenomena lead one to consider the possibility that national park areas may eventually come to act as ecological islands and some may already be experiencing relaxation.

We can now briefly examine two national park examples which may be demonstrating the results of the above influences: San Juan Island National Historical Park is located on San Juan Island in Washington State. The Island is the second largest island in the San Juan archipelago that separates Puget Sound from the Georgia Straights. The islands form a geomorphic arch across the northern end of the Puget Lowlands. Three islands: Orcas, San Juan, and Lopez account for 80% of the archipelago's landmass while the remaining mass consists of about 169 smaller named islands. The archipelago was covered by the great cordilleran ice sheets that flowed from the mountains of western British Columbia into the Puget Lowlands during the Pleistocene. At its greatest extent some 15,000 years BP, the glaciers buried the islands under 1800 meters of ice.

Recent studies of the islands' mammal fauna, information gleaned from scanty literature, and our own studies show that San Juan Island contains approximately 19 species of land mammals while the archipelago contains a total of 24 species (Table 1). Bounded within the two units of San Juan Island Historical Park (SAJH) may be found 14 mammal species. The notion that species number is proportional to the area is immediately evident if one plots the number of species against the logarithm of the geographic area, i.e., the species-area curve (Figure 1). Note that the Park (SAJH) fits comfortably on the curve. The actual number of species on the island and probably the Park has changed over time and such turnovers in species composition are consistent with the stated biogeographic influences (Table 2). The form of the changes, that the large and/or specialized species are those lost from the fauna, while the replacing species are the small generalized colonizers, seems to follow from the expectations, derived from known impacts of insularity, thus, giving the impression that the Park is functioning as an island. Alternatively, one could surmise that the fit of the Park to the species-area curve and the turnover data are simply artifacts of sampling and bear no theoretical relevance. That is, any comparable 700-hectare area on San Juan Island may show similar results. Unfortunately, there is no comparable area nor did the factors of time and money permit searching for such lands elsewhere in the archipelago. The resolution of this problem must await studies in future decades.

The second national park presents a different situation in several respects. In contrast to the preceding example where the number of species was compared to changes in area size, the next situation shows changes in species richness over time while the area remains constant (except for minor park boundary adjustments): Mount Rainier National Park is located somewhat west of the central Washington Cascades. Mount Rainier is a large Pleistocene strato-volcano exceeding some 4000 meters in elevation. The Park boundary encompasses about 97,000 hectares of forest, alpine tundra, glacier, and rock. The land on the east and south of the mountain is national forest land subject to multiple use management ranging from logging, grazing, mining, recreation, and all other comparable uses.

The northern boundary of the Park abuts a checker board of national forest and private lands in which alternative sections are owned by either the Weyerharuser ("The Tree Growing") Company or the U.S. Forest Service. These alternately owned lands are managed jointly under a series of mutually beneficial agreements. The west Park boundary is

[1]National Park Service, Cooperative Park Studies Unit. University of Washington, Seattle.

TABLE 1. Land mammal distribution on the San Juan Islands and Vancouver Island.

| | Vancouver[1] Island (321,000 ha) | San Juan[2] Archipelago (53,400 ha) | San Juan island (14,300 ha) | SAJH (709 ha) |
|---|---|---|---|---|
| Sorex obscurus | X | | | |
| S. palustris | X | | | |
| S. vagrans | X | X | X | X |
| Plecotus townsendii | X | | | |
| Eptesucus fuscus | X | X | X | X |
| Lasionycteris noctivagans | | X | X | X |
| Corynorhinus townsendii | X | X | | |
| Myotis lucifugus | X | X | X | X |
| M. yumanensis | X | X | X | X |
| M. evotis | X | | | |
| M. volans | X | | | |
| M. californicus | X | X | X | X |
| Oryctolagus cuniculus | X | X | X | X |
| Marmota vancouverensis | X | | | |
| Sciurus niger | | X | | |
| Tamiasciurus douglasii | X | X | | |
| Eutamias townsendii | | X | | |
| Castor canadensis | X | | | |
| Peromyscus maniculatus | X | X | X | X |
| Microtus townsendii | X | X | X | |
| Ondatra zibethica | X | X | X | |
| Rattus norvegicus | X | X | X | |
| R. rattus | X | X | X | X |
| Mus musculus | X | X | X | |
| Canis familiaris | ? | X | ? | |
| Vulpes fulva | | X | X | |
| Ursus americanus | X | | | |
| Procyon lotor | X | X | X | X |
| Martes americana | X | | | |
| Mustela erminea | X | | | |
| M. vison | X | X | X | |
| M. putorius | | | X | X |
| Lutra canadensis | X | X | X | X |
| Gulo luscus | X | | | |
| Felis concolor | X | | | |
| F. domesticus | ? | X | X | X |
| Cervus elaphas | X | X | X | X |
| Odocoileus hemionus | X | X | X | X |
| TOTAL (1975) | 31 | 24 | 19 | 14 |

[1]Gowan and Guiquet 1956.

[2]Schoen 1972.

TABLE 2. Turnover of mammalian species on San Juan Island, 1868-1975.

| Extinct 1868 - 1925 (4) | Successful Immigrants (6) 1868 - 1975 | Successful Native Species (13) 1868 - 1975 |
|---|---|---|
| Castor canadensis | Oryctolagus cuniculus* | Sorex vagrans |
| Canis lupus | Rattus norvegicus | Eptesicus fuscus* |
| Ursus americanus | Rattus rattus* | Lasionycteris notivagans* |
| Cervus elaphus | Mus musculus | Myotis yumanensis* |
| | Mustela putorius* | Myotis lucifigus* |
| | Felis domesticus* | Myotis californicus* |
| | | Peromyscus maniculatus* |
| | | Microtus townsendii |
| | | Ondatra zibethica |
| | | Procyon lotor* |
| | | Mustela vison |
| | | Lutra canadensis* |
| | | Dama hemionus* |

* Present in San Juan Island National Historical Park

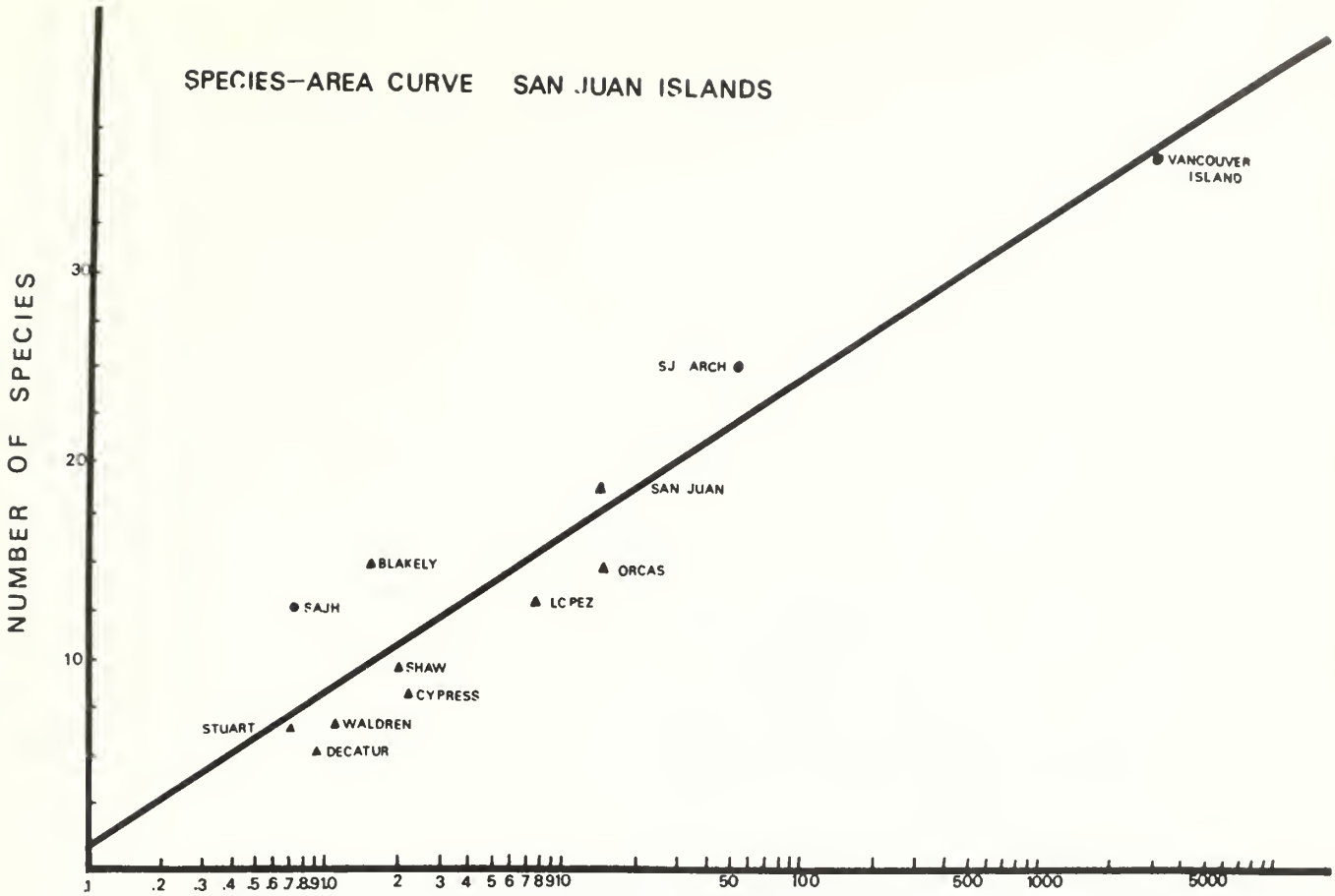



FIGURE 1. A species-area curve for the San Juan Island in which the number of species (ordinate) is plotted against the log of the area in thousands ($10^3$) of hectares (abscissa). (Line slope is $y = -16.78 + 8.25X$.) SAJH is the position of San Juan Island National Historical Park.

TABLE 3. Turnover of mammal species on Mount Rainier National Park.

I. Immigrations

A. 1920 - 1935

Plecotus townsendii
Erethizon dorsatum
Gulo luscus
Lutra canadensis
Mephitis mephitis

RATE: 1sp/3yrs

B. 1935 - 1976

Lasiurus cinereus

II. Extinctions

A. 1920 - 1935

Myotis volans
Rattus norvegicus
Gulo luscus
Lutra canadensis

RATE: 1sp/3.5yrs

B. 1935 - 1976

Scapanus townsendii
Scapanus orarius
Martes pennanti
Spilogale putorius
Mephitis mephitis
Canis lupus
Lynx canadensis

RATE: 1sp/5.7yrs

III. Turnover

A. 1920 - 1935

9 species in 15 years = 1sp/1.67yrs

B. 1935 - 1976

8 species in 41 years = 1sp/5.1yrs.

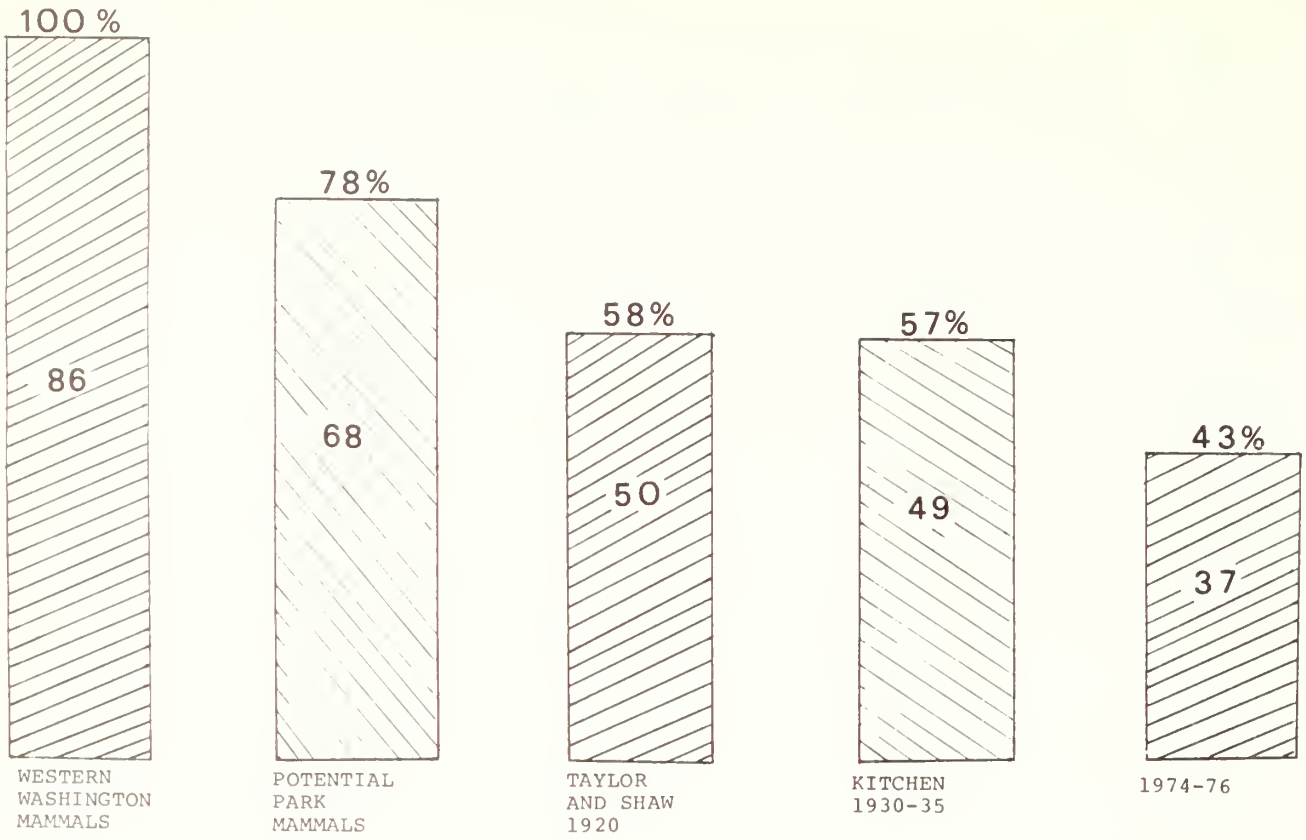



FIGURE 2. A figure showing the relative portion of land mammals west of the Cascade Mountains' crest in Washington State, by two authors (Taylor and Shaw 1920; Kitchen 1935) and this study.

largely state and private timberlands.

Early literature of the mammals of Mount Rainier National Park recorded 50 species present in the Park in 1920 (Taylor and Shaw 1927). By the mid-1930's, Kitchen (1935) reported 49 species could be found in the Park. The most recent study, which we have been conducting for the past 2 years verifies the presence of only 37 mammal species in the Park. This is an apparent extirpation of 13 ($\pm$ 2) species from Mount Rainier National Park since 1920 (Figure 2). We have checked as carefully as possible to determine the reliability of the early reports. Fortunately, most of the specimens collected by Taylor and Shaw are present in the U.S. National Museum's Biological Survey collection, while Kitchen's records consist largely of anecdotal observations by Park rangers and naturalists. By comparing these accounts with our own data, it is possible to estimate the insularity parameters of immigration and extinction rates (Table 3). Both immigration and extinction rates seem to be depressing over the past 40 years. This information suggests that perhaps relaxation is occurring and that a new equilibrium will be achieved at some future time; but at present, we simply do not have enough information to predict the final outcome, nor do we have enough to boldly state that the biogeographic theories posed are truly applicable to the situation.

Recent controversies over the utility of biogeographical notions to natural preserve design and management shed little light because the relevant data based for evaluating these ideas (and for evaluating alternative positions) and their efficacy to national parks is lacking (See Simberloff and Abele 1976; Diamond et al. 1976). If it can be demonstrated that the extinctions shown here are not a function of insularity, then alternative questions must be asked. Such alternatives must question those environmental influences which are known to disturb ecological systems and management practices or policies that may have led to the extinctions. Management programs in national parks often attempt to perpetuate a desired (static) situation in a natural system which is undergoing constant short- and long-term changes. These efforts are increasingly costly and in the long run, unlikely to succeed. Pragmatic programs designed to facilitate equilibrium processes are more realistic, and they must be encouraged if the national parks are to preserve primeval habitat remnants for future generations to experience.

LITERATURE CITED


COWAN, I. McT., and C. J. GUIGUET. 1956. The mammals of British Columbia. British Columbia Provincial Museum Handbook II. Victoria. 414 p.

DIAMOND, J. M. 1973. Distributional ecology of New Guinea birds. Science 179:759-769.

DIAMOND, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biol. Cons. 7:129-146.

DIAMOND, J. M., J. TERBORGH, R. F. WHITCOMB, J. F. LYNCH, P. A. OPLER, and C. S. ROBBINS. 1976. Island biogeography and conservation: strategy and limitations. Science 193:1027-1032.

KITCHEN, E. A. 1935. Checklist of the vertebrates of Mount Rainier National Park. USDI National Park Service pamphlet.

MacARTHUR, R. M., and E. O. WILSON. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N. J. 203 p.

SCHOEN, J. W. 1972. Mammals of the San Juan Archipelago: distribution and colonization of native land mammals and insularity in three populations of *Peromyscus manisulatus*. M.S. Thesis. Univ. Puget Sound. 119 p.

SIMBERLOFF, D. S., and L. G. ABELE. 1976. Island biogeography theory and conservation practice. Science 191:285-286.

TAYLOR, W. P., and W. T. SHAW. 1927. Mammals and birds of Mount Rainier National Park. USDI-Natl. Park Serv. GPO, Wash. D.C. 249 p.

WILSON, E. O., and E. O. WILLIS. 1975. Applied biogeography. *In* M. L. Cody and J. M. Diamond, eds. Ecology and evolution of communities. Belknap Press. Cambridge, MA.

# APPLICATION OF ISLAND BIOGEOGRAPHY THEORY TO REFUGE DESIGN: MAKING THE RIGHT DECISION FOR THE WRONG REASONS

L. G. Abele[1] and Edward F. Connor[1,2]

## INTRODUCTION

Dayton (1973) presented two examples of conceptual ecological models whose prediction appeared to be verified by field observation, but upon closer examination diametrically opposed mechanisms were actually indicated by the data. An analogy to Dayton's dilemma of "making the right prediction for the wrong reasons" has developed in attempts to apply island biogeography theory to the design of nature preserves. The right decision has been recommended, the preservation of maximum diversity, but the wrong strategy has been suggested. Furthermore, Erhenfeld (1976) cautions that ecological theory is not always compatible with the desires of conservationists.

The ethic of preserving maximum diversity is admirably and eloquently stated by Wilson and Willis (1976) and we wholeheartedly echo their sentiments. However. we disagree with the specific design recommendations of Terborgh (1974, 1975), Diamond (1975), Diamond and May (1976), and Wilson and Willis (1976), and show here that they have presented the wrong reasons for the right decision. These authors essentially contend that specific design recommendations regarding the size and shape of nature preserves can be derived from island biogeography theory, and that these recommendations represent the design strategy capable of preserving maximum diversity. They proceed to build a case for the construction of single large nature preserves as opposed to multiple small preserves, and make further recommendations concerning the shape of nature preserves. Two classes of evidence are presented in support of their recommendations; (1) arguments based on the species-area relationship, and (2) arguments based on the equilibrium theory of island biogeography, especially the phenomenon termed "relaxation." We offer here a preliminary examination of this complex problem and suggest that application of theory to conservation strategy is not as well supported by data as the literature would suggest.

## AREA

The species-area relationship is an empirical relationship that is consistent with the equilibrium theory of island biogeography (Simberloff 1974), but was derived long before and independent of island biogeography theory. The species-area relationship is simply a formalization of the observation that large areas usually contain more species than small areas. Three mechanistic explanations of the species-area relationship have been proposed, two prior to the advent of modern island biogeography theory, and one a prediction of equilibrium theory.

Habitat diversity has been the most popular explanation of the species-area relationship. It has long been proposed that species numbers increase with area because larger areas have more habitats and therefore species peculiar to particular habitats are more likely to be encountered when examining large areas. An alternative to the "habitat diversity hypothesis," also proposed prior to equilibrium theory yet based on island observations, is that islands passively sample a dispersing biota, larger islands intercepting a larger sample of invaders and hence a larger number of species. As a subsidiary prediction of equilibrium theory a third hypothesis was proposed; species numbers increase with area because species on larger areas (or islands) have on the average larger population sizes, and therefore a lower chance of becoming locally extirpated, so that at any one time more species will coexist locally on large islands than on small islands.

As often occurs in ecology, several factors may play a causal role, and good evidence exists that each of these three mechanisms contributes to the species-area relationship (Abele 1974; Harmon 1972; Simberloff 1976a; Abele and Patton 1976; Osman, 1977). However, biogeographers have as yet been unable to determine the 'proportional contribution' of these three mechanisms to the observation of a positive correlation between species number and area.

Graphically the species-area relationship has been represented in two forms; (a) with species numbers and areas untransformed (Figure 1), and (b) with species numbers and areas both logarithmically transformed (Figure 2). The curve in Figure 1 represents the usual shape of the relationship between species number and area, and is described by the equation

$$S = kA^z,$$

where S equals species number, A equals area, and k and z are constants. However, when species numbers and areas are examined in their untransformed modes data are fitted to the equation $S = zA+k$. The solid line in Figure 2 represents the same relationship with species numbers and areas logarithmically transformed. The line is both described by and commonly fitted to the equation $\log S = z\log A+\log k$. In both instances, the positive slope of the curves indicates the empirical result that species numbers are larger for large areas.

The major recommendation made for conservation practice and the design of biotic preserves, purportedly based on island biogeography theory, is that the largest single land area obtainable will preserve the greatest number of species and is therefore the best strategy (Terborgh 1974, 1975; Diamond 1975; Diamond and May 1976; Wilson and Willis 1975). However, this recommendation is predominantly based on the species-area relationship and is nothing more than an attempt to translate the long known monotonically increasing relationship between species number and area into a design strategy. Actually the species-area relationship is ambiguous on this point. Given that preserving the largest number of species possible is the goal to support for two conflicting strategies; (a) a single large preserve or (b) multiple smaller preserves with a combined area equal to the single large preserve.

The fact that species number is a monotonically increasing function of area supports the observa-

[1]Department of Biological Science, Florida State University, Tallahassee 32306.

[2]Tall Timbers Research Station, Route 1, Box 160, Tallahassee 32303.

tion that a large preserve will contain more species than a smaller one. However, the exact shape of the functional relationship between species number and area argues that Strategy b (multiple small preserves) may actually preserve more species. In Figure 1 the curve depicting the relationship between species number and area becomes asympotic (levels off) with large areas. Fewer and fewer species are added per unit area as larger areas are examined. In other words, the per unit area return in species preserved diminishes rapidly for large areas. The same pattern is revealed in Figfure 2 when log-species numbers and log-areas are plotted. The sloping dot-dash line represents a species-area relationship with a slope value of z = 1. At this slope value the return in species preserved per unit area is constant regardless of the absolute size of the area. Species-area relationships with slope values greater than 1 indicate that the per unit return in species preserved increases with large areas, and species-area relationships with slope values less than 1 indicate a decreasing return in species preserved per unit area with increasing area. Connor and McCoy (1979) have calculated from 100 species-area curves including multifarious taxa (e.g., birds, insects, plants, mammals, etc.) that the average slope value from actual observations is z = 0.3; much less than the value of z = 1 needed to maintain at least an equal return in species preserved per unit area. It would appear that in almost all natural situations the per unit area return in species preserved will always be much less for a large refuge than for a smaller one.

Related to this problem of diminishing return is a further ambiguity of the species-area relationship regarding conservation practice. For example, if a preserve is built with area A it is likely to have more species than a preserve of area B = ½A. However, as pointed out by Preston (1962) Simberloff (1974 and Simberloff and Abele (1976; but see comments by Diamond 1976; Terborgh 1976; Whitcomb et al. 1976) the species-areas relationship predicts that if one builds two preserves each of area B = ½A, the two smaller preserves together will contain more species than the

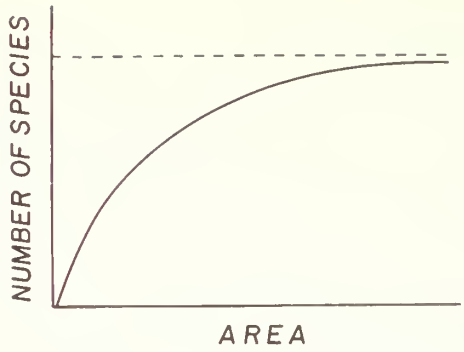



FIGURE 1. Plot of the species-area relationship for untransformed species numbers and areas, illustrating the asymptotic behavior of species number for large areas.

single large preserve. Figure 2 graphically illustrates this situation. Consider preserve A with $S_A$ species and area A, and a smaller preserve B with $S_B$ species and area B = ½A. Note that the distance between the points $S_A$ and $S_B$ is smaller than the distance between the points A and B. This indicates that preserve B with half the area of preserve A will contain more than half the species of preserve A, so that two preserves of area B will contain more species than preserve A, but comprise an equal land area. In essence, the species-area relationship predicts that two small preserves will contain more species than one large preserve. Figure 3 shows exactly what proportion of the species of a particular area will be preserved given that a certain proportion of the area is maintained as a refuge. In the example above, 50% of the land area preserves 81% of the species, and if only 10% of the land area were to remain still 50% of the species would be preserved.

We emphasize that although two small preserves are predicted, based on the species-area relationship to contain more species than a single large

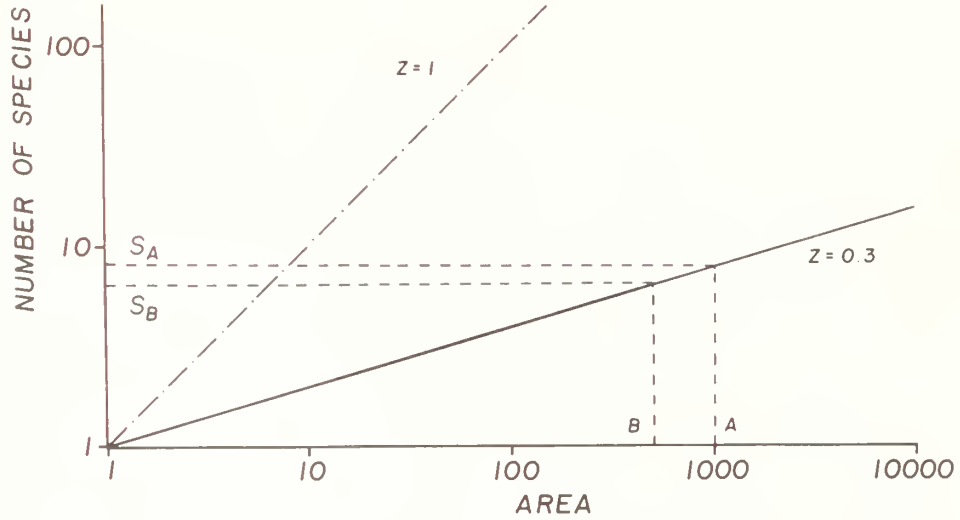



FIGURE 2. Plot of the species-area relationship for logarithmically transformed species-numbers and areas. The dot-dash line represents a species-area relationship with a slope value of Z = 1, indicating a constant return in species number independent of the absolute area. The solid line with a slope of Z = 0.3 indicates the usual situation found in nature. Point A represents a nature preserve with area A, and point B a preserve with area B = ½A. The dashed lines project these areas onto the species-area curve with Z = 0.3 and then to the vertical axis so that the number of species contained by each preserve can be determined (points $S_A$ and $S_B$). The small distance between points A and B, indicates that preserving half the area will preserve more than half the species, so that two small preserves of area B = ½A may contain more species than preserve A.

one of equal total area, we cannot predict a priori that the two small preserves will contain more species than a single large one since the two small preserves could potentially share many species. Realistically we may expect the two small preserves to share at least some species and to each possess some unique species, but without knowledge of the habitat requirements of the species considered it is impossible to determine which is the superior strategy, a single large or multiple small preserves.

A final comment on the implications of the species-area relationship for conservation practice is that the species-area relationship does not explain species numbers equally well in all regions. Based on 100 species-area curves (log-log), Connor and McCoy (1979) determined that the parametric correlation coefficient of the species-area relationship was significantly negatively correlated with latitude ($r = -0.3181$, $p = 0.0001$). This indicates that the per unit return of species preserved decreases from the tropics to the temperate zone. This further points out that the correct design formula for biotic preserves is different for each specific case.

## SPECIES EQUILIBRIUM AND TURNOVER

The equilibrium theory of island biogeography has been applied to the design and maintenance of parks and refuges. Its basic premise is that the biota of an island is in dynamic equilibrium between the immigration of species new to the island and local extirpation of those already present. Thus the total number of species remains about the same, but the composition changes over time. This change in composition without a change in species numbers is known as 'equilibrium turnover.' In assessing the occurrence and importance of equilibrium turnover we must be concerned with the extinctions of previously persistent, reproducing populations that disappear *independent* of secular environmental changes, specifically human influence (Lynch and Johnson 1974; Simberloff 1976a). A corollary to equilibrium turnover is the phenomenon of 'non-equilibrium turnover.' Non-equilibrium turnover is the result of an imbalance in extinction and immigrations and is attributable to secular environmental changes. In the case of parks and refuges it is usually caused by human influence. During non-equilibium turnover, changes in species numbers and compositional changes occur simultaneously.

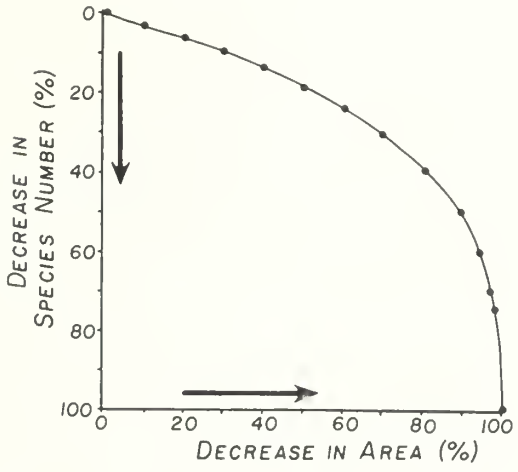



FIGURE 3. A plot of the percentage decrease in species number which accompanies a percentage decrease in area. For example, a decrease of 90% in area results in a loss of 50% of the species. The figure is based on $S = kA^Z$ where $Z = 0.3$.

The implication of equilibrium turnover for the design of nature preserves is apparent in that if equilibrium turnover is a significant phenomena, it would indeed be very difficult to design a refuge for any particular species or group of species since the composition of the refuge's biota would be expected to change constantly. If such were the case, designing preserves to increase species' persistence would be paramount. The implication of non-equilibrium turnover for preserve design is that the use and management both of parklands and surrounding regions can be expected to affect the number and composition of species that a preserve will contain. This is hardly a novel message, and anything but uniquely predicted by equilibrium theory. However, we are concerned here with the assessment of the significance of equilibrium turnover and the direction, magnitude, and time scale of non-equilibrium turnover (especially relaxation, species loss) caused solely by change in island's or a preserve's area and insularity.

### *Equilibrium Turnover*

There appear to be four sets of data that demonstrate turnover at equilibrium (1) arthropods on mangrove islands in the Florida Keys (Simberloff and Wilson 1969; Simberloff 1976a, 1976b) (2) birds of the Channel Islands off California (Diamond 1969) (3) birds of Karkar Island off New Guinea (Diamond 1971) (4) birds of islands off Britain and Mona Island off Peurto Rico (Terborgh and Faaborg 1973).

#### *Arthropods on Mangrove Islands*

In the experimental test of equilibrium theory Simberloff and Wilson (1969) measured turnover rates of approximately 0.5 species/island/day or 182 species/island/year. Such a high extinction rate would be cause for serious concern among those interested in refuge planning. However Simberloff (1976b) has carefully reexamined the data and suggests that much of the turnover observed was due to "pseudoturnover" or normal inter-island movement by transients and did not involve local extinction of long-term reproducing populations. Using conservative criteria Simberloff (1976a) estimates a minimum extinction rate of 1.5 species/island/year, a considerable reduction from the previous estimate of 182 species/island/year. Although an extinction rate of 1.5 species/year would be significant for a nature preserve, these values, computed from the mangrove island arthropod fauna, are not indicative of what can be expected of other taxa (birds, mammals, etc.) or the same taxa in other environments. Mangrove islands, situated on the constantly changing shoreline, certainly provide a more ephemeral environment (hence higher extinction rates) than the analogous upland forest does for its arthropod inhabitants.

#### *Birds on Islands*

Estimates of turnover rates for the avifauna of islands have been obtained by comparing species lists from surveys taken at different times. The assumptions have been that the islands are at equilibrium and that a changed composition with no change in species number is indicative of equilibrium turnover. For example, Diamond (1969) compared surveys of the birds of the Channel Islands taken in 1917 and 1968 and concluded that the islands were in equilibrium and that between 17 and 62% of the breeding species has been lost (and replaced by other species) over the 51-year period. Similar figures are reported by Diamond (1971) and Terborgh and Faaborg (1973). Diamond and May (1976) summarize these studies reporting turnover rates (per year) of 0.2 to 20% of the island's bird species for islands of 0.4 to 400 $km^2$. This corresponds to approximately 0.1 to 0.3 species/island/

year. The critical questions relevant to these studies are: Did the extinctions involve species which had previously persisted and reproduced on the islands and were the extinctions independent of human influence? Lynch and Johnson (1974) have addressed these questions with special reference to Diamond's (1969) report on the Channel Islands. They were able to avaluate 41 of the 48 claimed extinctions and concluded that 33 (80%) were either related to human activities or were the result of "pseudoturnover." They believe that of the realining species only two represent valid extinctions of reproducing populations. This would lower the estimated extinction rate from 0.10 species/island/year to about 0.004 species/island/year. While it is conceivable that Lynch and Johnson's conservative approach may have excluded some valid extinctions we are in general agreement with their conclusion that extinction rates have been greatly overestimated.

### *Relaxation*

Situations exist, particularly with respect to parks and refuges, where the initial area of forest or habitat decreases. Since species number is related to area, some change in species number can be expected (Figure 3) as already discussed. This process of reequilibration has been referred to as "relaxation" by Diamond (1972). The rate of species loss (extinction rate) generated by this process of insularization is important to park and refuge design in two ways. First, if extinction rates are related to the area of the preserve then the nature of the relationship may be germane to the question of single large or multiple small preserves. For example, if extinction rates are higher for small islands the persistence of species on small islands will be less than on large islands, and large islands would make better nature preserves. Second, what is the time scale over which extinctions caused by changing the area or more completely insularizing a preserve cover? If the time scale is short, we know that the activities in regions surrounding parks (e.g., urbanization and clear-cutting) will have an immediate effect on the diversity of species in parks. If the time scale is long, then it may be possible to allow short term high-yeild exploitation of these resources and make amends (e.g., reforestation) later, before extinctions occur.

Three data sets are pertinent to these questions; Diamond's (1972, 1975) analysis of relaxation times for the avifauna of islands off New Guinea, Terborgh's (1974, 1975) analysis of the West Indian and Barro Colorado Island avifaunas, and Simberloff's (1976b) analysis of the arthropod fauna of mangrove islands.

### *Arthropods on Mangrove Islands*

The relationship between island size and aspects of island biogeography has been discussed by Simberloff (1976a) and here we only summarize and comment on his results. A decrease in the size of mangrove islands resulted in a decrease in species numbers. However, there was no clear relationship between extinction rate and island size. Three rates rose and two declined with a decrease in area. Reequilibration from an oversaturated condition was rapid, all nine islands had reequilibrated within a year.

### *Land Bridge Islands and Birds*

Diamond (1972, 1975), Diamond and May (1976) and Terborgh (1974, 1975) estimate relaxation times and extinction coefficients for islands avifaunas using land bridge islands. The assumption is that islands separated from the source fauna by water less than 100 meters in depth were connected to the mainland (or source) about 10,000 years ago when sea levels were much lower. Thus these islands have experienced a change in area and presumably a change in species number. The original avifauna presumed to have been present is estimated and compared to both the species number present now and the species number predicted by the species-area relationship for that region. We have examined all relevant data (Abele and Connor, in prep.) and can only summarize our findings here. Diamond (1972, 1975) estimates the original species number for the land bridge islands to be 325, the entire lowland avifauna of New Guinea. This is biologically and statistically unrealistic, for as Diamond (1972, 1975) himself emphasizes, the distribution of New Guinea birds is extremely patchy and the probability of 325 species' breeding in an area the size of Misol (2040 $km^2$ compared to New Guinea 319,713 $km^2$) must approach 0. Similar comments apply to Terborgh's estimates. Both Diamond and Terborgh note that land bridge islands tend to fall above a species-area regression line for the respective regions. They cite this as evidence that the islands are 'supersaturated' with species. We have reexamined the New Guinea data and calculated a species-area regression for 67 islands (both with and without New Guinea included). If the land bridge islands are in fact supersaturated, one would expect the regression residuals to be significantly greater than the mean residual. Not a single island, including all land bridge islands has a residual three or more standard deviations from the mean, the usual criterion for outliners (Draper and Smith 1966). Only four islands are two standard deviations from the mean, one is negative and three are positive. These are Ritter (negative), already noted by Diamond to be vegetatively depauperate, a coral islet (positive) previously suggested by Diamond to be species poor (Diamond 1974), and two land bridge islands, Salawati and Botanta (both positive). It is true that land bridge islands tend to be above the regression line but this may be expected since they are close to the source fauna. Thus there is no evidence that New Guinea land bridge islands are supersaturated. We will deal with the West Indian islands elsewhere but Terborgh's (1975) calculation of extinction coefficients and their supposed inverse correlation with area deserve comment. It can be shown (Abele and Connor, in prep.) by simple algebraic substitution that Terborgh's formula for $K_3$ (extinction coefficient) reduces to $K3\propto 1/A$ (since the other terms in the right hand expression are all constants). Therefore his regression of $K_3$ against area is circular and the conclusion that extinction rates decrease with increasing area is trivial and tautological.

### *Barro Colorado Island*

Barro Colorado Island deserves special comment because it is the only island for which exist actual census of the original birds present. Willis (1974) and Wilson and Willis (1976) reviewed the data and concluded that of 209 original species 45 had become extinct over a 50-year period. They note that most (32) of these can be explained to be the result of habitat changes but the reasons for the other 13 remain elusive. Terborgh (1974, 1975) estimates an extinction coefficient for the island and a predicted loss of 16-17 species. This result has received wide acclaim as ". . . an acceptable account of reality . . .." (Terborgh 1975) ". . .gratifyingly in accord with the actual . . .." Diamond and May 1976) and ". . . dramatically confirmed the accuracy of his calculations . . . ." (Diamond 1975). Disregarding for the moment the mathematical circularity involved in the calculations (Abele and Connor, in prep.) we find (based on Terborgh's own data) that 95%

confidence interval for the estimate to be 7 to 81. We cannot agree that this is an acceptable account of reality. Our confidence in the data is further shaken by an examination of the original species numbers present on Barro Colorado. Since Chapman (1938) and Eisenmann (1952) list about 300 species, of which 253 they consider resident, the confidence interval around Willis's (1974) estimate of 209 species must also be fairly wide.

*Time Scale for Relaxation*

The relaxation times suggested by Diamond and Terborgh are on the order of 10,000 to 20,000 years. Is this reasonable? We have already noted that the arthropods of mangrove islands reached a new equilibrium level in less than a year. Regardless of the ultimate causes it is clear that major vegetational and avifaunal changes occurred on Barro Colorado in less than 50 years. Strong (1974a, 1974b) and Strong, McCoy and Rey (1977) have presented persuasive arguments that phytophagous insects equilibrate on introduced host plants within a few hundred years. This involves host plants switching, a process thought to require evolutionary time. We would suggest that whatever species loss may have occurred on land bridge islands, it occurred rapidly, lagging behind the actual sea level change very little.

The low values of equilibrium turnover calculated by Lynch and Johnson (1974) and Simberloff (1969) suggest that it has little significance for the design of nature preserves. Equilibrium theory predicts that extinction rates should be inversely correlated with area, but the experimental work of Simberloff (1976a) yielded no pattern. The inverse relationship between extinction rates and area reported by Terborgh (1974) for several West Indian Islands is based on circular mathematical reasoning and is therefore uninformative. The time scale of relaxation reported by Terborgh (1974, 1975) and Diamond (1972, 1975) is extremely long. However, the analyses of these authors are beset with many statistical problems, and are based only on inferences about original species numbers. Simberloff's (1976a) experiments suggest that the time scale of relaxation is very short.

## MAINTENANCE OF SPECIES COMPOSITION

A major problem in designing nature preserves is to determine a priori which species will be maintained. Island biogeography theory assumes that species with low abundances are more likely to be lost than common species. However, the presence or absence of a species from a particular preserve cannot be predicted simply by a knowledge of its abundance before the preserve is developed, but must include an in depth knowledge of the biology of the species in question. For example, low abundance "fugitive" species are extremely persistent when presented with a patchy environment.

Some empirical observations generally classed under the rubric of 'ecological truncation' are pertinent to this problem. Ecological truncation refers to the loss of specialists and of large members of ecological guilds. For example, there were originally 11 or so species of ant-following birds on Barro Colorado Island (Willis 1974) of which three became extinct or nearly so during 1960-70. These three were the largest members of the ant-following guild. Pelicans, ospreys, and eagles are three other examples. Large-bodied animals usually have large feeding territories (McNab 1963; Schoener 1968), as to the so-called top carnivores. These animals are extremely vagile and are likely to move in and out of even the largest nature preserves. The disappearance of the elk, wolves, and bear from Mount Rainier National Park is a perfect example of this problem (Weisbrod, this volume).

Somewhat similar to the absence of large-sized animals is the often reported absence of certain families of birds from islands. MacArthur, Diamond and Karr (1972) for example note the absence of certain families of birds from the Pearl Islands on the Pacific coast of Panama and conclude that it is unlkely to be accidental. However, only rarely (Simberloff 1974) has the question been asked, "What is the probability of these families being represented in a random sample of say, 46 species (e.g., Rey Island) of Panamanian birds?" For example, of 20 random draws of 59 species from the Panamanian avifauna 17 lacked families containing 20 or more species and three times families with 30 or more species were missed (Simberloff 1974). Only after the problems of random sampling probabilities have been factored out can the interesting ecological patterns be examined.

The emphasis on ecological truncation, the absence of certain families, and local extirpation have all been framed around islands without reference to these phenomena in mainland regions. For example the Harpy Eagle is no longer present on Barro Colorado (ecological truncation and local extirpation) but what is the probability of not only finding the species but finding it breeding in any 15.6 $km^2$ region of the adjacent mainland? How often do mainland species disappear from any subset of the region? What is the probability of finding jacamars, puffbirds and guans in any small region of the mainland? Studies such as those of Weisbrod (this volume), Moore and Hooper (1975), and Galli et al. (1976) can help to answer these questions. However, a more complete and sophisticated knowledge of species' abundances, regional movements, and habitat requirements are the only data capable of yielding the necessary predictive power to permit the effective and efficient design of nature preserves.

## DESIGN

The previous discussions have shown that it is a very risky business to attempt to predict a priori the single best design strategy in order to preserve maximum diversity without detailed studies of the habitat requirements of entire floras and faunas. It is at best premature to conclude that a single large preserve will be more effective in preserving maximum diversity than multiple small preserves, especially when the realities of the land acquisition process and the potential for placing smaller preserves in varied habitats are considered.

The design criteria of Terborgh (1974, 1975), Willis (1974), Diamond (1975), Wilson and Willis (1975) and Diamond and May (1976) all stress a single large area as being preferred for theoretical reasons. Implicit in the arguments in favor of a single large preserve is the connotation that small preserves are of less use. This is because most writers have dealt with vertebrates, particularly birds and mammals. A 1 $km^2$ refuge might be rejected as inappropriate for birds and mammals but it might be fine for some rather magnificant spiders or soil arthropods. Biologists know little of the population dynamics of vertebrates and almost nothing of invertebrates. We would not reject any amount of land from consideration as a refuge. As pointed out, arguments based on the species-area relationship are ambiguous on this point, and the extremely long relaxation times calculated by Terborgh and Diamond actually argue that we need not act with haste to forestall extinctions. The careful experiments of Simberloff (1976a), however, show that relaxation times for one fauna are rapid and that action may be needed now to prevent extinctions.

We also point out that reasonable design suggestions must distinguish between two possible roles for nature preserves; the prevention of local extirpations, and the prevention of ultimate extinctions. Approaches to this problem need to recognize both the various design goals and uses that nature preserves may be expected to fulfill. There is value in preventing local extirpation, availing the local biota to residents of a region, but on the periphery of a species' range it is dubious that disproportionate efforts should be made to preserve local populations when lesser efforts well within the distributional range of a species would be much more effective.

## CONCLUSION

We wish to reaffirm our support of the ethic of organic diversity and urge that mankind do as much as possible to preserve organic diversity and as little as possible to disturb it. Our complaint is with the uncritical acceptance and application of an insufficiently validated hypothesis. The large body of empirical observations which support conservation practices remains a firm foundation independent of any theory. The National Park Service can contribute to both the data base and the theory by continuing to support and enlarging many of the monitoring programs discussed at this conference. Many of the questions relating biogeography and conservation can be probed by simply following populations of animals in parks over a five to ten year period. Such projects would benefit everyone concerned. The National Park Service is guardian of a precious and irreplaceable national resource and this bears a special responsibility (and burden) to safeguard it.

## REFERENCES


ABELE, L. G. 1974. Species diversity of decapod crustaceans in marine habitats, Ecology 55: 156-161.

ABELE, L. G., and W. K. PATTON. 1976. The size of coral heads and the community biology of associated decapod crustaceans. J. Biogeo. 3:34-47.

CHAPMAN, F. M. 1938. Life in an air castle. D. Appelton-Century Company 250 p.

CONNOR, E. F. and E. D. McCOY. 1979. The statistics and biology of the species-area relationship. Amer. Nat. in press.

DAYTON, PAUL K. 1973. Two cases of resource partitioning in an intertidal community: Making the right prediction for the wrong reason. Amer. Nat. 107:662-670.

DIAMOND, J. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. PNAS 64:57-63.

DIAMOND, J. 1971. Comparison of faunal equilibrium turnover rates on a tropical island and a temperate island. PNAS 68:2742-2745.

DIAMOND, J. 1972. Biogeographic kinetics: Estimation of relaxation times for avifaunas of southwest Pacific islands. PNAS 69: 3199-3203.

DIAMOND, J. 1974. Colonization of exploded volcanic islands by birds: The supertramp strategy. Science 184:803-806.

DIAMOND, J. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. Biol. Conservation 7:129-146.

DIAMOND, J. 1976. Island biogeography and conservation: Strategy and limitations. Science 193: 1027-1029.

DIAMOND, J. and R. MAY. 1976. Island biogeography and the design of natural reserves. *In* R. M. May (ed) Theoretical ecology principles and applications. W. B. Saunders Co., Philadelphia, PA. 163-186.

DRAPER, N. R., and H. SMITH. 1966. Applied regression analysis. John Wiley & Sons, Inc. 407 p.

EHRENFELD, D. W. 1976. The conservation of non-resources. Amer. Sci. 64:648-656.

EISENMANN, E. Annotated list of birds of Barro Colorado Island, Panama Canal Zone. Smithsonian Miscellaneous Collections 117(5):1-62.

GALLI, ANNE E., C. F. LECK, and R. T. T. FORMANN. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk 93:356-364.

HARMON, W. N. 1972. Benthic substrates: their effect of fresh-water mollusca. Ecology 53:271-277.

LYNCH, J. F., and N. K. JOHNSON. 1974. Turnover and equilibria in insular avifaunas with special reference to the California Channel Islands. The Condor 76:370-384.

McARTHUR, R., J. DIAMOND, and J. KARR. 1972. Density compensation in island fauna. Ecology 53: 330-342.

McNAB, B. K. 1963. Bioenergetics and determination of home range size. Amer. Nat. 97:133-140.

MOORE, N. W., and M. D. HOOPER. 1975. On the number of bird species in British woods. Biol. Conserv. 8:239-250.

OSMAN, R.W. 1977. The establishment and development of a marine epifaunal community. Ecological Monographs. 47:37-63.

PRESTON, F. W. 1962. The canonical distribution of commonness and rarity I.II. Ecology 43:185-215, 410-432.

SCHOENER, T. 1968. Sizes of feeding territories among birds. Ecology 49:123-141.

SIMBERLOFF, D. 1974a. Equilibrium theory of island biogeography and ecology. Ann. Rev. Eco. Syst. 5:161-182.

SIMBERLOFF, D. 1974b. Models in biogeography. *In* T. J. M. Schopf (ed). p 160-191. Models in Paleobiology. Freeman, Cooper & Company, San Francisco, California.

SIMBERLOFF, D. 1976a. Experimental zoogeography of islands: Effects of island size. Ecology 57:629-648.

SIMBERLOFF, D. 1976b. Species turnover and equilibrium biogeography. Science 194:572-278.

SIMBERLOFF, D., and L. G. ABELE. 1976. Island biogeography theory and conservation practice. Science 191:285-286.

SIMBERLOFF, D., and E. WILSON. 1969. Experimental zoogeography of islands: The colonization of empty islands. Ecology 50:278-296.

STRONG: D. R. 1974a. Non-asymptotic species richness models and the insects of British trees. PNAS 71: 2766-2769.

STRONG, D. R. 1974b. Rapid asymptotic species accumulation in phytophagous insect communities: The pests of Cacao. Science 185:1064-1066.

STRONG, D. R., E. McCOY, and J. REY. 1977. Time and the number of herbivore species: the pests of sugarcane. Ecology 58:167-175.

TERBORGH, J. 1974. Preservation of natural diversity: The problem of extinction prone species. Bioscience 24:715-722.

TERBORGH, J. 1975. Faunal equilibrium and the design of wildlife preserves p. 369-380. *In* F. B. Golly and E. Medina (eds) Tropical ecological systems. Trends in terrestrial and aquatic research. Springer-Verlag: New York Ecological Studies Vol. 11.

TERBORGH, J. 1976. Island Biogeography and conservation: Strategy and limitations. Science 193: 1029-1030.

TERBORGH, J., and J. FAARBORG. 1973. Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. Auk 90:75-79.

WHITCOMB, R., J. LYNCH, P. OPLER, AND C. ROBBINS. 1976. Island biogeography and conservation: Strategy and limitations. Science 193:1030-1032.

WILLIS: E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecological Monographs 44:153-169.

WILSON: E., and E. O. WILLIS. 1975. Applied biogeography. *In* M. L. Cody, p. 522-534. and J. M. Diamond (eds) Ecology and evolution of communities. Harvard Univ. Press. Cambridge, Mass.

# PROSPECTIVE CONTRIBUTIONS OF A COMPUTER-BASED CONTINENTAL FLORA TO SCIENTIFIC INFORMATION NEEDS OF THE NATIONAL PARK SERVICE

Larry E. Morse and Jane I. Lawyer[1]

To be an effective interpreter of natural wonders and protector of diverse public lands, the U. S. National Park Service needs reliable, scientifically reviewed floristic information of many kinds. Traditional requirements for species-related knowledge about plants include specimen identification, contributions to interpretive programs, and interdisciplinary needs of anthropologists, historians, and paleontologists. The non-traditional questions raised in enlightened management of endangered populations and irreplaceable ecosystems also require answers based on reliable botanical data. At present, these diverse needs are partially fulfilled by regional floras and manuals, taxonomic monographs, ecological studies, and other traditional scientific works. However, the quality of such reference works varies considerably from region to region and taxon to taxon, and the information contained in them has never been synthesized satisfactorily and reviewed on a national scale.

Several years ago, the *Flora North America* project (based at the Smithsonian Institution) began such a synthesis, but this work was terminated abruptly by austerity budgets in 1973. *Flora North America* proposed as twin goals the production of a published floristic treatise on the vascular plants of North America north of Mexico, and, concurrently, the development of a computer-based information resource including these data and associated information (Shetler, 1971). A preliminary checklist was distributed, and contributions were solicited from hundreds of plant systematists, but work was suspended before any of these contributions could be completed, edited, and included in the data base.

Efforts are now being made to resume a modified *Flora North America* project with Department of the Interior sponsorship, as part of the Man and the Biosphere Program. The New York Botanical Garden is conducting a contract study in this area for the National Park Service, requiring investigation of the floristic information needs of the National Park Service and other selected land-management agencies, to determine which of their information needs could be served through resumption of a computer-based flora project. The following discussion presents some of the preliminary findings of the study.

First, a computer-based floristic information system would provide considerable support to scientific research in National Park areas, whether conducted by Park Service staff or by independent scientists. There are many lacks and ambiguities in the species-related botanical information available for the United States; if this knowledge were organized into a systematic review of continental scope, appropriate topics for future studies would be more evident. Meanwhile, great care would be needed to assure that the information-system design recognized the uneven quality and varying reliability of the available data (*cf.* Watson, 1971; Shetler, 1974; Morse, *in press*). This systematized floristic information base, if cautiously used, could also support modern information-retrieval procedures such as computer-based specimen identification techniques (Morse, 1975). Users of the computer system would have to realize, however, that such methods are only as good as their taxonomic reference data, and that it will take many years of research to achieve consistently high quality. Nevertheless, a modern continental synthesis of floristic information is an overdue task which would enhance the productivity of new research in many areas (Gates, 1971; Irwin, 1973; Raven, 1974).

The topic of legal-protection status of various taxa in various jurisdictions was not considered in the original FNA plans, but now deserves attention as an area where a centralized, computer-based information service could offer latest-available status reports to a large user community. Such a data base could be developed independently of *Flora North America*, but its coordination with FNA would provide a high quality scientific review particularly in the highly technical area of taxonomic synonymy. Another example of an area in which some coordination with FNA seems desirable is taxon-related management information (such as fire ecology, reproductive strategies, or sensitivity to feral animals); again, wide dispersion, up-to-date revision, and quality review of the information are important considerations.

The selection of new park properties (and designation of National Natural Landmarks) depends, in part, on a thorough awareness of the nation's biotic diversity. Here again a high-quality continental synthesis of knowledge of vascular plant species and their geographical and ecological distributions would be an invaluable reference source for management decisions concerning the conservation of our nation's biotic diversity in the National Parks and other wild natural areas.

## LITERATURE CITED

GATES, D. M. 1971. Flora North America: A data bank of systematic biology. BioScience 21:507.

IRWIN, H. S. 1973. Flora North America: Austerity casualty? BioScience 23:215.

MORSE, L. E. 1975. Recent advances in the theory and practice of biological specimen identification. pp. 11-52 in Biological Identification with Computers, R. J. Pankhurst (Ed.), Academic Press, London and New York.

MORSE, L. E. Some information-management problems raised by the international nature of systematic biology data. Proc. 5th Biennial CODATA Conference, Pergamon Press, Oxford. In press.

RAVEN, P. H. 1974. Plant systematics 1947-1972. Ann. Missouri Bot. Gard. 61:166-178.

SHETLER, S. G. 1971. Flora North America as an information system. BioScience 21:524, 529-532.

[1]New York Botanical Garden, Bronx, New York 10458.

SHETLER, S. G. 1974. Demythologizing biological data banking. Taxon 23:71-100.
WATSON, L. 1971. Basic taxonomic data; The need for organization over presentation and accumulation. Taxon 20:131-136.

# THE IMPACT OF EXOTIC PLANTS ON THE NATIVE VEGETATION OF THEODORE ROOSEVELT ISLAND

L. K. Thomas, Jr.[1]

## INTRODUCTION

Theodore Roosevelt Island is one of the parks of the National Capital Region of the National Park Service. Located in Washington, D.C., in the Potomac River (Figure 1) is is 35.74 hectares (88.32 acres) in area (National Capital Parks, 1970:56), approximately 1.1 km (0.7 mile) long and 0.5 km (0.3 mile) wide at its widest place (U.S. Geological Survey, 1965). The island consists of a core of micaceous schist surrounded by alluvium (Thomas, 1963:1,7). The highest elevation is about 13.1 m (43 ft., *ibid.*).

As early as 1792 the upland area was in agricultural use and the natural vegetation has been periodically disturbed from that time until the island was acquired by the National Park Service in 1932 (*ibid.*, 2, 49). Since acquisition, there have also been disturbances to the vegetation from developments: highway bridge, monument to Theodore Roosevelt, extensive plantings (*ibid.*, 2, 49, 50; U.S. National Park Service, 1968:8).

The natural vegetation of the upland is dominated by *Ulmus americana* L. (American elm), *Acer negundo* L. (boxelder), *Morus alba* L. (white mulberry), *Prunus serotina* Ehrh. (black cherry), *Fraxinus americana* L. (white ash), *Liriodendron tulipifera* L. (tulip-tree), *Quercus rubra* L. (northern red oak), and *Acer saccharinum* L. (silver maple) in about that order (Thomas, 1974:7). The forested alluvial deposits are dominated by *Acer saccharinum* L. (silver maple), *Fraxinus pennsylvanica* Marsh. (green ash), and *Salix nigra* Marsh. (black willow), while the nonforested deposits are dominated by a fresh water tidal marsh of *Peltandra virginica* (L.) Schott & Endl. (arrow-arum), *Acorus calamus* L. (sweetflag), *Typha angustifolia* L. (narrow-leaved cat-tail), and *Nuphar luteum* (L.) Sibth. & Sm. (spatter-dock) (*ibid.*, 7,8).

Because of their abundance, three exotic plant species were selected for ecological study in 1971: *Hedera helix* L. (English ivy), *Lonicera japonica* Thunb. (Japanese honeysuckle), and *Iris pseudacorus* L. (European yellow iris). The study which was terminated in 1974 was carried out to determine what native species, if any, were being replaced and what factors limit exotic abundance.

## METHODS

Each of the three exotic plant species was studied in two habitats in which it was abundant. The English ivy was studied on the island upland and the flood plain. The Japanese honeysuckle was studied on the upland under an intact understory where subcanopy trees and shrubs were present and in an upland area where subcanopy trees and shrubs had been removed. The European yellow iris was studied in the open marsh near the tidal gut and back near the tree line in the marsh-swamp transition.

In all six of these habitats square meter plots were laid out in several experimental designs. In noncontrol plots exotic plant biomass was removed, dried, and weighed. Invasion of native and other species into some of these plots was noted.

Light stations, using Ozalid type light meters (Friend, 1961), were set up at the plots and in similar habitats without the exotics. Light was determined as a percent of open sunlight, therefore, meters were also placed as controls in an open field on the island. In addition controlled light experiments were run in both the English ivy and the Japanese honeysuckle.

Surveys were made of the elm trees on the island and their vigor and relationship with the two exotic evergreen vines: English ivy and Japanese honeysuckle. All down trees on the island were surveyed along with their relationship with these same exotic vines.

The topography of the marsh and swamp-marsh transition was determined as well as a number of soil factors as they related to presence or absence of the European yellow iris.

Altogether there were 190 experiments and surveys which were statistically analyzed.

## RESULTS

Light is a strong limiting factor for Japanese honeysuckle (Figure 2). Growth increases with light intensity. This evergreen vine is a twiner and it overwhelms and kills small trees and shrubs, and suppresses reproduction especially of the tree species American elm, black cherry, and tulip-tree which are among the dominants on the island upland.

Light is not as strong a limiting factor for English ivy (Figure 2), but on the upland no factor is stronger. On the flood plain, the water table limits growth and distribution of the ivy. In both of these habitats the ivy suppresses growth of herbs.

On the flood plain the impact of this exotic vine is about the same as the impact of the flood from hurricane Agnes. The impact of this ivy on upland herbs exceeds this. This tendril evergreen liana is not limited to climbing small trees; it shades and kills out understory and overstory trees. Examination of log cross sections from overstory sized trees covered with English ivy shows suppressed ring growth in the other rings. The English ivy takes over Japanese honeysuckle areas.

When the canopy is opened by a tree falling, vines of both English ivy and Japanese honeysuckle are encouraged. A great boost, however, is given to English ivy growth when an American elm tree is cut (for management of Dutch elm disease).

[1]National Park Service, National Capital Region, Washington, D.C. 20242.

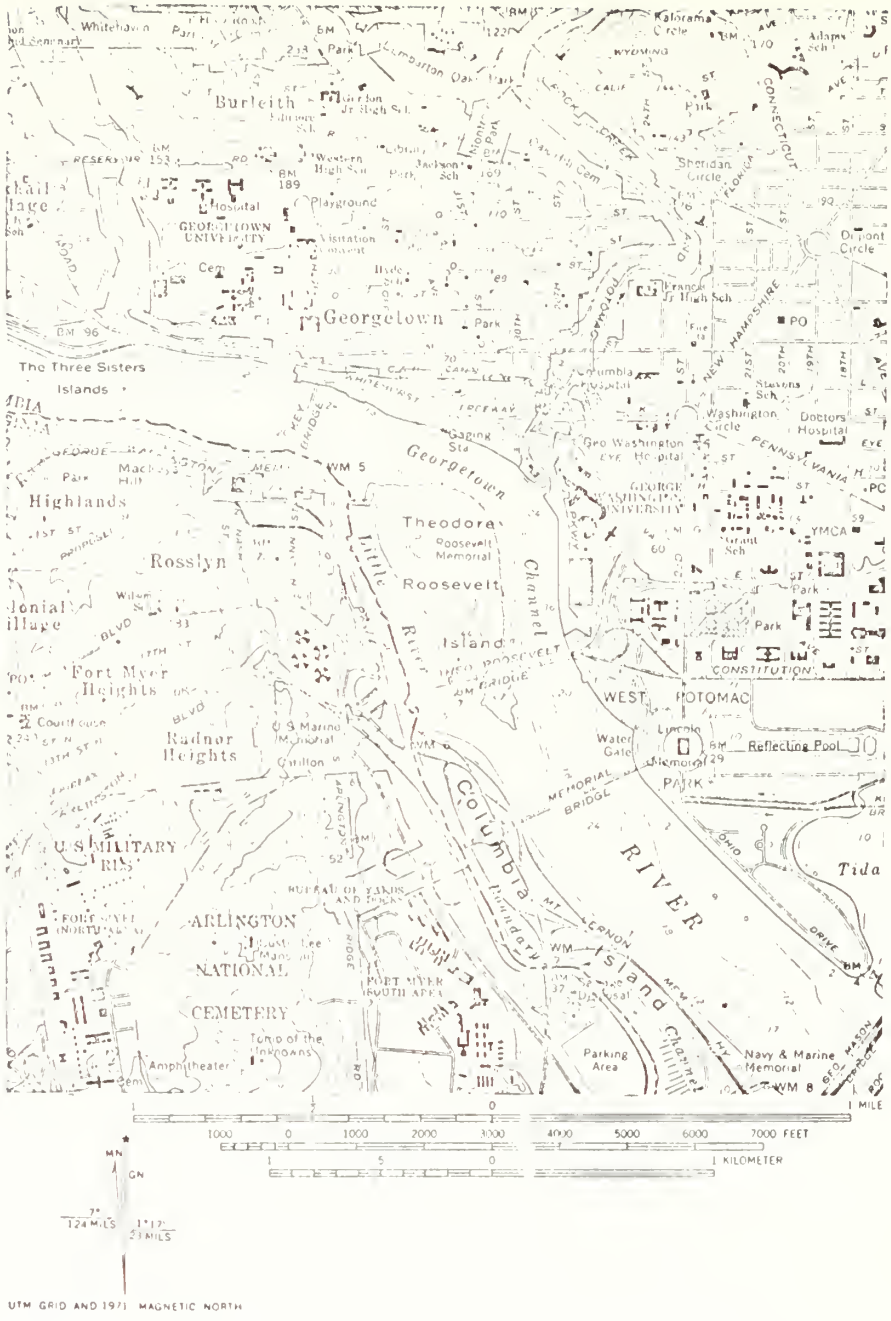



FIGURE 1. Theodore Roosevelt Island and vicinity.

For the European yellow iris the length of time it is inundated comes closest to a limiting factor. The longer the inundation, the slower the growth. By assuming this as the limiting factor a rise in the river level during the growing season was accurately predicted. Trash in the marsh increases the microtopography and functions as any raised surface in marshy habitats by encouraging the iris. The iris takes over arrow-arum areas. In the swamp-marsh transition, sweetflag takes over iris areas. Iris is associated with soil hardpan, especially in this transition area.

## DISCUSSION AND CONCLUSIONS

Once Japanese honeysuckle becomes established, its suppression of tree reproduction and killing of small trees and shrubs changes not only the composition of the forest, but its structure as well. With less woody plants the area becomes more sunlit, thus Japanese honeysuckle tends to create its own best habitat.

The killing of trees by English ivy appears to result both from shading out the tree leaves and compressing (in the case of heavy ivy growth) the

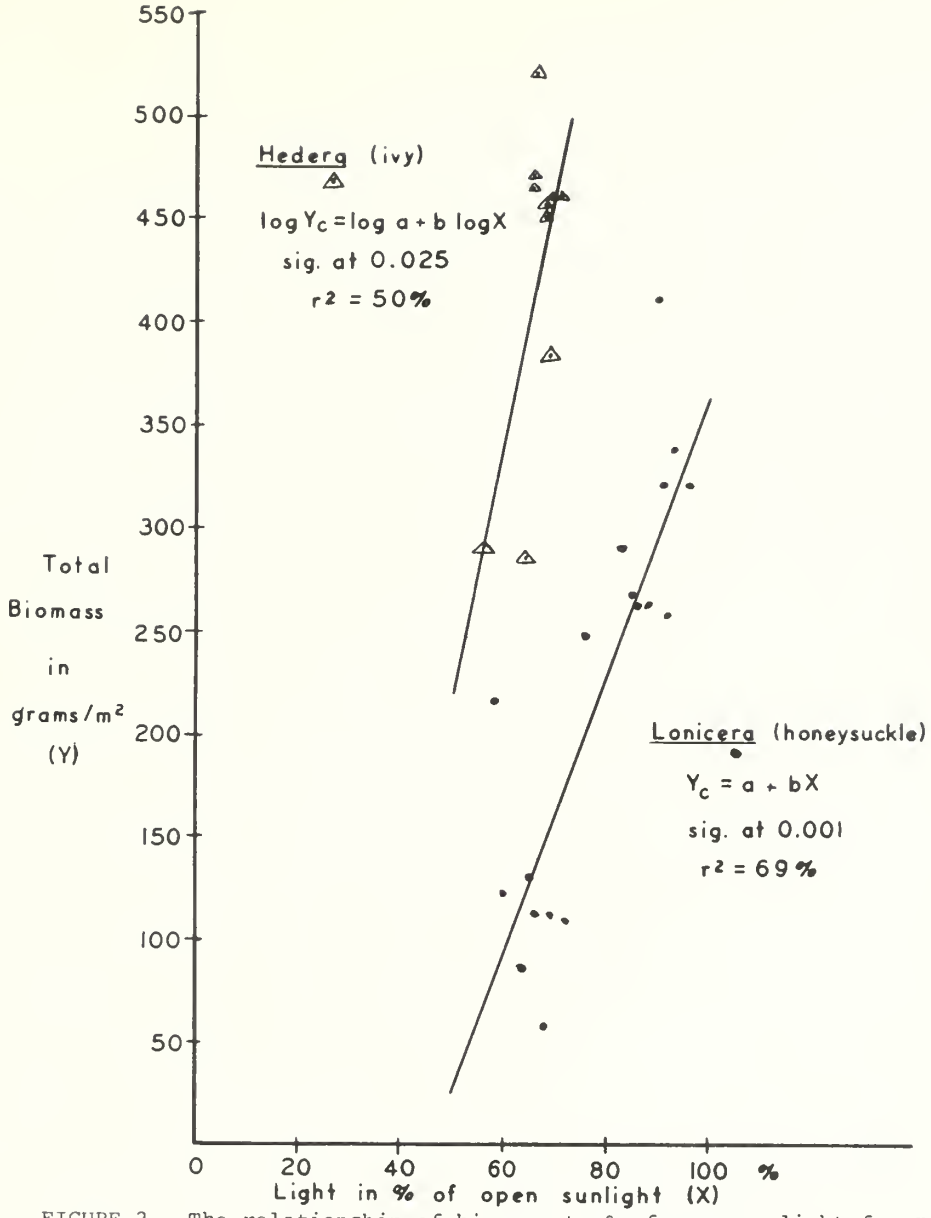



FIGURE 2. The relationship of biomass to % of open sunlight for *H. Helix* (English ivy) and *L. japonica* (Japanese honeysuckle).

vascular tissue to prevent or slow down food translocation and water uptake. American elms are particularly vulnerable, and this is probably due to reduced vigor from Dutch elm disease and root compaction from the many trails on the island.

Overall, the consequences of the establishment of these two ornamental vines are that the forests (except the swamp) are being destroyed and succession is being directed toward a vine dominated community. The ultimate community will be dominated by English ivy and the management for the control of Dutch elm disease is an important factor in encouraging this ivy.

Since the European yellow iris replaces the arrow-arum which may be an important wood duck (*Aix sponsa* (L.)) food supply in the nesting season (Martin *et al.*, 1951:447; Stewart and Robbins, 1958:85), these ducks may be in jeopardy. Stewart and Robbins (1958:21) consider this bird as one of the primary species of breeding birds in the Coastal Plain of Maryland and the District of Columbia. Since the island straddles the Piedmont and Coastal Plain physiographic provinces (Thomas, 1963: 7, 39), the further possibility exists of reducing the range of a primary species of breeding bird.

Once the iris gets established on a site, its rhizomes ramify the soil and in growth compact that soil to create a hardpan. With the drier hardpan plus a slightly raised mat of rhizomes, more favorable conditions are created for iris growth, thus the iris apparently helps to create its own best habitat.

In the swamp-marsh transition area, this iris appears to outcompete the willows (*Salix*) for mineral soil and thus eliminate the willow stage from the normal marsh to swamp succession. It thus short-circuits succession and provides a seed bed for swamp trees such as green ash.

At the present time this short-circuit is being slowed down because of a rise in the river level during the growing season. This makes the marsh and adjacent swamp-marsh transition wetter for a longer period of time and hence less favorable for iris growth.

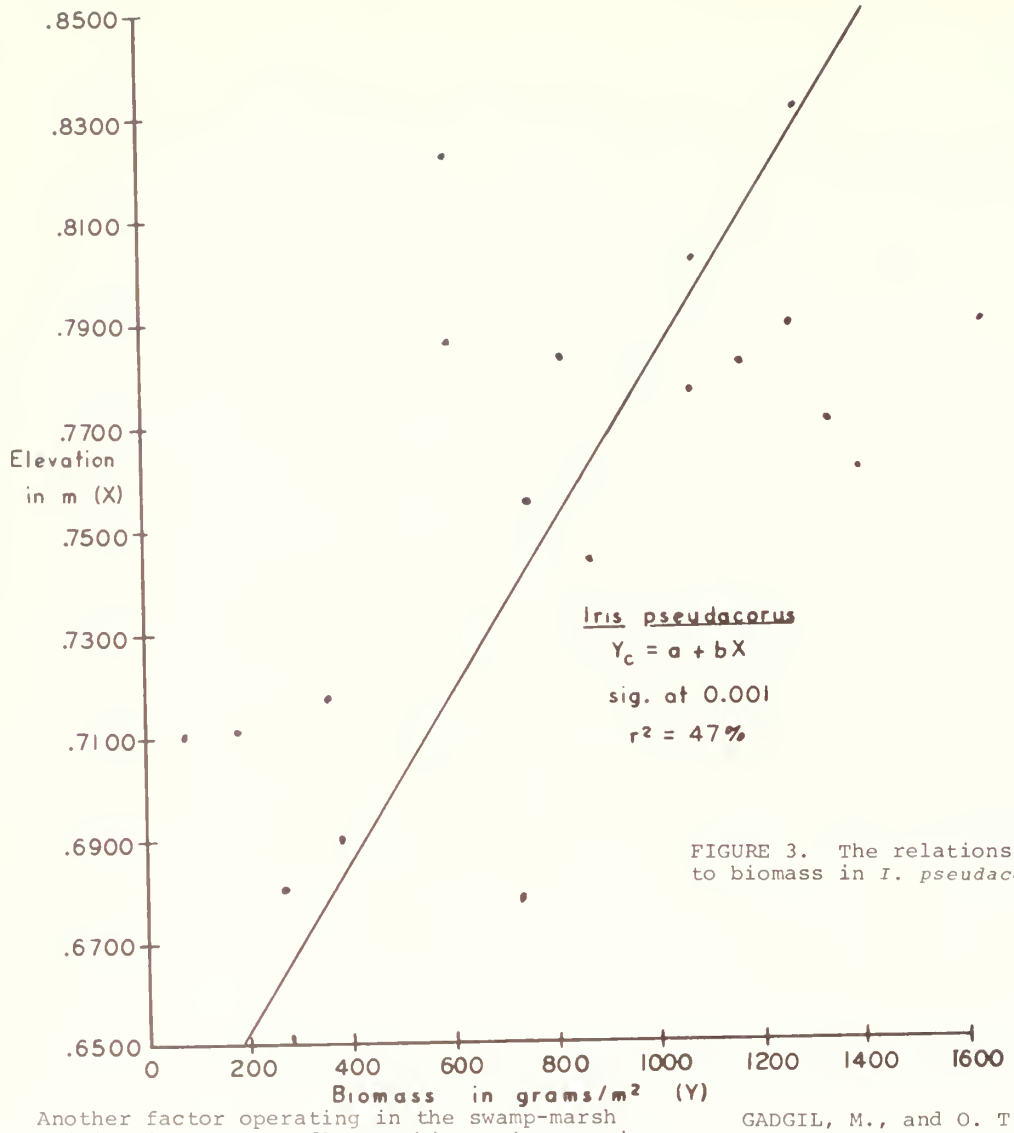



FIGURE 3. The relationship of topography (elevation) to biomass in *I. pseudacorus* (European yellow iris).

Another factor operating in the swamp-marsh transition is the sweetflag. This native species is outcompeting the iris, and in so doing it confirms the r- and K- selection theory. The sweetflag behaves as a K- strategist by putting most of its resources into vegetative structure, while by comparison the European yellow iris is an r-strategist that produces a lot of seed. According to the theory (see Gadgil and Solbrig, 1972: 14, 17-20) the r-strategist (the iris) will be most successful in a density-independent mortality environment and the K- strategist (the sweetflag) will be most successful in a density-dependent one. Thus one could predict that in the emergent zone of marsh vegetation where both these species live, that the K- strategist will do better as the zone fills with vegetation and density-dependent factors become more important. This is what is actually happening in the marsh.

All three of the exotic plant species studied were established before the island became a park forty-four years ago. They are all associated with disturbed areas, and in every case they are altering the native vegetation.

REFERENCES CITED

FRIEND, D. T. C. 1961. A simple method of measuring integrated light values in the field. Ecology 42:577-580.

GADGIL, M., and O. T. SOLBRIG. 1972. The concept of r- and K- selection: evidence from wild flowers and some theoretical considerations. The American Naturalist 106(947):14-31.

MARTIN, A. C., H. S. ZIM, and A. L. NELSON. 1951. American Wildlife and Plants. Dover Publications, Inc., New York. 500 pp.

NATIONAL CAPITAL PARKS. 1970. Reservation List, January 1, 1970. United States Department of the Interior, National Park Service. 69 pp.

STEWART, R. E., and C. S. ROBBINS. 1958. Birds of Maryland and the District of Columbia. Bureau of Sport Fisheries and Wildlife, United States Department of the Interior. North American Fauna, No. 62. 401 pp.

THOMAS, L. K., JR. 1963. Geomorphology and Vegetation of Theodore Roosevelt Island. National Park Service Scientific Report No. 2. 61 pp.

_____. 1974. The impact of Three Exotic Plant Species on the Native Vegetation of a Potomac Island. Ph.D. Dissertation, Duke University, Durham, North Carolina. 281 pp.

UNITED STATES GEOLOGICAL SURVEY. 1965. Washington west quadrangle, 7.5 minute series (topographic).

UNITED STATES NATIONAL PARK SERVICE. 1968. Master-plan, Theodore Roosevelt Island, Washington, D.C. United States Department of the Interior, National Park Service. 52 pp.

# THE STATUS OF FIVE EXOTIC WOODY PLANTS IN THE TENNESSEE DISTRICT OF GREAT SMOKY MOUNTAINS NATIONAL PARK

Jill Baron, Christine Dombrowski and Susan Power Bratton[1]

This report describes the occurrence and status of five non-native plant species within the Tennessee side of Great Smoky Mountains National Park. The research project attempted to determine where the plants are located, whether their populations are expanding or contracting, and what impact, if any, they have on the native flora. Management of exotic plants is important for two reasons. The first, more vital reason is the preservation of an irreplaceable native flora. Plants that are in a delicate balance with their environment may not survive competition with introduced species. The second reason is certainly aesthetic. Non-native plants growing along the roadsides obscure the native flora, giving visitors a false impression about the structure and composition of the plant communities in the park.

The Resources Management Plan (of 1969) for the Great Smoky Mountains proposed that the exotic plants in the park be divided into three management groups:

1. Exotic plants which are displacing present native species and control is practical

2. Exotic plants which are displacing present native species and control is not practical

3. Exotic plants that remain static or those that have been declining in present years

(III-A-33 Resources Management Plan)

Plants included in Group 1 were kudzu *(Pueraria thunbergiana)*, mimosa *(Albizzia julbrissin)*, and tree-of-heaven *(Ailanthus altissima)*. Although all three species have been slated for control, at present, only an active eradication program for kudzu has been initiated. Research has been conducted on mimosa leaf wilt at the National Park Service Science Center at Bay St. Louis, Mississippi, but no field tests have been made in the park. Japanese honeysuckle *(Lonicera japonica)* was included in Group 2. Control was therefore not recommended. No specific species were included in Group 3.

In addition to kudzu, mimosa, tree-of-heaven, and Japanese honeysuckle, this study includes the Princess tree *(Paulonia tomentosa)*, which frequently associates with mimosa, and quickly invades large road cuts, particularly those near rivers.

## METHODS

The field research for this report was carried out in the summer of 1975. Two hundred and seventy miles of trails and roads on the Tennessee side of the park were observed to determine the extent of the invasion of woody non-native plants. Roads walked included the Cade's Cove Loop Road, Laurel Creek Road, Tremont Road, Little River Road, Newfound Gap Road, Greenbrier Road, the Bypass, the Spur, and Highway 73 to Greenbrier. The trails were chosen to represent a variety of forest types and elevations. Some manways and abandoned roads were also covered. About three hundred sitings of the five exotics in question were recorded. At each site we took the following information:

1. The exact location of the plant(s), including the coordinates on the 7.5 minute topographic maps, and a written description of the location

2. Elevation above sea level

3. Slope and aspect - slope was estimated or measured using a Brunton pocket transit; aspect was measured with a compass

4. Site type - the investigators noted whether the plants were growing around old home sites and fields, along streams or rivers, or along roads or trails

5. Forest type and understory type - this included the estimated age of the stand

6. Site disturbance - this included evidence of human intervention such as mowing or grading, and evidence of recent "natural" disturbance such as hog-rooting

7. Population of the exotic - the investigators noted the number of mature plants and seedlings present at a site, the presence of flowers or fruits, and any indication of vegetative spreading and reproduction

8. Area of exotic distribution in square meters

9. Affect on neighboring plants - the vines, kudzu and honeysuckle could be placed into one of three categories according to their impact on their closest neighbors. The first category was "slight", which indicated the plant was not growing on other species and generally had a scattered distribution. Individual plants or shoots were small. The second category was "moderate", which indicated that the plant was growing on other species or making solid clumps, excluding other species. The third category was "great", which indicated that the plants were climbing on trees or strangling other species. The three tree species had little impact other than shade on their neighbors, and tended to be too scattered to completely exclude other species. Therefore, no categories of impact were developed for these.

10. Nearest neighbors - in order to quantify the community type, the investigators recorded the names of the ten nearest herb species, and the species of each of the ten nearest trees (greater than 4 inches in diameter at breast height) and of the ten nearest shrubs (less than 4 inches DBH).

[1]National Park Service, Uplands Field Research Laboratory, Great Smoky Mountains National Park, Gatlinburg, Tennessee.

## RESULTS AND THE ANALYSIS OF THE STATUS OF THE INDIVIDUAL SPECIES

### *Lonicera Japonica*

In the course of this study, Japanese honeysuckle was recorded 86 times. Of these occurrences, 83 percent were in a successional forest dominated by *Liriodendron tulipifera*. The species composition of the successional tulip tree forest type (Whittaker 1964, Howe and Bratton 1975) varied along a moisture gradient. At the drier sites *Pinus virginia, P. strobus, Quercus coccinea, Q. rubra and Q. alba* were common. Trees found at wetter sites were *Plantanus occidentalis, Juglans nigra, Carpinus caroliniana,* and *Liquidambar styraciflua*. Several vines common in successional forests were often present as nearest neighbors to the honeysuckle. These were *Rhus radicans, Parthenocissus quinquefolia, Vitus* spp., *Rubus* spp., and the herbaceous vine *Amphicarpa bracteata*.

Herbaceous species commonly found growing near the honeysuckle along the roadsides included native species such as *Fragaria virginiana, Potentilla* spp., and *Polystichum acrostichoides,* and non-native species such as *Plantago major, P. lanceolata, Cynodon dactylon, Eluesine indica, Trifolium pratens, T. repens,* and *T. procumbens.* Around the old homesites *Panicum* spp., *Aster* spp., *Solidago* spp., *Agrimonia* sp. *Fragaria virginiana, Potentilla* spp., *Polystichum acrostichoides,* and the exotic *Dioscorea batatas* were common. Altogether, over a third of the herbaceous species associated with the honeysuckle were exotics themselves.

Seventeen percent of the records for the honeysuckle were in areas with no mature canopy at all. The impact of the honeysuckle on its neighbors depended on the presence of a canopy. Of the stands occurring under a canopy, one-fourth were judged as having heavy impact, half had a moderate impact, and one-fourth had slight impact on its neighbors. This could be due to the competition provided by the established grasses. Forest floor herbs in contrast, seemed to offer less resistance to invading honeysuckle, and in some areas are completely excluded by a heavy ground cover of the vine.

The impact of a clump of honeysuckle was also related to its area. The smallest clumps, as might be expected, tended to have the least effect on their neighbors. Clumps from 6 to 30 $m^2$ were usually moderate in their effect. The largest honeysuckle clumps graded from areas of little impact to those of heavy impact. The large stands with little impact were found on the roadsides where they were sparse and probably frequently cut. The shoots tended to be small and scattered.

The lowest elevation where honeysuckle was found was 1,200 feet. The highest elevation was 3,360 feet. Most of the sightings occurred between 1,400 and 2,000 feet above sea level. The plants at the higher elevations were small and pale suggesting altitude may be a limiting factor in the distribution of the species in the park. It is important to note, however, that most of the low elevation forest in the park is successional. A majority of the old homesites in the park are below 2,200 feet and the forests below this elevation are regenerating after farming, logging or burning.

The impact of the honeysuckle was related to elevation. The greatest impact was found in stands growing at elevations less than 2,000 feet. Above 2,000 feet the density of the stands and the impact decreased steadily. Above 3,000 feet the stands had almost no effect at all on the surrounding plants.

Honeysuckle was found on slopes ranging from 0 degrees to 90 degrees. Over half (63 percent) of the sightings were in areas with 0 to 10 degree slopes. This appears with site type: 84 of the site locations were homesites and roadsides, areas which are primarily flat. Twelve of the honeysuckle clumps were on slopes greater than 40 degrees. Of these, two had only slight impact, seven had moderate impact, and three had great impact on the neighboring plants.

Seventy-three of the honeysuckle sightings were on roadsides, ten on old homesites, and three by riversides. Our field time was not divided equally between the three different site types, since a majority of the time was spent on the roads. However, this does not fully account for the difference in occurrence by site type. Many old homesites investigated had no honeysuckle. A homesite with mimosa seedlings would often have no honeysuckle and vice versa. Honeysuckle may not have been common as an ornamental, or it may have been common but unable to survive in the shade of the successional forest. The three riverside sightings were all between Little River Road and Little River. In these areas, the honeysuckle was growing up relatively steep banks. No honeysuckle was found growing right by the water. The presence of Japanese honeysuckle on all of the roads investigated suggests that it needs an open canopy to become established. Once established, however, it may invade nearby forests. Most of the stands of the honeysuckle were confined to road cuts and forest edges, but several dense clumps went back 6 to 8 meters under the trees. Two locations on the Little River Road above Sugarlands Visitor Center had very dense stands that went into the forest at least 15 meters. The density of these stands decreased markedly inside the canopy, presumably due to shade.

### *Albizzia julibrissin*

In the course of this study, mimosa was recorded 87 times. Although 80 of the sightings were near tulip tree successional forest, none of the mimosa plants were actually growing under closed canopy. Seven sightings were in open areas. The tree was found growing along the same wide moisture gradient as the honeysuckle. Mature individuals were observed growing along stream banks as well as more xeric areas such as road cuts near pine-oak forest.

The herbaceous species found in association with mimosa along the roadsides and around the old homesites are largely the same as those associated with the Japanese honeysuckle. Trees growing by streams rarely had any herbs near them. Some sedges were found, as well as *Campsis radicans, Amphicarpa bracteata* and *Solidago* spp.

Only sixteen of the mimosa sightings included mature trees or clumps of mature trees; the remaining seventy-one sightings included only seedlings. As many as 1,000 seedlings were recorded on one data sheet if the seedlings were all in the same vicinity. There were no mature mimosa plants around the old homesites which were

being overgrown by the forest community. At many of the other mimosa sites, mowing probably removed most of the seedlings the first year. Shade from forest trees may also negatively affect seedling survival.

Mimosa was found at a maximum elevation of 2,420 feet and at a minimum elevation of 1,160 feet. It was most common between 1,200 and 2,000 feet. Note that the maximum elevation presently recorded for Japanese honeysuckle was 1,000 feet higher than the maximum elevation recorded for mimosa. Mature individuals of mimosa were found between 1,200 and 2,150 feet. The species is certainly found at lower elevations outside the park but 2,400 feet may be about the upper altitudinal limit of mimosa in the Great Smoky Mountains.

Most of the mimosa (68 percent) was found growing on slopes of 0 to 10 degrees, but the slopes of some of the mimosa locations were as steep as 90 degrees.

Mimosa seedlings have very little impact on the native flora. They were sparsely spread along roadsides and around old homesites. Since mimosa seeds are very light, the seed sources for this heavy production of seedlings are probably outside the park as well as inside the park boundary, seedlings would probably reestablish themselves within a year.

Around homesites, roads and stream banks, mimosa was usually found in two sizes: small seedlings (6 to 10 cm) or mature trees (up to 10 meters in height). The general lack of intermediate growth stages is further evidence that most seedlings do not survive their first year, largely because of mowing. The lack of intermediate stages may also indicate that the mimosa population is stable or declining, outside of the open areas around buildings and recent roadcuts.

*Paulownia tomentosa*

Of the eight individuals of princess tree found, five were growing on or at the base of cliffs. The other three were growing on open ground close to streams. Four of the sites had slopes of less than 10 degrees and four of the sites had slopes of 80 to 90 degrees. The tree was found at a maximum elevation of 1,716 feet and a minimum elevation of 1,160 feet. Six trees were growing in isolated positions, away from any other trees. The other two, which were growing by streams, had *Platanus occidentalis, Liriodendron tulipfera,* and *Betula lenta* as nearest neighbors. Princess tree is not common in the park and seems to grow only in areas where it has little competition.

*Ailanthus altissima*

Only one stand of tree-of-heaven was found in the sample area. There were more than twenty stems and many seedlings. This group is possibly a single clone, originating from one root. One tree was in fruit. Neighboring trees were *Prunus* sp., *Malus* sp., *Plantanus occidentalis,* and *Liriodendron tulipifera*. Shrubs present were *Aralia spinosa, Robinia pseudo-acacia,* and *Liquidambar styrifolia*. The herbs were typical of roadside successional flora: *Ambrosia* sp., *Albizzia julibrissin* (present as a seedling), *Fragaria virginiana, Panicum* sp., *Plantago major, P. lanceolata, Solanum carolinese* and *Viola* sp.

*Pueraria thunbergiana*

There is an active management program to eliminate kudzu from the Great Smoky Mountains National Park. No kudzu was found in the course of this study.

## DISCUSSION - IMPLICATIONS OF PLANT DISTRIBUTIONS FOR MANAGEMENT

Looking at the distributions of exotic plants for the Tennessee side of Great Smoky Mountains National Park, several patterns of importance to management appear. These include:

1. Exotic vascular plants are generally not found in virgin forests in the Smokies. Unlike the wild boar *(Sus scrofa),* which has invaded forests where there was a minimum of previous human interference, the exotic plants now present in the park are dependent on human activity, such as mowing or grading, to provide a suitable habitat for their establishment. The native vegetation seems to be able to out-compete the exotics, as long as the native forest communities are not subject to unnatural disturbance.

2. The woody exotics appear to be confined in their altitudinal distribution. Even though the roads in the park extend above 6,000 feet, the woody exotics drop out at 3,400 feet and below. The higher elevations may not be subject to invasion by non-native woody exotic species, or any invasion may be slower and easier to control. There are, of course, vigorous clumps of exotic herbs present along the roads, even at the highest elevations.

3. The non-native woody species are not only confined to low elevations, but are also confined to one general type of successional forest, the tulip tree type and its variations. This forest type itself is largely an artifact of human activity. Aside from the Japanese honeysuckle, the woody exotics do not grow well under the forest canopy and tend to be along roads, and in the openings around old buildings. This further restricts the distribution of these species in the park.

4. The populations of these species in the park are not very large. If one were to consider only the saplings and the mature individuals of the three tree species surveyed, there were barely 20 sightings over 270 miles of roads and trails (and the area sampled included some of the best possible habitat available in the park).

5. The age structure of the populations does not indicate an impending rapid expansion of the species. The lack of large number of saplings of the three tree species implies that few seedlings are surviving, and that in the next few years there will be few additional mature plants to replace those already in the park.

6. The species included in this survey have been present in the area of the park for quite a number of years, but have not undergone a real population explosion (unlike the wild boar or the chestnut blight). A vine like Japanese honeysuckle probably spread quickly after the abandonment of the

agricultural land in the park, but the same species may now actually be losing area to the new growth of forest. Unfortunately, since no datum has been kept on the status of exotic species in the park, one cannot determine at present if the populations of these species are increasing or decreasing.

7. With the exception of the Japanese honeysuckle, these species have very little impact on the native flora. The populations are too small and scattered and are too restricted to disturbed sites to have much effect.

8. These woody exotics tend to be along the roads and near park buildings, where they are highly visible to visitors. In fact, the areas which have the heaviest visitor use have the greatest numbers of exotics.

## PROPOSED MANAGEMENT STRATEGY

*Prevention of further problems with exotic plants:*

Although there is no way to insure that exotic vascular plants will not invade the native plant communities in the park, certain management policies make problems with exotics less likely. First, and foremost, disturbance of the native forest communities should be avoided as much as possible. This is especially important in the case of virgin forest. Cutting and grading should be minimal. Cleared and mowed areas serve as reservoirs for vascular exotics. Roads are the main invasion routes into the center of the park. Large road cuts provide excellent habitat for species like mimosa and princess tree.

Secondly, grazing damage should be kept to a minimum. Overgrazing by deer, wild hogs or other species may give exotic species a competitive advantage over the native inhabitants of a site.

Thirdly, the Park Service should be careful about introducing exotic species not already present in the park. When possible, native species should be planted around the visitor centers and residence areas. Care should be exercised when reseeding disturbed areas.

*Management for the non-native species now present in the park:*

Before outlining a management plan for exotic plants, it is necessary to realize that certain park programs tend to encourage an exotic flora. The park will never be completely free of exotic vascular plants, as long as there are roads and lawns in the park. Most of the non-native herbs established at these sites are not a threat to native plant communities, however, and the non-native herbs are largely confined to the disturbed habitats. Several exotic species are relics of earlier agricultural practices and tend to occur in areas now managed as historical sites rather than as natural areas. Cades Cove, for instance, probably has a greater biomass of exotic plants than any area of comparable size in the park. Many of the forage plants on which both the deer and the cattle subsist are exotics.

Because of the impossibility of eliminating vascular exotics from the park (and it remains to be seen if this is even desirable), the investigators suggest dividing the park into zones for the purpose of managing exotic vascular plants. The zones are:

ZONE 1: The exotic-free area - this includes the virgin forest areas in the park, forest and heath balds with little previous human disturbance, and the high elevation forest, both logged and unlogged, which have no exotics at the present time. Most of these areas support few, if any, exotics now and are the areas where invasion by exotics is least desirable. At the moment no active management program is needed in these areas, but any stands of woody exotics which are discovered should be removed at once. Botanists visiting these sites will hopefully report any unusual plants to park personnel.

ZONE 2: The buffer area - this includes sites which adjoin areas in Zone 1 and roads and disturbed areas which pass through areas in Zone 1. Absolute exclusion of woody exotics should also be practiced here. At present only the Newfound Gap Road needs to be watched.

ZONE 3: The non-management area - this includes low elevation second growth forests, old fields, old home sites and other successional areas toward the outside edge of the park and generally below 3,000 feet in elevation. These areas have large populations of exotics, but are largely inaccessible to control. No management is recommended unless future study indicates expansion of the exotic populations in these areas and an increase in the impact on the native flora. Present data indicate that normal successional processes will tend to slowly exclude many of the non-native species and reduce their populations.

ZONE 4: The managed area - this zone includes roadsides, visitor use areas, residence areas, and other places subject to continual human disturbance. These are the sites within the park which have the greatest populations of exotics, and are also the areas most visible to the public.

The control of some of the woody exotics could well be conducted as a program incidental to normal maintenance. In many of the areas with concentrations of exotic plants, the Park Service is cutting or mowing. If the maintenance crews could identify small saplings of the species in question they could pull them out by the roots. In general, with mimosa and the other woody exotics, removing seedlings is probably more trouble than it is worth. Saplings are the best age class to attack. Root-sprouts can be controlled by recutting at close time intervals. Honeysuckle might be cut off at the base.

## LITERATURE CITED


BRENDEN, E. V. 1960. Progress report on control of honeysuckle and kudzu. Proc. 13th Annual Mtg. Weed Conf. 187-93.

BROCKMAN, C. F. 1968. Trees of North America. Golden Press. New York. 280 pp.

FERNALD, M. C. 1970. Gray's manual of botany. 9th Ed. D. Van Nostrand Co., Cincinnati. 1632 pp.

HOWE, T. D. and S. P. Bratton. 1976. Winter rooting activity of the European wild boar. *Castanea*. 41:256-264.

NATIONAL PARK SERVICE. 1970. Compilation of the administrative policies for the national parks and national monuments of scientific significance (Natural Area Category). U.S. Govt. Printing Office. Washington, D.C. 147 pp.

NATIONAL PARK SERVICE. 1974. Final environmental statement natural resources management plan. Hawaii Volcanoes National Park. Offset 143 pp.

PETERSON, R. T. and M. MCKENNEY. 1968. A field guide to wildflowers of northeastern and north-central North America. Houghton Mifflin Co. Boston. 420 pp.

RADFORD, A. E., H. E. AHLES, and C. R. Bell. 1968. Manual of the vascular flora of the Carolinas. Univ. of N. C. Press, Chapel Hill. 1183 pp.

SYMONDS, G. W. D. 1963. The shrub identification book. M. Barrows and Co., New York. unnumbered.

SYMONDS, G. W. D. 1958. The tree identification book. William Morrow and Co., Inc. New York. unnumbered.

U. S. DEPARTMENT OF AGRICULTURE, FOREST SERVICE. 1974. Seeds of Woody plants in the United States. U.S. Dept. Agric., Agric. Handb. 450. U.S. Govt Printing Office, Washington, D.C. 883 pp.

WHITTAKER, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Mong. 26:1-80.

# THE ORIGINAL SURVEY NOTES OF THE PICTURED ROCKS AND APOSTLE ISLANDS NATIONAL LAKESHORES AND THEIR USE IN RECONSTRUCTING ORIGINAL FORESTS[1]

D. J. Frederick[2], L. Rakestraw[3], C. R. Eder[2], R. A. Van Dyke[2], B. J. Griewe[2], and M. A. Anderson[2]

## INTRODUCTION

Pictured Rocks and Apostle Islands National Lakeshore are two of the latest additions to the National Park System. Pictured Rocks, established in 1966 with an authorized area of 66,500 acres (26.912 ha), stretches 35 miles (56.32 km) along the southern shore of Lake Superior between the towns of Munising on the west and Grand Marais on the east of Alger County, Michigan. The Apostle Islands Lakeshore was created in 1970 and encompasses 42,011 acres (17,002 ha) consisting of 20 islands and a section of mainland on the Bayfield peninsula in Ashland and Bayfield counties, Wisconsin.

Both lakeshores offer an unsurpassed variety of natural scenic beauty. Pictured Rocks boasts multicolored sandstone cliffs, broad sand beaches, sand bars and dune, and numerous waterfalls and streams. The Apostle Islands archipelago, the northernmost land area in Wisconsin offers densely forested islands ranging in size from 3 to 10,000 acres (7.4 to 2,471 ha) sand beaches, rocky shorelines with sculpured arches and a unique early history.

A variety of soils are found ranging from those of sandstone origin on both areas with varying mixtures of organic material and glacial drift to the famous red clays of the Apostles. Several outwash features occur at Pictured Rocks including the Kingston Plains and the Grand Sable Dunes.

The present vegetation of both lakeshores is quite varied, the composition depending on topography, soil conditions, land use and fire history. Better-drained upland areas generally support Northern hardwoods with sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton) and basswood (*Tilia americana* L.). Beech (*Fagus grandifolia* Ehrh.) is a common associate on such mesic areas at Pictured Rocks, while it is completely absent on the Apostle Islands. Northern red oak (*Quercus rubra* L.) is often an associate on the Apostle Islands, while it is less common at Pictured Rocks. On both areas, the poorer drained upland soils support hemlock (*Tsuga canadensis* (L.) Carr.), red maple (*Acer rubrum* L.) and elm (*Ulmus americana* L.). The sand and outwash soils support white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Ait.) and jack pine (*Pinus banksiana* Lamb.). The lowland areas support stands of northern white cedar (*Thuja occidentalis* L.), tamarack (*Larix laricina* Du Roi K. Koch), balsam fir (*Abies balsamea* (L.) Mill.) and black spruce (*Picea mariana* Mill B.S.P.).

Vegetation surveys have been made of Pictured Rocks (Read 1975). However, recent information is lacking for most of the Apostle Islands. Beals and Cottam (1960) made the first extensive survey, and only recently individual islands have been sampled (Larson 1975; Northland College 1975; Stadnyk et al. 1974).

[1]Supported by a National Park Service contract to Michigan Technological University.

[2]Department of Forestry, Michigan Technological University, Houghton 49931.

[3]Department of Social Sciences, Michigan Technological University, Houghton.

The forests of these two lakeshores have undergone significant changes with the advance of civilization. Logging, quarrying, land clearing for agriculture plus repeated fires over much of the land, have all contributed to these changes. Thousands of acres of land originally supporting magnificent stands of white pine, red pine and hemlock in the eastern portion of Pictured Rocks on the Kingston Plains is now open grassland with only a scattering of tree cover. The present state being the result of exploitative logging and repeated wild fires. Islands in the Apostles which originally supported dense, high quality stands of sugar maple, yellow birch and red oak have been repeatedly high-graded, often burned and now support scattered unmerchantable culls, sprout origin hardwoods and poor quality aspen.

The early history of man's incursions into these two areas began with French explorers in the early 1600's and fur trading in 1659 (Ross 1960). Later, missionaries and more fur traders and the outpost of LaPoint was established on Madeline Island in the Apostles. During the early part of the 19th century, the fur trade declined and commercial fishing activity increased. By the mid-19th century, explorers like Douglass Houghton, Lewis Cass, Henry Schoolcraft, C. S. Jackson and Joseph Norwood had arrived. They made observations and wrote descriptions of portions of both areas. Surveyors arrived during this time to establish the township and section lines and to describe the physical features of the land.

### *The Original Survey and Surveyors*

Several methods can be used to help reconstruct original forest. These include inference based on existing present-day forests, examiniation of old growth remnants, historical accounts and records of early land surveyors (Daubenmire 1968). Original surveyor's records have been used by many researchers to help construct vegetation maps (Kenoyer 1933; Elliott 1953; Potzger et al. 1956; Lindsey et al. 1965). They have been the most commonly used method of reconstructing early forests (Bromley 1935). They possess the special advantage of having been written on the spot according to a previously determined plan and constitute a definite sample of the vegetation (Bourdo 1956).

The township lines of Pictures Rocks were established by William Burt in 1841. Burt was Michigan's master surveyor and inventor of the solar compass (Chope 1976; Stewart 1935). He is recognized for accuracy and completeness of his surveys and descriptions (Bourdo 1954; Laapala 1974). He was particularly concerned with his crew's accuracy in addition to his own. Once he found fraud by one of his crews, and resurveyed alone seven townships on his own time and expense (Bourdo 1954).

Fellow surveyors of the time were equally impressed with Burt. William Ives wrote of Burt's knowledge of surveying, completeness of his work and dedication to his job while often working under very difficult circumstances (Ives 1850).

William Ives and George Adair established the interior section lines at Pictured Rocks between 1850 and 1855. Ives had previously worked with Burt and displayed much the same skill in surveying

and ability to write detailed descriptions of his observations. Like Burt, Ives was an exceedingly conscientious field man and often wrote more than was required. Ives has been described in Hubbard (1898) by Lane ". . . I cannot let Ives' name go by without special note of the fine character of the work he did. Working far from civilization, through an extremely rough and densely wooded country . . . he turned out work far surpassing that customary on the linear survey . . .." In addition to his survey records, Ives kept a personal diary which has given us a closer look at his personality. Both men did work of the highest quality and much of what they wrote is valuable historical information.

George Adair was also noted for good quality field work at Pictured Rocks. Apparently, his close association with Ives resulted in his conscientious recording of field data and detailed descriptions of the area's physical features.

The township and section lines of the lands within the Apostle Islands Lakeshore were surveyed during 1852 and 1857 by three separate surveyors; J. Allen Barber, Elward L. Baker and Elisha L. Norris. Very little written information exists on these men compared to that of the Pictured Rocks surveyors. An insight into their personalities must be made through an analysis of their written survey descriptions and comparing them with the work of men like Burt and Ives.

Land subdivision techniques today are well standardized but during the period when Pictured Rocks and the Apostle Islands were surveyed, the instructions for surveyors changed (Stewart 1935). The instructions for 1855 were the guide book for practically all surveys until the end of the contract system in 1910 (Dodds 1943). The major differences between instructions of the 1840's and those of 1855 were in the amount of details required and the manner in which they were recorded. All instructions specified that four bearing trees be recorded both at townshop corners and at section corners on township and range lines. The diameter of each bearing tree was estimated and distance to the corner recorded. Each tree was blazed facing the corner, and scribed with the letters "B.T".

Early instructions specified that bearing trees at quarter corners were to be located in adjacent quadrants, while later instructions specified they be in opposite quadrants.

At Pictured Rocks, Ives and Adair recorded four bearing trees at interior section corners in addition to those on township and range lines. At Apostle Islands only two trees were recorded at interior corners.

The instructions of 1843 and 1850 stipulated that at least one or two trees directly intersected by a survey line be designated as line trees and be recorded as to species, estimated diameter, and exact distance between every two corners. Instructions of other years stipulated that *all* trees which the line intersected be recorded. Line trees were double blazed, one blaze directly above the other. The Apostle Island surveyors failed to record any line trees. At Pictured Rocks usually two to four were recorded on each section line.

The recording of other details by the surveyors is quite interesting and has been useful in our delineation of the presettlement vegetation reconstruction. Major changes in cover types were reorded and chainages given. Also, understory shrubs and herbs were sometimes recorded. At each section corner, tree species were recorded in order of their prevalence on the preceding section line. Very complete information of this type was recorded for Pictured Rocks while at the Apostle Islands, the surveyors evidently had limited knowledge of forest vegetation and their notes reflect this.

While establishing lines, surveyors were required to record major changes in topography, soils, line intersections with lakes, streams, and marshes and the incidence of windfalls. They also were required to estimate the size of these latter features and their distance to the corner. Again, descriptions for Pictured Rocks show a very complete and detailed record while there were obvious omissions at the Apostle Islands. Several instances of streams, lakes and marshes not being recorded were found on the western half of Outer Island and Stockton Island.

When the survey of a township was completed, the surveyor was required to draw a plan and write an overall description. The township descriptions for Pictured Rocks were detailed and often contained several paragraphs. In addition to physical descriptive information, personal accounts of the men, their thoughts and experiences were included. Conversely, township description for the Apostle Islands were brief, usually not more than a few sentences. Therefore, on the Apostle Islands, we placed more emphasis on bearing trees in our work of reconstructing the original forests.

A number of variables will influence the validity and usefulness of any given survey for delineating vegetation types. Bourdo (1956) has described in detail variables contributing to errors in type map construction from original notes and how one could determine any bias.[4]

Even though disadvantages exist, many of the original surveyors produced accurate and detailed work and it constitutes by far the best record we have of original vegetation types. Other methods such as memories of persons familiar with the area are frequently inaccurate due to lack of scientific training. Only records written down shortly after observation can be trusted and in some instances these must be interpreted in terms of the background and personality of the writer at the time (Duabenmire 1968). Although true randomness is not an attribute of the General Land Office Survey, the survey records do constitute a sample of the vegetation recorded on the spot according to a predetermined plan. They constitute a definite sample of the vegetation and thus are usable for quantitative as well as qualitative analysis (Bourdo 1956).

## METHODS

Data were transcribed from the original survey notes of the Pictured Rocks and Apostle Islands which were available on microfilm. U.S. Geological Survey maps and county soil survey maps were used in conjunction with the survey notes for final forest vegetation typing.

From the survey notes, the following information was recorded:

---

[4]Whether bearing and line trees were chosen by the original surveyors without regard to species, conditions, size or other factors and represented a random sample has been considered by other reseachers. Tree attributes such as decay resistance of the wood (witness tree durability), bark smoothness (scribing ease), species commonness (corner relocation made easier), or wood value (probability of being cut in the future) may introduce bias in selecting trees for witnessing corners. Obviously selection of bearing trees was not strictly random. The major concern is not whether bias was present, but whether it would negate the use of survey data for type map construction. There presumably is less problem with line trees for their recording depended strictly on location. However, not all trees falling "on line" were necessarily recorded.

1. The species and diameter of all bearing trees and their direction and distance from all section corners.

2. The species, diameter and location of all line trees.

3. The intersection of all lines with natural or other noted features.

4. The species prevalence on each section line and the intersection of any forest type boundaries.

5. Notes on animal life and evidence of human presence or settlement.

All information was transcribed to blank township sheets at a scale of two inches per mile.

A one-way analysis of variance was used to determine if species or diameter bias was evident for section and quarter corner trees. Each tree witnessing a section or quarter corner constituted one observation from the population. The extent of bias between species and within diameter classes was tested using the Neuman-Keuls method, a variation of the Q-test (Snedcor 1956).

Importance values (Mottam and Curtis 1956) were computed for all species recorded by the surveyors by summing relative density, relative abundance and relative frequency. This was done separately for both lakeshore areas. Each section and quarter corner was considered a sample point for determining relative frequency.

For map placement of forest type line boundaries, the species and number of occurrences of each bearing and line tree for each section line was first listed. For the Apostle Islands, only bearing trees were used because line trees were not recorded during the survey. The product of the importance value and the number of occurrences of each species per section line was calculated. This total was then compared to the list of species in their order of prevalence originally recorded by the surveyors for each section line. With few exceptions the ordering of species on these two lists was similar. Adjacent section lines were similarly inspected and the degree of contagion of bearing and line trees noted. Each type was named on the basis of the dominant species. Dominance was based on the surveyor's species prevalence list for each section line and the product of bearing and line tree occurrences by species and their respective importance values. U.S. Geological Survey maps were then superimposed on the data sheets for elucidating topography, and detailed soils maps consulted before final type line placement was made. Where possible, classification and naming of forest types followed the major cover type classification of the Society of American Foresters (SAF 1940). At Pictured Rocks, seven types were classified according to SAF. Due to the complexity and alternation of dominant species on the mesic sites, four new types were created.

On the Apostle Islands, twelve types were delineated, ten of which followed the SAF, while two were created.

A method was attempted at coding and storing in the computer all information used manually in type line designations. This was done on a trial basis for Pictured Rocks. We are attempting to produce a plotted type map by inputing bearing tree data and calculating importance values and integrating this with soils and topographic information. We hope such a computer generated map will be comparable in accuracy and detail with the hand drafted map.

The present vegetation cover of both areas was determined from existing timber type maps, aerial photographs and ground reconnaissance. For Pictured Rocks some timber maps were available for former Cleveland-Cliffs Iron Company lands now within the Lakeshore boundary. For the Apostle Islands, type map information was available from published sources (Larson 1975; Northland College 1975; Stadnyk et al. 1974), state and federal agencies. Vegetation data collected by Northland College during 1974-75 were also used to construct type maps of several islands. Based upon this information, a generalized comparison was made with the original vegetation.

## RESULTS AND DISCUSSION

From the original surveyor's data and descriptions of the Pictured Rocks and Apostle Islands areas, vegetation type maps of considerable detail were drafted using bearing trees, soils and topographic information. Included on these maps were locations where the surveyors recorded animal sightings, windthrows, natural features and evidence of human presence.

Results of the statistical tests on section and quarter corner trees showed some bias by the surveyors for selecting certain species and diameters. After close inspection, the bias found was expected and not considered critical in this work. For example, small diameter trees (less than 6 inches), intolerant or short-lived species were not chosen as witness trees when other species were available. Other studies have shown preference by surveyors for medium size trees (Bourdo 1956). Exceptionally large, old and defective trees were also avoided where possible.

The attempt at producing a computer generated type map is incomplete. However, the three sets of data including: bearing trees, soils and topographic information were successfully stored in the computer in a form usable for assigning types. A program was also developed that assigns cover types based on importance values to each section and quarter corner. A program to incorporate soils and topographic information with the bearing tree data is still to be completed. However, a program which produces a listing of all three data sets for each section and quarter corner including importance value cover types is complete and can be used to simplify hand calculations.

Large scale exploitation and disturbance of the original forests of both areas began in the 1880's with the logging of the white pine. In the following paper, Dr. Rakestraw will discuss the land use history of the Apostle Islands in detail. Therefore, I will concentrate on the Pictured Rocks area and identify the land use practices which have had the greatest influence on the complexion of the present forest vegetation.

The relative effect of various land use practices at Pictured Rocks has depended on several factors, one of the most important being the site.

Little compositional change has occurred on the bottomland sites. Much of the spruce, fir, cedar and tamarack has been cut only lightly. These areas have generated very well.

The mesic forests have undergone moderate compositional change and reduction in average tree size. High value species such as sugar maple and yellow birch have been cut heavily. Hemlock has also been cut heavily and has suffered from subsequent fires and post logging decadence. Records of cuttings on former Cleveland-Cliffs Iron Company lands in the eastern portion of the Lakeshore show heavy selective cutting beginning in the early 1940's. Approximately 50% of the volumes were removed in the form of merchantable logs and chemical wood. These

cuttings continued on a 10-20 year interval until the Park Service acquired the lands. More clearcut logging was done in the western sections for charcoal wood (Richard Ewalt, pers. comm.).

A major compositional change is presently occurring in the wetter mesic forest areas with the elimination of the American elm by Dutch elm disease (*Ceratocystis ulmi* (Buism.) C. Moreau).

The xeric forest composed of white pine, white pine-red pine and white pine-hemlock types has undergone the greatest change since the original survey. Virtually all the forests of these types has been destroyed. Clearcut logging followed by repeated fires not only eliminated the few remaining uncut trees and logging slash but also destroyed the thin organic layer, exposing the bare sandy soil. Today the area supports mainly grasses, braken fern (*Pteridium aquilinum* (L.) Kuhn.) and a few scattered clumps of aspen, (*Populus tremuloides* Michx.) white birch (*Betula papyrifera* Marsh.) and small pine plantings.

## CONCLUSIONS

By comparing and contrasting the surveyors and the data and descriptions they recorded for these two areas, several factors become apparent. Considerable difference exists between the surveyors of these two areas and the detail of their work. This directly affected the use of these data for reconstructing the original forest vegetation. Although selection of bearing trees by the surveyors was not truly random, the survey records did constitute a vegetation sample recorded according to a previously determined plan.

The value of type maps of any area using original survey notes are contingent upon the preceding factors plus the instructions to the survey crews at the time the survey was done. If researchers acquaint themselves with this information and establish the validity of the data they use, vegetation maps can be produced that are accurate and have several practical uses.

One of the primary values of such maps is their use as an ecological data base for planning and management. By determining the original forest vegetation, a better understanding of the potentials of the area can be realized. Also by comparing the original forests with present conditions, a better understanding can be gained of the influence of natural and man-related disturbances and the local processes of succession. For example, the use of fire as a management tool might be adopted more readily after understanding its natural place in succession on certain sites.

Finally, for these two areas our original vegetation map should be a valuable addition to the interpretive program. Vegetation changes over the last 125 years have often been dramatic. To acquaint the public with this history not only makes them better informed but also allows them to appreciate and understand management decisions made by the Park Service on these public lands.

## BIBLIOGRAPHY


BEALS, E. W., and G. COTTAM. 1960. The forest vegetation of the Apostle Islands, Wisconsin. Ecol. 41:743-751.

BOURDO, E. A. Jr. 1954. A validation of methods used in analyzing original forest cover. Ph.D. Diss. Univ. of Michigan, Ann Arbor, Michigan. 207 pp.

BOURDO, E. A. Jr. 1956. A review of the general land office survey and of its use in quantitative studies of former forests. Ecol. 37:754-768.

BROMLEY, S. W. 1935. The original forest types of southern New England. Ecol. Mono. 5:61-89.

CHOPP, I. E. 1976. William Austin Burt--Surveyor and inventor (1792-1858). Surveying and Mapping 36:249-253.

COTTAM, G, and J. T. CURTIS. 1956. The use of distance measurements in phytosociological sampling. Ecol. 37:351-360.

DAUBENMIRE, R. 1968. Plant Communities: A textbook of synecology. Harper and Row, New York. 300 pp.

DODDS, J. S. 1943. Original instructions governing public land surveys (1815-1955). Powers Press, Ames, Iowa. 215 pp.

ELLIOTT, J. C. 1953. Composition of upland second growth hardwood stands in the tension zone of Michigan as affected by climate and man. Ecol. Mono. 23:271-288.

HUBBARD, L. L. (ed.). 1898. Alfred G. Lane, "Isle Royale" *In*: Geological Survey of Michigan. Vol. VI, p. 4.

IVES, W. 1850. Diary of William Ives. State Historical Collections, Ann Arbor, Michigan.

KENOYER, L. A. 1933. Forest distribution in south western Michigan as interpreted from the original land survey (1826-1832). Mich. Acad. Sci., Arts, and Letters, Papers. 19:107-111.

LARSEN, W. C. 1975. Vegetation ecology of Bear Island--Apostle Islands National Lakeshore. Masters Thesis, Michigan Technological University, Houghton, Michigan, 91 pp.

LAPPALA, D. D. 1974. Retracement and evidence of public land surveys. U.S. Dep. Agr. For. Serv. Rpt. 52 pp.

LINDSEY, A. A., CW. B. CRANKSHAW, and S. A. QUADIR. 1965. Soil relations and distribution map of the vegetation of presettlement Indiana. Bot. Gaz. 126:155-163.

NORTHLAND COLLEGE. 1975. Vegetation surveys of the Apostle Islands. Unpublished data held by Sigurd Olson Instit., Northland Coll., Ashland, Wisc.

POTZGER, J. E., M. E. POTZGER, and J. McCORMICK. 1956. The forest primeval of Indiana as recorded in the original U.S. land surveys and an evaluation of previous interpretations of Indiana vegetation. Butler Univ. Bot. Stud. 13:95-111.

READ, R. H. 1975. Vascular plants of Pictured Rocks National Lakeshore, Alger County, Michigan. Mich. Bot. 14:1-43.

ROSS, H. H. 1960. LaPoint--Village outpost. Edwards Bros. Inc., Ann Arbor, Michigan. 200 pp.

SOCIETY OF AMERICAN FORESTERS: COMMITTEE ON FOREST TYPES. 1940. Forest cover types of the eastern United States. Soc. Amer. For. Washington, D.C. 39 pp.

SNEDECOR, G. W. 1956. Statistical methods. (5th ed.) Iowa State Univ. Press, Ames, Iowa. 534 pp.

STADNYK, L., R. L. VERCH, and B. A. GOETZ. 1974. Stockton Island survey: An ecological survey and environmental study of Stockton Island, Apostle Islands National Lakeshore, Northland Coll. Rpt., 71 pp.

STEWART, L. O. 1935. Public land surveys: history, instructions, methods. Meyers Printing Co., Minneapolis, Mn. 202 pp.

# ORIGINAL FOREST VEGETATION AND LAND USE HISTORY OF THE APOSTLE ISLANDS NATIONAL LAKESHORE[1]

L. Rakestraw,[2] D. J. Frederick, [3] C. R. Eder[3], R. A. Van Dyke,[3] and B. J. Griewe[3]

## INTRODUCTION

In 1930, Harlan Kelsey, a National Park Service Collaborator, made a report on the Apostle Islands. In it he wrote:

> What must have been once a far more striking and characteristic landscape of dark coniferous forest has been obliterated by the ax followed by fire.
>
> This unfortunately is the most universal aspect of the islands themselves as viewed from the water--the virgin forest having been ruthlessly exterminated, mostly within the last 5-20 years. It will probably take 50 to 100 years to reproduce, even in a measure, those wonderful oak and evergreen growths and to restore the original charm and beauty, of this mature primeveal forest. The ecological conditions have been so violently disturbed that probably never can they be more than remotely reproduced...the hand of man has mercilessly and in a measure, irrevokably destroyed their virgin beauty... (Kelsey 1931).

What were the patterns of land use and abuse that called forth Kelsey's comment 45 years ago? To answer this, we must examine the land use of the area from an historical point of view.

The twenty-two Apostle Islands are situated north of Ashland, Wisconsin. The number of islands has changed over the years as Sand and Rock Islands have been destroyed by wind and wave erosion. At the time Captain H. W. Bayfield made his geological survey of the lakes in the 1820's, there were 23 islands (Bayfield, 1829). The islands are composed of red sandstone in roughly parallel beds, with a topsoil of clay and sandy clay. The exposed sandstone is highly susceptible to wave erosion. On the north side of some islands and on the mainland from the National Park Service Headquarters to Bark Point, large sea caves are common. On the southern ends of many islands are rocky and sandy beaches, sometimes enclosing lagoons. The relief of the islands is low and gentle. The highest point, on Oak Island, is 480 feet above lake level (Bayfield 1929; Martin 1965).

Except for Madeline Island, the early history of the Apostle Islands has not been researched. There is ample data on the Indian settlements on Madeline, but little on the other islands. Except for an Indian sugar grove on Oak Island, tangible evidence is lacking that these islands were subject to fishing and food gathering activities (GLO notes, 1852-57). The impact of aboriginal use of the islands was slight, unlike the effects of the Indians' practice of silverculture on the sugar maple groves of Isle Royale (Ives 1847).

Before the land survey period of 1850-57, the first settlement by the white man was limited to Madeline Island. While this island is not part of the National Park System, a brief account of man's settlement and activities there is necessary to place our story in perspective. Settlement began in the late 17th century when a French trading post was established on the southwestern end of the island. A series of other forts, fur trading posts, missions, and dwellings were made in the next century and a half, as the French interests were succeeded by the British fur trading interests. Subsequently the American interests predominated. During the American period, the American Fur Company established a settlement of about 300 people at La Pointe. Between 1837 and 1840, the American Fur Company carried on a large fishing enterprise, that embraced all Lake Superior waters from Whitefish Pond to Grand Portage (Ross, 1960; Rakestraw, 1968).

At the time the surveyors began their work (1852-57), Madeline Island had an area of settlement extending along its western shore, with a series of clearings, pastures, farms, dwellings, warehouses, and churches. A sizeable amount of white and red pine had been cut for construction, fuel, and cooperage. The cutover area had regenerated predominantly to aspen (GLO notes and plates, 1952-57; oss, 1960).

With the exception of three small areas, there was little trace of man's activities on the islands during the 1850's. General Benjamin Armstrong built a house on the southern tip of Oak Island (Armstrong, 1927). The clearing composed about 40 acres (GLO notes and plates, 1852-57). William Wilson built a house and cleared some land on Hermit Island (Ross, 1960). The American Fur Company built a small fishhouse on Stockton Island, near Quarry Bay (GLO notes and plates, 1852-57).

Speculators, promoters, and settlers came with the arrival of the railroad about 1870, and the extension of the lumbering, mining, and fishing frontiers to the area. The cities of Bayfield and Ashland were established, and the islands became the economic hinterland for these booming cities (Chapple, 1973; Chapple, 1974; Burnham 1974). A large variety of promotional and speculative enterprises developed in the area.

A boom period for fisheries began in the 1870's. Successor fisheries to the American Fur Company took over its buildings, warehouses, and cooper ships on Madeline Island. By the 1870's, the railroad reached Chequamegon Bay, and the fish could be shipped fresh as well as salted or smoked to Milwaukee, Chicago, and Minneapolis markets. The cities of Duluth and of Superior were established, and provided venture capital for the fisheries. Fishing became a major

[1]Supported by a National Park Service contract to Michigan Technological University.

[2]Department of Social Sciences, Michigan Technological University, Houghton.

[3]Department of Forestry, Michigan Technological University, Houghton 49931.

occupation at Bayfield. At first gill nets were used, and as time went on, pound nets came into use. The shallow water and sandy bottom were well suited to this type of fishing. In 1885, there were 15 pound net settings along the coastline from Sand River to Bark Point, and Oak, Manitou, Stockton, and Otter Islands all had pound net settings near their shores. In 1886, Bayfield shipped 310,000 pounds of whitefish, 200,000 of Lake trout, 10,000 of sturgeon, 40,000 of herring, and 15,000 of pike. In addition, they smoked or salted 800,000 pounds of whitefish, 305,000 of trout, 31,000 of siskowit, and 10,000 of herring (Smith and Snell, 1891).

The end of the frontier period for fishing came about 1890, with changes both in organization and in technology. The A. Booth Company of Chicago moved to Duluth and came to dominate the fishing industry on Lake Superior. The "hot head" gasoline engine was invented in Duluth in the 1890's and soon gasoline engine boats began to replace the graceful Mackinaw boats. As the Germans and Scandanavians moved into the Midwest, herring fishing became more important. Norwegian, Finn, and Swede-Finns replaced the former French and Indian fishermen (Rakestraw, 1968; Chapple, 1974).

Selections from the *Ashland Press* for 1872 suggest the development of other commercial activities. For example, "Basswood Island is doing things in the brownstone and hemlock exploitation business. Who says that the resources and natural advantages of Lake Superior are not looking up?" (June 22, 1872). On the activities of Mr. Pendergast on Michigan Island: "He has a hennery as well as a nursery, and Michigan Island is prospering." It was noted that he had sold 3,000 fruit trees that year (September 28). William Knight ran a large advertisement for his woodyard on Oak Island: "On the direct channel to Duluth, on Oak Island, and a large supply of dry hard and hemlock wood is kept on hand" (October 12).

Quarrying on the islands lasted from about 1870 to 1900. Four quarries were established for obtaining the fine brownstone found on the islands. Two of these were located on Basswood Island, a short-lived one owned by John C. Breckinridge, a Kentuckian who had served as Vice-President under Buchanan; and a larger one, owned by Milwaukee interests, the larger quarry operated from 1869 to 1893. They combined cutting of hemlock for bark with quarrying. On Hermit Island, Frederic Prentice in 1891 established a large operation with 100 men employed. This quarry closed operations about the turn of the century. On Stockton Island in 1889 the Michigan Company established a large operation which ceased operations about 1900. These quarries ceased operating because of business and financial problems, increased use of steel girders for city construction, and the growing demand for the light-colored Bedford sandstone which lessened the demand for the dark stone from these island quarries (Buckley, 1896).

The Apostle Islands were exploited for a variety of types of timber after 1870. Early cutting included the harvesting of hemlock bark for tanneries, the cutting of fuel for steamboats, the use of pine and oak for fish barrels, and the clearing of forest lands to make room for gardens. About 1880, the search for white pine began. The islands were systematically logged for pine and most of the merchantable pine had been cut by 1900 (Roth, 1898; Lumber Inspector Records, 1890-1908). This was the era of animal logging and log rafting (Roth, 1898; Wisconsin Lumber Inspector Records, 1891-1898).

After the white pine was logged off, the search for Northern hardwoods and hemlock continued and tractor logging replaced animal power. One operator was John Schroeder, who also brought in timber from the north shore and later rafted pulpwood. Schroeder conducted railroad logging on Outer Island and Michigan Island during the 1920's (Wisconsin Lumber Inspector Records, 1891-1908; Wisconsin DNR Files, 1959-70; Apostle Islands, 1970). Since hardwood logs do not float well, barges were used to take logs to the mainland. After World War II, war surplus landing craft were used. Most of the large mills at Ashland and Bayfield were closed by this time and many of the logs were railed to more distant mills.

Tourism and home building began on the islands on a large scale after 1870. Excursions by railroads and boat lines brought vacationers. Large hotels were built in Ashland and Bayfield (Burnham, 1974; Chapple, 1974). Excursion boats took visitors to the outlying islands, and Madeline Island became the home of nabobs from the Midwest and East (Ross, 1960). In 1886, Sam Fifield established a summer camp, and later lodge, on Sand Island. Subsequently, other private homes were built on the island. With the rise in value of lake property and the general prosperity of the period after World War II, many of the islands came into private ownership. After the lights were automated, lighthouse buildings were often leased or bought (Chapple, 1973).

How have these multitude of activities affected the islands and their vegetation over the past 125 years? The question may be answered first in general terms, and then in relation to specific groups of islands.

1. *Fishing*. Every island, including tiny Gull Island, has been occupied at one time or another by fishermen. For the most part they were seasonal visitors, coming in the spring and leaving in the winter. There were some exceptions to this as both Sand and Rocky Island had year round resident fishermen for many years (Chapple, 1973). Fishermen built cabins, constructed docks, wharves, warehouses and storage houses for their nets, using local woods. They cut wood for fuel, but probably relied a great deal on driftwood or logs escaped from log rafts. Poles were cut for pound net settings. Most fishermen had vegetable or flower gardens, fertilized by fish offal. These activities were limited in extent, however, and were located on the outer periphery of the islands.

2. *Lighthouses*. Five lighthouses were established on the Apostle Islands: Michigan Island (1857); Raspberry (1862); Outer (1874); Sand (1881); and Devil's (1891). Areas of the individual lighthouse reservations varied from two to 16 acres; a total of about 34 acres was taken up by these reservations. Like the fishermen's establishments, these were small, local disturbances (Lighthouse Clipping Files, National Archives).

3. *Quarrying*. The quarrying on Basswood, Hermit, and Stockton Islands had extensive effects on the vegetation. Quarrying involves clearing

vegetation, removing the overburden, and cutting out the rock beds, thereby disturbing the drainage and altering site stability. It involved building roads, wharves, warehouses, smithys, houses for workers, barns for draft animals, and vegetable gardens for the crew. These activities had profound effects on fairly extensive areas along the edges of Hermit, Basswood, and Stockton Islands.

4. *Agriculture.* Agriculture was common on many of the islands, but this practice had a minor disturbance effect due to the small acreages involved. An exception to this was the agricultural activities on Sand Island which were extensive and of prime importance.

5. *Lumbering.* Lumbering has had the most profound effect on the islands. The logger searched the islands systematically for pine and hemlock, then northern hardwoods. By 1931, Arno Cammerer, Associate Director of the National Park Service, could report that there were no longer any virgin stands of timber on any of the islands except Outer Island, which was then in the process of being logged off (Cammerer, 1931). Effects of this logging depended on several factors: the site characteristics, type of stand, type of cutting, whether fire followed the operation, and whether the land was later used for agriculture. Fire generally followed the white pine logging on most of the islands. The more xeric sites have regenerated back to some pine, but mostly aspen, paper birch and tolerant conifers. The mixed hardwood-pine and hemlock stands have reverted to Northern hardwoods, aspen and paper birch. Hardwood logging was a high-grading proposition, with the best quality sugar maple, yellow birch and other species removed. The result is scattered relics of the original stand and poor quality second growth.

One additional aspect of the disturbance history should be mentioned. With these activities, exotic plants were often introduced to the islands. Apple trees are still found on some old agricultural sites. In the era of animal logging, grain and hay were brought to the island as fodder. Seeds from these germinated, and often flourished. Harlan Kelsey, in 1930, followed a logging road on one of the islands and came to a clearing. There he found timothy four to five feet high, red clover and red top three to four feet high, and white clover two feet high (Kelsey, 1930).

Some additional examples of the land use history may be cited by examining specific islands or groups of islands.

Sand Island may be classified by itself, since it is the only island that has had continuous occupancy for nearly a century. A Norwegian fishermen settled on the island in 1870, and later farmed. In 1886 and in 1910, resorts were set up -- one at the southeastern end of the Island and the other at West Bay. Other farmers and fishermen came to the Island; roads were built, a post office established, and a telephone line run to the mainland. A great deal of land was cleared for gardens and pasture, and we have records of some fires.

The Island was logged before 1898, again in 1906, probably removing all the white pine. It was logged again in the 1940's for hardwoods, and again in the 1970's. It is now a complex of abandoned fields and forests composed largely of mixed Northern hardwoods, aspen and paper birch. Some soil erosion has been caused by tractor skidding during the most recent operations.

Stockton and Oak Islands had a similar history of exploitation. Oak was a steamboat landing, later exploited for pine, and in the 1920's was heavily cut over for hemlock and hardwoods. It was burned over in 1943. Stockton was cut over for pine in the 1890's, had a quarrying operation during the same decade, and was cut over for hardwoods at a later period. An extensive fire swept the south shore in 1929 or 1930. Since 1959, both islands have been under protection as part of a State Forest, and some recovery from this past history has occurred. A cruise of Oak Island in the 1960's indicated only about three million board feet of merchantable hardwoods on the Island. This low volume reflects the past high grade type cuttings.

Hermit and Basswood are both medium-sized islands with a common history of quarrying activity. This activity has shaped the southern half of both islands. Both had extensive gardening activity, and apple trees are still found on Hermit Island. Both were cut over for white pine, hemlock, and hardwoods. Field examination of Basswood revealed a great deal of pulpwood cut, corded, and left in the woods. Today there is very little high quality timber on either island.

Michigan and Outer Islands have a common history of being logged by railroad in the 1920's. Highgrade logging with conventional equipment has followed several times since then. Outer also had devastating fires in 1930. The present forests consist of scattered sawtimber size culls and young sapling and pole size Northern hardwoods, aspen and paper birch. Cedar, balsam fir, and spruce are common understory species.

The other islands show a similar history of exploitation and change in vegetation types after logging. Cat Island is a typical example. Originally called Hemlock Island because of its large stands of hemlock, it was purchased by Frederic Prentice in 1887 for its hemlock, pine, and cedar. It was logged and relogged. At present, hemlock is no longer an important species; the dominant species are young Northern hardwoods, with some cedar and balsam fir in the understory.

As Kelsey noted in 1930, remarkable and far reaching changes had occurred. In some instances, even greater changes have occurred since then. This historical and ecological background can be the subject of many specialized studies by the historian, and as background for future ecological studies.

## BIBLIOGRAPHY


APOSTLE ISLANDS NATIONAL LAKESHORE, 1970. Hearings: Parts I and II. Washington, D. C.

ARMSTRONG, B. G. 1927. Reminiscenses of life among the Chippewa, Part 2. Wisconsin Magazine of History, SS. 4 pp. 287.

BAYFIELD, H. W. 1829. Outlines of the geology of Lake Superior. Trans. of the Literary and Hist. Soc. at Quebec, Vol. 1, pp. 1-43.

BUCKLEY, E. R. 1896. On the building and ornamental stones of Wisconsin. Wisc. Geol. Surv. Bull. 10, Madison, Wisconsin.

BURNHAM, G. M. 1974. The Lake Superior country in history and in story. Ashland, Wisconsin 464 pp.

CAMMERER,A. 1931. Apostle Islands. *In*: Proposed National Monuments, Apostle Islands, RG 48, National Archives, Washington, D.C.

CHAPPLE, J. C. 1973. Apostle Islands source book. Ashland, Wisconsin. 8 p.

CHAPPLE, J. C. 1974. Ashland County, Wisconsin, Ashland, Wisconsin.

GENERAL LAND OFFICE SURVEY NOTES AND PLATES, Apostle Islands, 1852-57. National Archives, RG 48.

IVES, W. 1847. Survey notes of William Ives, General Land Office Survey. State Historical Collections, Ann Arbor, Michigan.

KELSEY, H. 1931. Report on the Apostle Islands National Park project, January 31, 1931. *In*: Proposed National Monuments, Apostle Islands, RG 48, National Archives, Washington, D.C.

LIGHTHOUSE CLIPPING FILE, no date. RG 26, National Archives, Washington, D.C. copies at NPS Hdqtr., Apostle Islands National Lakeshore, Bayfield, Wisconsin.

MARTIN, L. 1965. The physical geography of Wisconsin. Madison, Wisconsin pp. 446-478.

RAKESTRAW, L. 1968. Commercial fishing of Isle Royale. Report to the National Park Service, Houghton, Michigan.

ROSS, H. 1960. LaPointe: Village outpost. Edwards Brothers, Ann Arbor, Michigan, 200 pp.

ROTH, F. 1898. Forestry conditions and interests of Wisconsin. Wisc. Geol. and Nat. Hist. Survey Bull. No. 1.

SMITH, H. M., and M. Snell. 1891. A report of the fisheries of the Great Lakes in 1885, *In*: Report of the commissioner of fish and fisheries, 1887, House Misc. Document 133, 50th Congress, 2nd Session, Washington, D.C. pp. 31-70.

WISCONSIN, DNR FILES, 1959-70. Wisc. State Hist. Soc. Univ. of Wisc., Madison.

WISCONSIN LUMBER INSPECTIONS RECORDS, 1891-1908. Wisc. State Hist. Soc. Univ. of Wisc., Madison.

# ECOLOGY OF THE SAND VEGETATION OF THE APOSTLE ISLANDS[1]

Carol A. Jefferson[2]

## INTRODUCTION

The Apostle Islands, covering 77 square miles, form an archipelago of 22 islands in Lake Superior. They consist of glacial till and Pleistocene red clays overlying ancient sandstones. Sandy beaches, spits, tombolos and cuspate forelands are of more recent lacustrine origin. Adjacent lies the Bayfield Peninsula, with a 10-15 mile sand covered ridge, the Bayfield Hills, which forms the northern terminus of the Wisconsin pine barrens. The dominant vegetation of the wilderness islands is second-growth mixed deciduous-conifer forests with relict stands of *Tsuga canadensis, Betula lutea, Pinus strobus* and *Abies balsamifera - Picea glauca*. Parallel ridges and runnels, with the runnels filled with wetlands, typify the sand regions.

Previous research on the sand vegetation of the Apostles has been minimal. Curtis (1959) listed the species of beach and dune communities based on two locations in this area, also noting their marked difference from dune vegetation along Lake Michigan. Murphy (1931) discussed the geography of the northwest Wisconsin pine barrens, commenting specifically on the open nature of the barrens and how fire exclusion probably resulted in dense growth of *Pinus banksiana*. Buss (1956) examined the plant succession on a sand plain in northwestern Wisconsin. Concurrent with this present study, Barbara Coffin studied the geomorphology and vegetational development of the Stockton Island tombolo. Results of her study are described elsewhere in these proceedings. An 1872 map of the LaPointe Light Station on Long Island indicates that the vegetation is a forest of stunted, scattered *Pinus banksiana*, interrupted by narrow marshes--vegetation similar to that occurring on Long Island today.

Vegetational disturbances include selective logging for *Pinus strobus* and *P. resinosa*, deer browsing, fire and settlement. Today only Madeline Island has permanent residents, but both Stockton and Long Islands were seasonally occupied by Indians who fished and gathered berries (Ross, 1960). Presumably the Indians burned the woods, as they did on the peninsula (Murphy, 1931), to enhance *Vaccinium* production. Selective logging for pines occurred intermittantly between 1870 and the 1940's on spits on the islands and peninsula. Nearly every site visited showed evidence of logging and subsequent burns. Deer are present on several of the islands; their most visible impact is the elimination of *Taxus canadensis*, which is preferentially browsed (Beals, 1958).

The purpose of this study was to identify upland and wetland plant communities on sandy substrates in the Apostle Islands and to determine the successional development and status of the vegetation. An ecological understanding of these fragile areas may aid personnel of the Apostle Islands National Lakeshore in locating and managing recreation areas and campsites.

## METHODS

During the summers of 1975-1976, 27 stands and five line transects were sampled for plant species cover. Stands had homogeneous vegetation and were generally in excess of four acres. Ground cover vegetation was recorded in 28, 20 x 50 cm plots, shrubs in one 25/5m plot, and trees in one 25 x 15m plot per stand. In each stand the largest representative of each dominant tree species was aged by counting growth rings. Depth of the humus in the soil was also recorded. The point-quarter method was used to sample along transects.

An importance value equaling one half of the average percent cover and frequency of each species in each stand was calculated. Stands were then synthesized into communities by the relevé method. Finally an ordination of communities by floristic values and soil development was executed End points for the floristic axis represented communities on the most xeric and hydric sites.

## RESULTS

Seven upland and five wetland communities resulted from the relevé sorting: *Ammophila breviligulata; Pinus banksiana/Vaccinium* sp./ *Cladonia* sp.; *Pinus resinosa; Quercus borealis/ Vaccinium* sp. - *Pteridium aquilinum/Danthonia spicata; (Tsuga canadensis) - (Betula lutea)/Taxus canadensis; Abies balsamifera; Picea mariana; Potamogeton* sp. (pond); *Juncus* sp. (marsh); *Alnus rugosa/Chamaedaphne calcyculata/Sphagnum* sp.; *Larix laricinia/Betula pumila/Sphagnum* sp.; and *Myrica gale/Juncus* sp. (a deflation plain).

Table 1 lists the species present in the communities with importance values in excess of 20. These data indicate that the *Pinus and Quercus* dominated communities are closely related floristically, as are the *Alnus and Myrica* wetlands. The most important factors dictating community composition of the wetlands is probably saturated soils and *Sphagnum*. The *Pinus and Quercus* communities are both open woods on ridge tops with well drained sands and little humus accumulation. The *Abies* community was in all cases 30 years old or less and occupied openings in the *Tsuga-Betula* forests and *Pinus resinosa* stands. With *Acer rubrum, Abies* invades non-reproducing *Pinus banksiana/Vaccinium/Cladonia* woods, in the absence of recent fire and/or heavy growth of *Pteridium*. The presence of occasional mature *Pinus strobus* trees, many saplings, and frequent stumps, indicates that this species may be codominant with *P. banksiana* in unlogged forests. Each of the forest communities may be invaded by *Sphagnum*, accompanied by elevated water tables, resulting in a raised bog moving up the edge of old dunes.

The ridge and runnel system of sand deposition provides a template for studying succession, because the ridges parallel to the lake shore and at distal ends of spits are the youngest geologically.

[1]This study was supported in part by Sigma Xi, the National Scientific Research Society.

[2]Department of Biology, Winona State University, Winona, Minnesota.

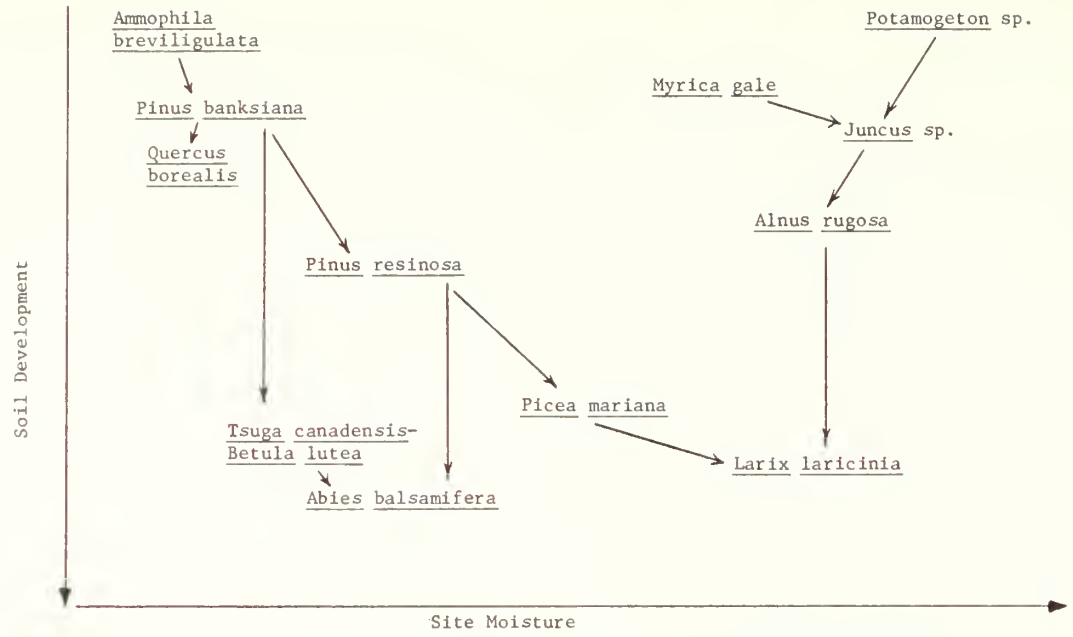



FIGURE 1. Sand plant community succession, Apostle Islands. (Communities designated by dominant species.)

Thus transects running across and along the dune system follow historical vegetational development, aside from perturbations. The patterns of development in the tombolos are more complex. Figure 1 shows succession patterns derived from the transect data, combined with the results of the floristic-edaphic ordination.

## DISCUSSION

Vegetational variations between the peninsula and the islands and among the islands can be attributed to three factors, the presence of deer, human activity, and the time of formation of the sand landforms, modified by climatic changes and the ability of the species to disperse.

The effects of deer on forest vegetation of the Apostle Islands has been extensively discussed by Beals (1958) and Beals and Cottom (1960). The deer on Otter, Cat, Stockton, Hermit and Madeline islands have virtually eliminated *Taxus canadensis*.

Logging and fires have kept *Pinus* woods on spits in the islands and on the peninsula in an early successional state. However, recent efforts to control fires on Madeline, Sand and Stockton islands seems to have resulted in the reduction of *Pinus banksiana* and upland *Picea mariana* regeneration, and increased colonization of *Acer rubrum* and *Abies*. Fires have been suppressed on Long, Michigan and Raspberry islands by Light Station personnel since the late 1800's. A couple of years ago fire burned the dune vegetation on the east side of Stockton Island, severely reducing the populations of *Juniperus communis, Pinus strobus* and *Vaccinium,* which are making little or no comeback. In the pine barrens region of the peninsula, wild fires have been restrained since the establishment of Chequamegon National Forest in the 1930's, with a resultant forestation by dense, uniformly aged stands of *P. banksiana* (Curtis, 1959).

Logging severely decimated stands of *Pinus strobus* and *P. resinosa,* so that only a few, isolated stands of mature pines remain. Dating of many pines by annual ring counts show that the pines are either 100, 60 or 30 years old, thus indicating the dates of logging. *Pinus strobus* regeneration seems to be the best on the sites with less humus accumulation, where *P. resinosa* is regenerating better.

*Quercus borealis* occurs in abundance only on spits of the peninsula and on Madeline and Long Islands. All of these areas were sites of permanent Indian habitation, thus the oaks may have been originally planted for acorn production. On Outer, Michigan and Stockton islands each of the solitary oak trees growing on the sand is in close proximity to twentieth century fishing camps, and the trees are all less than 60 years old. Such individuals may have been planted or accidentally transported by man.

On the other hand, *Quercus* distribution may reflect its inability to disperse to sand regions on the off shore islands in the time period that the sand areas have been habitable for plants.

Probably the most important determinant of forest and wetland communities is the age of formation and colonization of the sand features. Abandoned lake shores, benches and beaches have been documented on the Bayfield Peninsula (Cahow, 1971) and presumably similar features occur in the islands. The last continental glaciers retreated from this region about 11,500 years ago. During the peak of the Wisconsin, Glacial Lake Duluth rose to 1085 feet above sea level, covering all of the Apostle Islands and much of the Bayfield Peninsula, except the Bayfield Hills. Ten thousand years ago, Glacial Lake Minong occupied the present basin of Lake Superior, but water levels were at 450 feet, 248 feet below present lake levels (Farrand, 1969). Since that time the earth

TABLE 1. Community composition, species importance values >20. (Communities indicated by dominant species.)

| | Ammophila | Pinus banksiana | Quercus | Pinus resinosa | Tsuga-Betula | Abies | Picea | Larix | Alnus | Myrica | Juncus | Potamogeton |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Betula papyrifera | | | | | | + | + | | | | | |
| Abies balsamifera | | | | + | + | + | | | | | | |
| Pinus resinosa | | | | + | | | | | | | | |
| Picea mariana | | | | | | | + | | | | | |
| Amelanchier sp. | | | | + | | | | | | | | |
| Pinus strobus | | + | + | | | | | | | | | |
| Betula lutea | | | | | + | | | | | | | |
| Tsuga canadensis | | | | | | | | | | | | |
| Acer rubrum | | | + | | | | | | | | | |
| Acer spicatum | | | | | | | | | | | | |
| Pinus banksiana | | + | + | | | | | | | | | |
| Quercus borealis | | | | | | | | | | | | |
| Picea glauca | | | | | | + | | | | | | |
| Juniperus communis | | + | | | | | | | | | | |
| Taxus canadensis | | | | | | | | | | | | |
| Larix laricinia | | | | | | | | + | | | | |
| Betula pumila | | | | | | | | + | | | | |
| Alnus rugosa | | | | | | | | + | + | + | | |
| Myrica gale | | | | | | | | | + | + | | |
| Chamaedaphne calyculata | | | | | | | | + | + | | | |
| Salix humilis | | | | | | | | | | + | | |
| Salix interior | | | | | | | | | | + | | |
| Salix lucida | | | | | | | | | | + | | |
| Cladonia sp. | | + | | + | | | | | | | | |
| Hudsonia tomentosa | | + | | | | | | | | | | |
| Commandra richardsonia | | + | | + | | | | | | | | |
| Vaccinium sp. | | + | + | + | | | | | | | | |
| Gautheria procumbens | | + | + | + | | | | | | | | |
| Gaylussacia baccata | | | + | + | | | | | | | | |
| Melampyrum lineare | | + | + | + | | | | | | | | |
| Danthonia spicata | | + | + | + | | | | | | | | |
| Arctostaphylos uva-ursi | | | + | + | | | | | | | | |
| Maianthemum canadense | | + | + | + | + | | | | | | | |
| Pteridium aquilinum | | | + | + | | | | | | | | |
| Epigea repens | | + | + | + | | | | | | | | |
| Clintonia borealis | | + | + | + | | | | | | | | |
| Trientalis borealis | | + | + | + | | | | | | | | |
| Cornus canadensis | | | + | | | | | | | | | |
| Deschampsia flexuosa | | + | | | | | | | | | | |
| Ammophila breviligulata | + | | | | | | | | | | | |
| Lathyrus maritimus | + | | | | | | | | | | | |
| Artemesia caudata | + | | | | | | | | | | | |
| Sphagnum sp. | | | | | | | | + | | | | |
| Juncus effusis | | | | | | | | | + | + | + | |
| Hieracium aurantiacum | | | | | | | | | | + | | |
| Carex rostrata | | | | | | | | | + | + | | |
| Calla palustris | | | | | | | | + | | | | |
| Carex lasiocarpa | | | | | | | | + | | | | |
| Vaccinium oxycoccus | | | | | | | | + | | | | |
| Juncus gerardi | | | | | | | | | | | + | |
| Scirpus validus | | | | | | | | | | | + | |
| Juncus canadensis | | | | | | | | | | | + | |
| Equisetum arvense | | | | | | | | | | + | | |
| Oenanthera biennis | + | | | | | | | | | | | |
| Potamogeton illinoensis | | | | | | | | | | | | + |
| Potamogeton natans | | | | | | | | | | | | + |
| Nuphar variegatum | | | | | | | | | | | | + |
| Brasenia schreberi | | | | | | | | | | | | + |
| Utricularia intermedia | | | | | | | | | | | | + |

has slowly rebounded, and new shoreline sand deposits undoubtedly developed with the falling, and later, rising lake levels.

A study of the present lake depths among the islands indicates that when the lake was 150 feet shallower, the islands were interconnected in three clusters, with Outer, Michigan and Stockton islands isolated by themselves. The clusters consisted of Chequamegon Point - Long Island - Madeline Island; Basswood - Hermit - Oak - Otter - Rocky - Devil's - North Twin - South Twin - Cat - Bear - Raspberry - Sand - York - Eagle islands and the peninsula; and Manitou Island - Ironwood Island. This depth was chosen because inter-island similarities in sand vegetation closely follow these clusters and because the lake may have been at this level by the time the climate had warmed enough to support vegetation similar to today. Even during the lake's lowest post-Pleistocene level, Michigan Island probably was not connected to the rest of the islands.

Despite the limitations of this analytic method, these postulated island clusters and isolations may account for the presence of *Chimaphilia umbellata* on Long Island, the peninsula and Outer Island; *Quercus* on Long Island, Madeline Island and the peninsula, and the absence of *Pinus banksiana, Picea mariana,* and *Larix* on Michigan Island. The wetland vegetation on the islands is more homogeneous than the forests, except that the diversity of strand line plants decreases with the distance from the peninsula.

Older deposits seem to be indicated by a red, coarse grained sand, with a deep humus layer, forested by *Tsuga-Betula* and *Abies* communities, while the adjacent depressions are bogs. These deposits occur on the inner edge of cuspate forelands and tombolos, and were probably formed from exposed sand flats that blew inland, forming dunes, as the lake level dropped. The dunes were later stabilized by plants as the climate warmed, perhaps 4000-5000 years ago.

To gain a precise picture of the rates of deposition and colonization of the sand, dating of bog sediments and determination of historical lake levels will be necessary.

A comparison of forest and wetland plant communities of the Apostle Islands to similar communities in northern Wisconsin, as described by Curtis (1959) and others, indicates that the island communities have lower species diversity, especially in hepatics and deciduous trees. The island region is at the northwest limit of the continuous *Tsuga* forest and several of its species. Curtis (1959) noted that, as in the islands, *Abies* invades openings in *Tsuga* and *Pinus strobus* forests occupying rich soils. Wetland communities of the islands are lower in species diversity.

The most striking difference between the sand vegetation of the Apostle Islands and northern Wisconsin is the lack of *Myrica asplenifolia* as a dominant shrub in the pine barrens. This species does not occur on the islands, nor occurs on any peninsula spits, although it is abundant only 5-10 miles inland. The explanation for this distribution may be lack of a micronutrient or symbiont. *M. asplenifolia* is a nodulated nitrogen fixer, as is *M. gale* which is abundant on deflation plains and the edges of bogs in the islands. Levy's (1970) list of plant species in the openings in the sand barrens has 74% of the prevalent species in common with the *Pinus, Quercus* and *Ammophila* communities in the islands.

## CONCLUSION

This study indicates that the sand vegetation of the Apostle Islands is similar to vegetation elsewhere in northern Wisconsin, but has fewer species. Discontinuities in species distribution between the islands may be the result of historical connections and barriers. Seven upland and five wetland communities were identified, with upland vegetation culminating in *Tsuga canadensis-Betula lutea* or *Abies balsamifera* forests, and wetlands becoming *Sphagnum* bogs.

## LITERATURE CITED


BEALS, E. 1958. The phytosociology of the Apostle Islands and the influence of deer on the vegetation. M.S. Thesis, University of Wisconsin, Madison.

BEALS, E. and GRANT COTTOM. 1960. The forest vegetation of the Apostle Islands, Wisconsin. Ecology 41:743-751.

BUSS, I. O. 1956. Plant succession on a sand plain, northwest Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. 45:11-20.

CAHOW, A. C. 1971. Abandoned shorelines and related geomorphic features of Bayfield County, Wisconsin. M.S. Thesis, Michigan State University.

CURTIS, JOHN T. 1959. The vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press, Madison. 657 p.

FARRAND, WILLIAM R. 1969. The Quaternary history of Lake Superior. Proceedings of the 12th Annual Conference on Great Lakes Research. pp. 181-197.

LEVY, GERALD. 1970. The phytosociology of northern Wisconsin upland openings. Amer. Midland Natar. 83:213-237.

MURPHY, R. E. 1931. Geography of the northwest pine barrens of Wisconsin. Trans. Wis. Acad. Sco. Arts Lett. 45:11-20.

ROSS, HAMILTON H. 1960. LaPointe--village outpost. University of Michigan Press, Ann Arbor. 200 p.

# PLANT DISTRIBUTION IN RELATION TO GEOMORPHIC PROCESSES ON PRESQUE ISLE TOMBOLO, STOCKTON ISLAND, LAKE SUPERIOR

Barbara Ann Coffin[1]

## ABSTRACT

The origin of the ridges and troughs that form a double tombolo, two bars of sand joining Presque Isle Point to the main body of Stockton Island, in the Apostle Islands region of western Lake Superior is related to the history of water level, currents, and wind. The inception of the Presque Isle tombolo began approximately 5500 years ago, as the lake level began to retreat from the Lake Nipissing stage, 185.3 m (608 ft) above sea level. A series of parallel ridges were formed as the water level lowered, culminating with a final barrier beach formed on the northeast shoreline of the tombolo. This outer beach is identified as an Algoma beach formed between 3200 and 2500 B.P. Sediment and radiocarbon analyses support this interpretation.

The diverse topography of the tombolo provides habitats for distinct vegetation communities. Four different topographic zones were identified: active dunes, interdune hollows, stabilized dune/beach ridges, and inter-ridge troughs or filled lake basins. Single vegetation plots were studied in the sand dune and bog communities of Presque Isle tombolo according to the Braun-Blanquet relevé system. Relevés were arranged according to species occurrence. Organized in this manner, the relevés fall into three major groups: hydric, mesic, and xeric. Boundaries between adjacent plant communities are visibly distinct, but when tabulated they represent a nearly continuous gradient from hydric to xeric communities. By measure of structure and composition, five different vegetation types are recognized from this gradient: lake dunes, northern conifer forest, northern mixed forest, shrub carr, and open bog.

A combination of topographic zone, vegetation type, moisture status, degree of exposure, and dominant species define twelve major plant communities. Topography and moisture status are key factors influencing the distribution and composition of plant communities. On a broad scale, the age of substrate is not so important as water level in understanding successional relationships on the tombolo. Within each community, cyclic patterns rather than linear patterns characterize successional development.

Presque Isle tombolo demonstrates the dynamic relationship between physical and biotic processes in natural ecosystems.

## INTRODUCTION

Parallel dune and beach ridges separated by linear bogs form a double tombolo, consisting of two bars of sand and gravel joining together what were formerly two islands. The Presque Isle tombolo stretches approximately 2 km between the main body of Stockton Island and the point of Presque Isle (Figs. 1 & 2). Stockton Island is part of the Apostle Islands archipelago, located off the north-central shore of Wisconsin in the western half of the Lake Superior basin. This area of diverse topography displays a heterogeneous array of distinct plant communities, inhabiting a landform created by sediments deposited and rearranged by the interaction of wind, currents, water level fluctuations, and lake ice. Physical and biotic factors create gradients along which species align in a continuum from abundant to absent. This paper demonstrates how geomorphic processes and geologic events continuing since glacial times have interacted dynamically with vegetation development.

## STUDY AREA

Stockton Island is now administered by the National Park Service as part of the Apostle Islands National Lakeshore, established in 1970. Previous to its inclusion within the National Lakeshore, it was administered by the Wisconsin Department of Natural Resources; it was recognized as a unique area of scientific value (Tans & Read 1975).

The Apostle Island National Lakeshore is classified as a recreation area of the National Park Service. Plans for the development and management of Presque Isle Point at this time includes construction of campsites (summer 1976) and maintenance of a trail (already in existence) on the southwest ridge of the tombolo, bordering the lakeshore. On the northwest side of the tombolo there is to be no camping, only foot travel. The wetlands of the area, lagoons and floating bog mats, are so difficult to traverse on foot in summer that their deterioration by visitors is not anticipated. The area is largely inaccessible from the mainland in winter because of shifting ice packs.

It is hoped that further development will not occur. The sandy substrate of the ridges is an easily erodible surface, part of a delicate vegetation-environment system, which under heavy human traffic could be drastically altered. Because it is an unusually well developed example of a double tombolo and supports a unique array of dune, bog, and forest communities, it is of considerable importance in the preservation of ecological diversity and as a study area for investigators and observers of natural history.

## PHYSICAL ENVIRONMENT

To facilitate an accurate understanding of the tombolo formation as the physiographic foundation upon which the existing vegetation has developed, a knowledge of the physical environment is necessary. Specifically relevant to such an understanding is a reconstruction of the glacial geomorphic, and climatic events of the Quaternary. Particular attention is given to the processes directly related to the formation of the Apostle Islands and subsequently Presque Isle tombolo.

[1]Department of Botany, University of Minnesota, St. Paul 55108.

*Geologic history of the Lake Superior basin.*-- The Lake Superior basin is composed mostly of Precambrian rocks, the Jacobsville Sandstone. The basic structure of the basin was formed in Late Precambrian time when folding and faulting created the synclinal structure that exists today. The bedrock exposed in the Apostle Islands is the red quartzose unfossiliferous Bayfield Sandstone (Thwaites 1912). Within the islands, bedrock exposures are generally restricted to the northern and eastern shorelines, where cliffs carved by wave action protrude from beneath a mantle of till and lacustrine clays (Engstrom 1972).

Glaciation during the Pleistocene was a major factor shaping the present-day topography in the Lake Superior basin and adjacent areas. The most recent advance of the continental ice sheet, about 12,000 years ago, covered the entire basin of Lake Superior. As this ice sheet retreated northward a series of lakes was formed from the meltwater. The shorelines cut by these meltwater lakes provide evidence for the reconstruction of the Superior basin lake-level history. Interpreting this evidence is complicated by the following considerations: 1) the effect and extent of post-glacial crustal uplift on the present elevations of past shorelines, 2) positions of "hinge lines", north of which rebound has occurred, 3) submergence by flooding of shorelines south of the "hinge lines", and 4) the elevations of potential outlets utilized by the meltwater lakes during their existence. As evidence on each of these is accumulated through new research, previous hypothetical explanations must be altered to conform.

Study of the glacial history in Lake Superior began as early as 1850 with the expedition of Louis Agassiz. The descriptions by Agassiz were followed by more detailed study of glacial features by Taylor (1894), Leverett (1929), Sharp (1953), and Hough (1958). Farrand's research (1960) on former shorelines has presented the most recent acceptable hypothesis for understanding Quaternary history (Fig. 3). Additional research and radiocarbon dates have since somewhat altered Farrand's original time scale (Lewis 1969, Saarnisto 1975). However, Farrand must be credited with building a framework that can be modified and strengthened as future research dictates.

The western Lake Superior basin was filled with glacial ice for the last time during the Nickerson phase of the Superior Lobe, approximately 12,000 years ago (Wright and Watts 1969). The glacial meltwater lakes first formed following retreat of this ice cover, flowed south through the Moose River and then through the Brule River outlet to the Mississippi River (Fig. 4). With further retreat, lower outlets in the upper peninsula of Michigan were opened, and the water flowed east into the Michigan and Huron basins (Farrand 1960). During this period much of the lacustrine sediments that now cover the islands was probably laid down. The lake level became progressively lower as outlet channels were freed of ice. This trend ended with the low Houghton stage (8000 B.P) when the water level stood only 100 m (360 ft) above mean sea level (MSL). At this time waters from Huron, Michigan, and Superior basins drained northeast through the North Bay outlet to the Ottawa River (Fig. 4). Glacial rebound caused uplift of this principal outlet, and lake levels began to rise, culminating at 185.3 m (608 ft) MSL, the Lake Nipissing stage. It is now believed that the Nipissing high level occurred approximately 5500 years ago, contrary to the traditional date of 4000 years B.P. (Lewis 1969, Saarnisto 1975).

Because of uplift of the North Bay outlet, flow was transfered to the Illinois River outlet and the Port Huron outlet (still in use today between Lakes Huron and Erie), and the lake level again began to fall as these outlets eroded. The lake level fell approximately three meters to the Lake Algoma stage, 182 m (596 ft) MSL, where it stabilized during a halt in the erosion of the Port Huron outlet. Renewed lowering formed the minor Sault stage, with shorelines identified at 178.6 m (586 ft) MSL (Farrand 1960). This trend ceased about 2200 years ago, when glacial rebound caused uplift of the bedrock sill at Sault St. Marie, raising the water level in the Superior basins (Farrand 1969). Rebound has continued, accounting for the gradual rise to the present level of Lake Superior at 193.6 m (602 ft) above sea level (USDC 1976). Since Lake Superior emerged as a separate lake, rebound has progressively elevated the northeast shore, and flooded the shores that lie south of the isobase of zero uplift.

The general topography of the Apostle Islands tells much of how they fit into the glacial history of the Lake Superior basin. The most recent ice sheet moved across the islands in a NE-SW direction, parallel to the long axes of many of the islands and the channels between them. Presumably, old glacial valleys were flooded, and subsequent isolation of high land surfaces, in combination with erosion, formed the islands (Collie 1901). Thus a change in lake level has important implications for the construction or destruction of islands and connections between islands.

*Geomorphology of tombolos.* -- The term tombolo is Italian in origin, describing the classic examples of these features found on the Italian coast (King 1959). Although not a commonly studied feature, tombolos have been described in Italy, the classic Orbetello tombolo (Gulliver 1899), New England (Johnson 1919), and Magdalen Islands, Quebec, and North Cape, New Zealand (Farquhar 1967). Tombolos are created by a combination of factors: longshore currents, beach drifting, winds (here in combination with ice), waves, and water-level change. They are originally formed by the development of a single spit or by the convergence of two or more spits.

The direction of prevailing and storm winds are basic to understanding the origin of a tombolo. The waves (and here ice) are the agents that transmit wind energy into the kinetic energy that builds spits and tombolos. The waves most effective in building underwater bars are those that come from the direction of maximum fetch (Farquhar 1967). Longshore currents, created by waves meeting shorelines obliquely, cause deposition of underwater bars of sand (King 1959). Sediments carried by these currents are deposited at right angles to the direction of dominant on-shore wave action.

The way in which underwater bars emerge to form spits or tombolos is controversial. Johnson (1919) states that wave action alone is capable of building a submerged bar above a water surface of constant elevation. According to Evans (1972), however, subaqueous ridges are not built above a water surface of constant elevation by the work of waves depositing material from the bottom. Lewis (1931, 1932) states that the emergence of spits is the result of deposition by obliquely approaching waves during major storms. The importance of ice action on lake shore is examined by Scott (1926).

He explains the ramparts found on the shores of lakes to be formed in part by "ice-jam", the movement of beach material by ice shoved on shore by wind and wave action. These hypotheses all become of secondary importance if there are major fluctuations in water level. A falling water level will expose previously submerged ridges.

In the case of the Presque Isle tombolo, two separate spits extended from the main body of Stockton Island enclosing a triangular lake (now bog). Convergence of these spits ($S_a$, $S_b$ of Fig. 2) joined Presque Isle Point to the main body of Stockton Island, forming what is described as a double tombolo. Farquhar (1967) states that double tombolos are formed by waves that approach the tied islands at different angles on the lee side. This is in agreement with Engstrom's (1972) findings that cuspate forelands, spits, and tombolos have a preferred orientation in the Apostle Islands, the southern (lee) side of the islands. The Presque Isle tombolo projects southward from the lee shore of Stockton Island. The action of prevailing winds (see Climatology) and particularly storm winds from the northwest and northeast in the fall and from the southwest in the summer can account for the development of two separate spits at this site.

*Climatology.* -- The climate of the Apostle Islands is basically continental, moderated by the presence of Lake Superior. At Ashland, a coastal town 48 km (30 mi) south of Presque Isle Point. Winters are cold with average January temperatures of -10.6°C (13°F), and summers are cool with average July temperatures of 19.4°C (67°F). Average annual precipitation is 70 cm (29 in) (USDC 1974a).

Climate parameters of particular importance to the study of processes involved in tombolo formation, include prevailing wind directions and duration and extent of ice cover. The closest source of compiled wind data is Duluth, Minnesota, approximately 100 km (63 mi) west of Presque Isle (USDC 1974b). Winds of Beaufort force 3 and greater, capable of producing waves of significant dimensions, were extracted from the Duluth statistics. Prevailing winds during the months of May, June, and August are easterly. Beginning in September and continuing through April, and also in July, prevailing winds are from the west and northwest.

Storm winds in the summer are from the west and southwest, and during the autumn from the northeast. The most severe weather occurs during November. In this season the intensely different polar and tropical air masses converge and, assisted by heat energy from the relatively warm unfrozen lake, create cyclonic storms, commonly referred to as "northeasters". Typically these storms begin with winds from the SE (35 to 40 mph, or 56 to 64 kph), later shifting to the NW (72 to 96 kph or 45 to 60 mph), and finally veering into the NE coming straight down the lake parallel to its Minnesota north shore (Loy 1962).

The extent of ice cover is important because of the potential for movement of beach sediments by ice packs. Estimates of ice-cover duration are made from the USDC (1976) and Marshall (1967). Navigation for Ashland harbor is closed on the average from December to April. Marshall's statistics suggest that the duration of ice cover is greater in the channels separating inner islands than those separating outer islands. The northeast side of the Presque Isle tombolo, due to its location in the eastern outer limits of the Apostle Islands, is exposed during most of the winter to the action of wind-driven ice packs.

## VEGETATION

The Apostle Islands and northern Wisconsin are classified as part of the northern-hardwoods forest, described by Kuchler (1964) as tall, broadleaf deciduous forests with an admixture of needleleaf trees. Beal and Cottam (1960), who studied the forests of the Apostle Islands, agree that they contain representative forests of northern Wisconsin but recognize some important differences. Most salient of these is the scarcity of well-drained habitats. Upland areas on the islands usually resemble lowland areas on the mainland. Beal and Cottam (1960) found the dominant trees in the upland forests to be *Betula lutea* (Yellow Birch), *Thuja occidentalis* (Northern White Cedar), *Betula papyrifera* (Paper Birch), and *Acer saccharum* (Sugar Maple). Sand spits when sufficiently elevated above the water table are dominated by *Pinus resinosa* (Red Pine) and *Pinus strobus* (White Pine). The bog communities are typical of northern Wisconsin, dominated by ericaceous shrubs, sedges, and sphagnum moss, and support in some areas a scattered population of *Picea mariana* (Black Spruce) and *Larix laricina* (Tamarack).

A survey of the vegetation of Stockton Island (Annonymous 1974) identifies Yellow Birch-Maple and pure Maple stands as the forest type dominant on the main body of the island. Presque Isle Point, once a separate island, is described as a mesic area of mixed conifer and hardwood species.

The Presque Isle tombolo supports a composite of sand dune and bog communities. The sand-dune communities are found in varying states: actively aggrading dunes and stabilized dunes (supporting either a xerophyllous population of low herbaceous and shrubby plants or covered with a forest canopy). The big communities include a filled lake basin with firm sedge-sphagnum mats supporting trees, narrow strips of wet sphagnum bog filling troughs between old beach ridges, and open ponds with long, linear sedge-sphagnum mats.

Beach and sand dune communities have been the object of considerable study world wide. Dune environments provide ideal laboratories for the study of dynamic change in a natural system. Cowles (1899) in his classic work in the Lake Michigan dunes looked at the relationship between vegetation and physiography in terms of successional development. He found that a dune system functioned as an excellent habitat for observation of plant formations that are rapidly passing into other types by reason of changing environment. The interrelation of physical and biotic factors was continued, in the Lake Michigan dunes, in more specialized studies by Olson (1958 a, b, c, & d) and Lang (1958). Studies of similar focus have been conducted on both the Atlantic and Pacific coasts. Some of the more comprehensive studies include Oosting and Billings (1942), Cooper (1958, 1967), Martin (1959), and Au (1974).

Bogs have been studied extensively in glaciated landscapes in many locations over the entire northern hemisphere. Bogs are of remarkably uniform structure and composition throughout circumboreal regions. The term bog, as defined by Curtis (1959), refers to a soil-vegetation complex composed of a specialized group of herbs and low shrubs growing on a wet, acid soil of peat. The two flowering-plant families most commonly encountered are the Ericaceae and Cyperaceae, which create a canopy over a ground covering of sphagnum moss. Studies of bogs in the adjacent states of Minnesota and Michigan

include those of Conway (1940), Gates (1942), and Heinselman (1970).

## METHODS

The dual approach to understanding the Presque Isle tombolo requires methods which elucidate both vegetational and topographic patterns, and biotic and physiographic processes. Field work was conducted during parts of both the summers of 1975 and 1976. The studies conducted the first summer explored the present topography and vegetation by reconnaissance and general ecological survey. During the second summer extensive coring and systematic analysis of the vegetation were completed.

Most important in the interpretation of topographic features was a careful study of the literature on water-level history of Lake Superior. To provide verification and further evidence for this interpretation, transects were established in the large triangular bog (B of Fig. 2), along which probes were made and cores were taken systematically. A 4.8-cm-diameter Livingstone piston sampler (Cushing and Wright 1965) was used for coring when a continuous sample was desired. A 1.6-cm-diameter Davis sampler (Wright *et al.* 1964) was used for collecting data on depths and contact zones of sediments in the bog basin. Content of organic matter was determined by loss on ignition for representative samples from eight meters of sediment. A composite of five peat samples from 6.54 m depth at station 18 on transect A was dated by radiocarbon analysis by Geochron Laboratories, Cambridge, Mass.

A topographic and vegetation profile 140 m long, (Fig. 7 & located on Fig. 8 B-B') was laid out across the long axis of the tombolo approximately at right angles, 30°N of east. Elevations were measured from the lake-level datum on August 30, 1975 by use of an Abne hand level. Depth to the water table under the highest dune ridge was measured (August 31, 1976) by driving down a tube with a flattened tip and perforated lower portion (to admit ground water), according to the technique described by Turnoch and Lawrence (1953). After the tube had been in place 24 hours, a split bamboo stick attached to a calibrated nylon thread, was lowered until it touched the water surface, and the depth below the soil surface could be calculated.

The vegetation analysis, described not only composition but the structure of the community in relation to the physiography of the habitat. The following techniques for gathering information were utilized: (1) aerial photography (Abrams Aerial Survey, Lansing, Mich. July 1974) and a personal flight (July 1976), (2) reconnaissance on foot, (3) compilation of relevés according to the Zurich-Montpellier school of phytosociology (Braun-Blanquet 1932) at twenty-five locations, (4) symbolic representation of vegetation on a topographic profile (Fig. 7), (5) construction of a vegetation map (Fig. 8), and (6) collection of voucher specimens (identified and deposited in the University of Minnesota Herbarium). Plant nomenclature follows Gleason and Cronquist (1963).

Because of the high degree of homogenity within a given unit, boundaries of plant communities are in most cases clearly demarcated in relation to topography. Relevés were located in each major topographic unit on the tombolo. It was ascertained by testing with sample plots of several sizes that a 10 x 40 m area was sufficient for sampling the vegetation of each unit. This size was modified in some areas, for example some of the beach ridges were not 10 meters in width. For each relevé, all species of vascular plants and abundant non-vascular genera were recorded on the Braun-Blanquet cover-abundance scale (Table 1) (Mueller-Dumbois and Ellenberg 1974). Additionally, details of slope, aspect, altitude, height of vegetation, soil characteristics, and physiographic features were noted in a full description of the relevé site.

## RESULTS AND DISCUSSION

### *Origin of Presque Isle tombolo*

The model of lake-level history in the Lake Superior basin worked out by Farrand (1960, 1969), modified by Saarnisto (1975), and here summarized in the introduction, is used to interpret the origin and development of the Presque Isle double tombolo. It is believed by the present writer that this geomorphic feature developed as the lake level began to retreat from the high Nipissing stage, 188 m (608 ft) MSL. The high period for this stage was approximately 5,500 years ago (Saarnisto 1975). Thus the two forested dune ridges ($S_a$, $S_b$ of Figs. 2 & 5), which enclose the large triangular-shaped bog (B of Figs. 2 & 5), were formed as the lake retreated from the Nipissing high level.

It is likely that the dune ridges were superimposed on exposed underwater ridges of sand, which had been formed as the lake level rose from the low Houghton stage. The rising lake level may have caused increased erosion of adjacent bedrock shorelines, augmenting the amount of material available for deposition of underwater bars. A falling water level is one explanation for the emergence of underwater bars between Presque Isle Point and Stockton Island. The other alternative is that underwater bars emerged prior to the water-level drop because of other factors: high storm waves, ice push, or gradual deposition. In the latter alternative, a falling water level, which would have followed the establishment of the emerged bars (spits), would merely have exposed new material and initiated further growth of the existing spits. Thus the emergence of underwater bars prior to or concurrently with the falling water level does not affect the subsequent development of the emerged surface. Presque Isle tombolo probably formed as the falling water level, aided in beach drifting and longshore currents, caused elongation of the emerged spits, eventually connecting Presque Isle Point to Stockton Island. Dunes would have developed on these spits as increasing amounts of beach material were exposed to wind action by lower lake levels.

As the water level continued to fall, beach ridges ($S_c$ of Figs. 2 & 5), still visible on the northeast side, were formed. The beach ridges that mark the falling lake level were deposited during major storms by ice push or by combination of these processes and the retreating water level. The absence of beach ridges on the southwest side of the tombolo is attributed to the lesser magnitude and frequency of storms and winds that strike that shoreline. Additionally, the fetch of the waves is considerably less on the southwest shore than the northeast shore. The beach ridges are evidence that the wind and wave conditions on the northeast shoreline can build shore structures, whereas the wind and wave conditions on the southwest shoreline do not possess this potential.

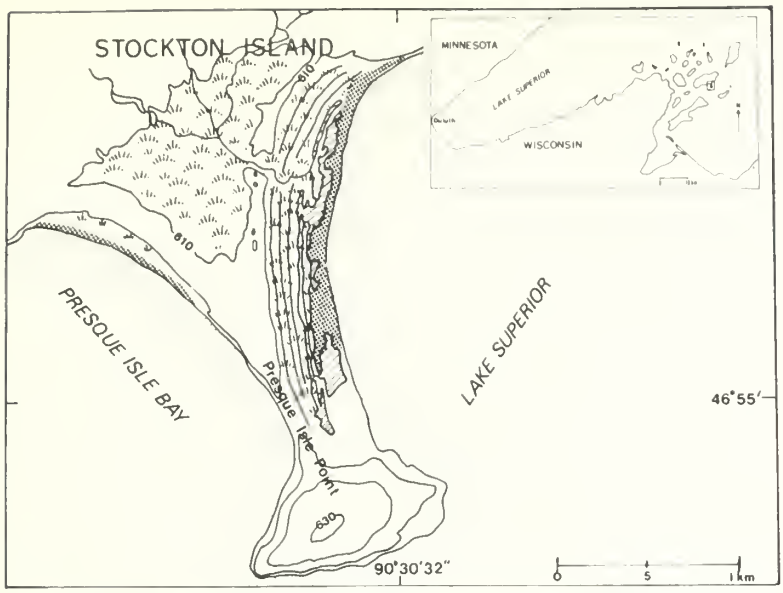



FIGURE 1. Map of Presque Isle tombolo and its location in the western half of the Lake Superior basin.




FIGURE 2. Vertical aerial-photograph of Presque Isle tolbolo $S_a$ & $S_b$ - forested dune-ridges, $S_c$ - parallel ridges and troughs $S_d$ - barrier beach/dune ridge, and B - large triangular-shaped bog.

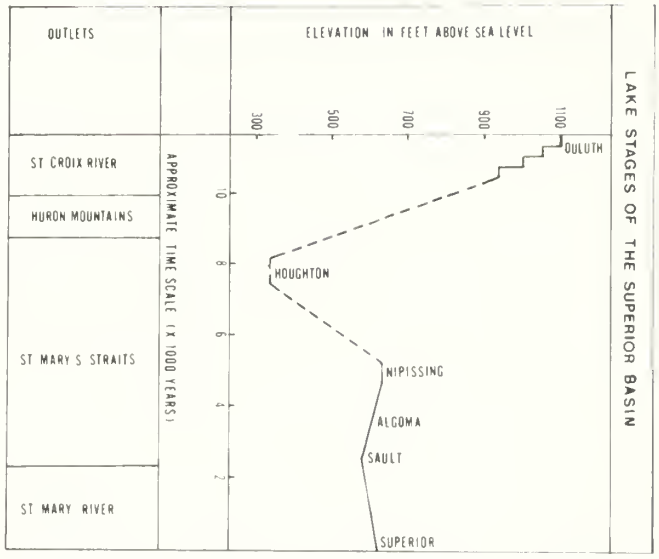



FIGURE 3. Profile illustrating approximate elevation, age, and outlet of the post-glacial lakes of the Lake Superior basin (adapted from Farrand 1960).




FIGURE 4. Map showing the outlets used by meltwater lakes formed by the retreating Wisconsin icesheet.

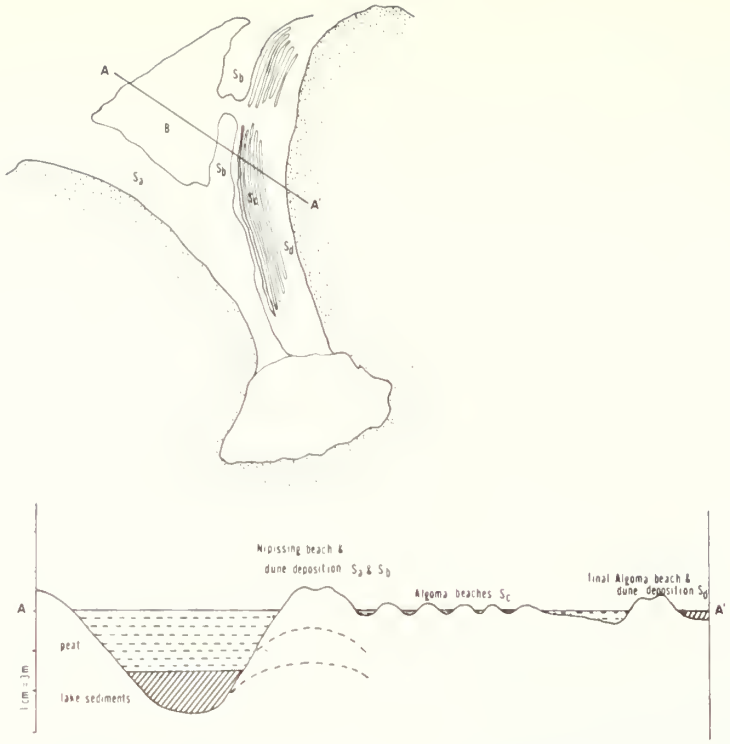



FIGURE 5. A reconstruction of the historical development of the Presque Isle tombolo.

TABLE 1

KEY TO RELEVE SYMBOLS

| Stratum Symbol | Rating Symbol |
|---|---|
| T - tree layer (height greater than 5 m) | cover degree - abundance |
| saplings (height 1 to 5 m) | |
| seedlings (height less than 1 m) | r - single occurence |
| S - shrub layer | + - occasional, cover less than 5% |
| $S_1$ - (woody plants less than 1 m) | 1 - plentiful, cover less than 5% |
| $S_2$ - (woody plants 1 to 5) | 2 - very numerous, cover 5-25% |
| H - herbaceous layer | 3 - any number of individuals, cover 25-50% |
| forbs | 4 - any number of individuals, cover 50-75% |
| graminoids | 5 - any number of individuals, cover 75-100% |
| G - ground layer | |
| moss | |
| lichens | |

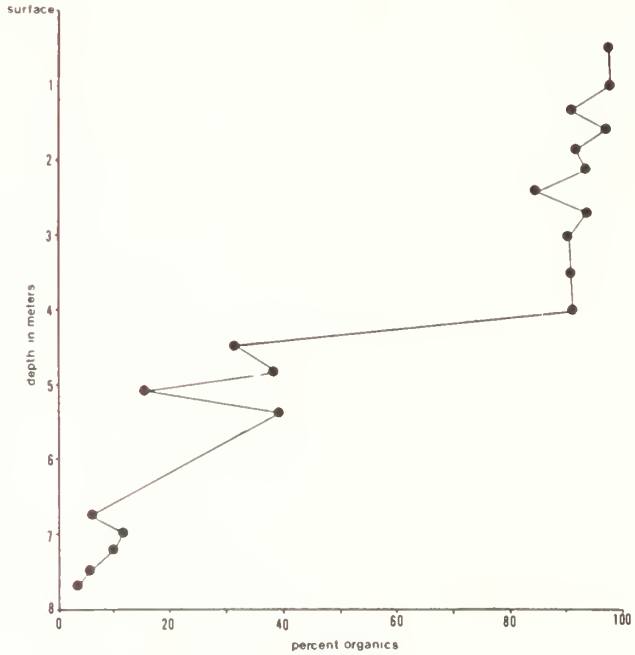



FIGURE 6. Percent of the organic matter in bog sediments as a function of depth from surface.

TABLE 2A. Summary chart of species present in the tree layer and shrub layer in 25 releves on Presque Isle tombolo.

SUMMARY TABLE FOR RELEVÉS

| | HYDRIC | | | | | | | | | MESIC | | | | | | | | | XERIC | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | poorly drained | | | | | | | | | | | | | | | | | | well drained | | | | | | |
| Relevé number | 25 | 20 | 17 | 15 | 13 | 21 | 11 | 6 | 9 | 24 | 18 | 16 | 14 | 12 | 10 | 8 | 23 | 5 | 19 | 7 | 4 | 3 | 1 | 22 | 2 |
| total no. of species | 24 | 21 | 18 | 8 | 20 | 16 | 15 | 15 | 13 | 24 | 8 | 14 | 14 | 15 | 19 | 16 | 23 | 30 | 22 | 21 | 10 | 11 | 24 | 8 | 9 |
| **TREE LAYER** | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pinus strobus* | | | | | | | | + | | | | | 1 | 2 | 1 | r | 2 | 2 | 2 | | + | 3 | + | + | + |
| *Betula papyrifera* | | | | | | | | | 1 | | | | 1 | 1 | + | + | 1 | 2 | 2 | 1 | | | + | r | + |
| *Picea mariana* | 1 | | | | | r | + | 2 | | | | | | 2 | 4 | 5 | | + | | 1 | | | + | | + |
| *Pinus resinosa* | | | | | | | | + | | | | | | 1 | + | | 2 | 3 | | 1 | | 3 | + | | |
| *Acer rubrum* | | | | | | | | | | | | | | | + | r | 1 | 2 | 1 | + | | | | | |
| *Abies balsamea* | | | | | | | | | + | | | | | | | + | | + | 1 | | | r | | | |
| *Sorbus americana* | | | | | | | | | | | | | | | | r | + | | | | | | | | |
| *Tsuga canadensis* | | | | | | | | | | | | | | | | | r | | 2 | | | | | | |
| *Pinus banksiana* | | | | | | | | | | | | | | | | | | | | | | | r | | |
| *Thuja occidentalis* | | | | | | | | | | | | | | | | | | | | | | | | + | |
| *Betula lutea* | | | | | | | | | | | | | | | | | | | 2 | | | | | | |
| *Populus grandidentata* | | | | | | | | | | | | | | | | | | | | + | | | | | |
| *Larix laricina* | + | | | | | | | | | | | | | | | | | | | | | | | | |
| **SHRUB LAYER** | | | | | | | | | | | | | | | | | | | | | | | | | |
| Shrub II | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Amelanchier sp.* | | | | | | | | | | | | | | | | | + | + | | | | + | | | |
| *Alnus rugosa* | | | | | | | | | | | | | | | | | | | | | | | | | r |
| *Physocarpus opulifolius* | | | | | | | | | | | | | | | | | | | | | | | | | r |
| Shrub I | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Chamaedaphne calyculata* | 2 | + | 3 | 2 | + | 2 | 4 | | + | | 3 | 3 | 2 | 2 | | | | | | | | 4 | | | + |
| *Myrica gale* | 1 | + | 3 | 2 | + | 2 | | 2 | + | | 3 | 3 | 2 | 2 | + | | | | | | | 3 | | | |
| *Andromeda glaucophylla* | 1 | r | r | r | | 1 | + | | + | | + | r | | + | | | | | | | | | | | |
| *Kalmia polifolia* | 1 | r | | + | | + | 1 | | r | | | 1 | 1 | 1 | | | | | | | | | | | |
| *Vaccinium macrocarpon* | + | | 1 | 1 | | | | | | | 1 | 1 | 1 | + | | | | | | | | | | | + |
| *Vaccinium Oxycoccus* | 1 | 1 | + | | + | 1 | + | | | | | | | | | | | | | | | | | | |
| *Ledum groenlandicum* | 1 | | | | | | 2 | 2 | + | | | | 1 | | + | + | | + | | + | | | | | |
| *Vaccinium angustifolium* | | | | | | | | + | | | | 2 | 2 | + | 1 | + | + | 2 | | 2 | 3 | | 2 | | |
| *Gaylussaccia baccata* | | | | | | | | | + | | | 3 | 3 | | | | | 1 | | 1 | 1 | + | 1 | | |
| *Vaccinium myrtilloides* | | | | | | | | | | | | 2 | 2 | | | | + | 2 | + | 2 | | | | | |
| *Gaultheria procumbens* | | | | | | | | + | | | | | | | | | + | 1 | 1 | + | | | | | |
| *Gaultheria hispidula* | | | | | | | | | + | | | | | | + | + | | 1 | | | | | | | |
| *Juniperus communis* | | | | | | | | | | | | | | | | | | | | 1 | 1 | | | + | + |
| *Spirea alba* | | | | | | | | | | + | | | | | | | | | | | | 1 | | | + |
| *Salix humilis* | | | | | | | | | | | | | | + | | | | | | | | | | | |
| *Prunus pumila* | | | | | | | | | | | | | | | | | | | | | | | | | + |
| *Arctostaphylos uva-ursi* | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| *unknown #49* | | | | | | | | | | | | | | | + | | | | | | | | | | |
| **Saplings** | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pinus strobus* | | | | | | | | | | | 1 | + | + | + | | | | 1 | | | | | | + | |
| *Betula papyrifera* | | | | | | | | | | | | + | + | + | + | | + | + | | | | | | + | |
| *Picea mariana* | | 1 | | | | | | + | | | | | + | + | | | | + | | + | 1 | | | + | |
| *Pinus resinosa* | | | | | | | | | | | | + | + | | | | | 1 | | + | | | | | |
| *Acer rubrum* | | | | | | | | | | | | | | | + | | + | + | | + | | | | | |
| *Abies balsamea* | | | | | | | | | | | | | | | | + | | + | | + | | | | | |
| *Thuja occidentalis* | | | | | | | | | | | | | | | | | | | | | | | | + | |
| *Larix laricina* | | 1 | | | | | | | | | | | | | | | | | | | | | | | |

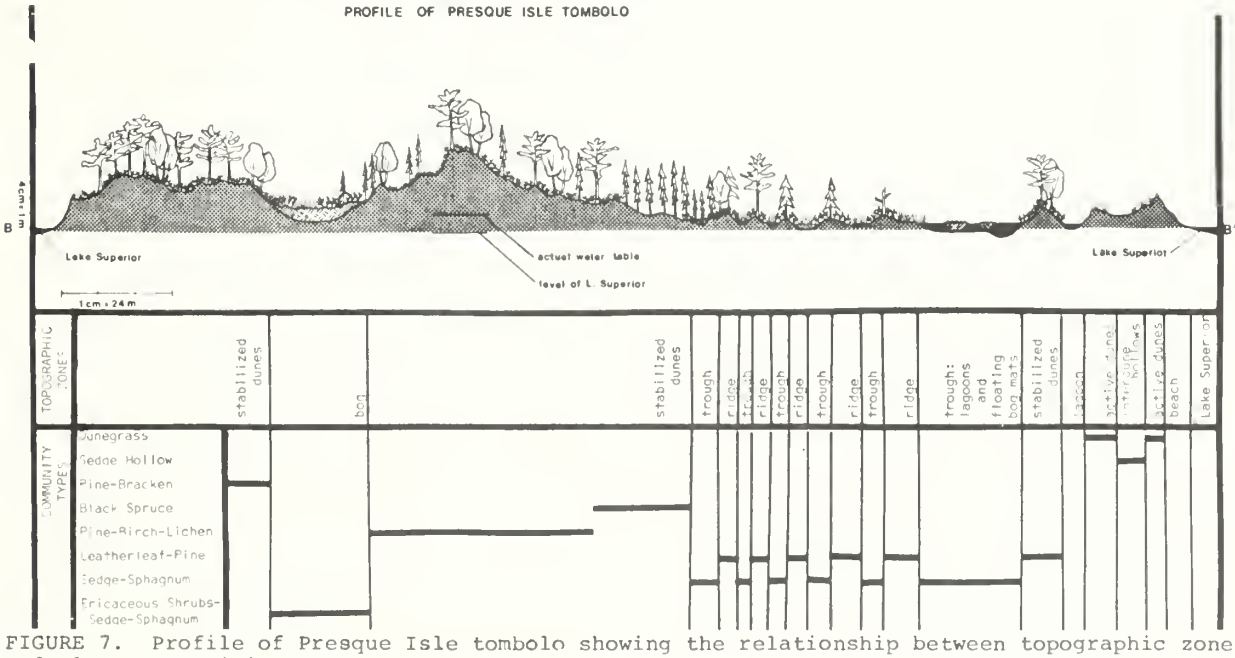



FIGURE 7. Profile of Presque Isle tombolo showing the relationship between topographic zones and plant communities.

TABLE 2B. Summary chart of species present in the herb layer (forbs) in 25 releves on Presque Isle tombolo.

| | SUMMARY TABLE FOR RELEVÉS | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | HYDRIC | | | | | | | | | MESIC | | | | | | | | | | XERIC | | | | | | |
| | poorly drained | | | | | | | | | | | | | | | | | | | well drained | | | | | | |
| Relevé number | 25 | 20 | 17 | 15 | 13 | 21 | 11 | 6 | 9 | 24 | 18 | 16 | 14 | 12 | 10 | 8 | 23 | 5 | 19 | 7 | 4 | 3 | 1 | 22 | 2 |
| total no. of species | 24 | 21 | 18 | 8 | 20 | 16 | 15 | 15 | 13 | 24 | 8 | 14 | 14 | 15 | 19 | 16 | 23 | 30 | 22 | 21 | 10 | 11 | 24 | 8 | 9 |
| HERB LAYER | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Herbs (forb.) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Sarracenia purpurea* | 1 | 1 | | + | | + | 2 | + | r | | | r | | | | | | | | | | | | | | |
| *Drosera rotundifolia* | 1 | 1 | 1 | | | 1 | 1 | | r | | | | | | | | | | | | | | | | | |
| *Calopogon pulchellus* | 1 | 1 | + | + | | + | | + | | | | | | | | | | | | | | | | | | |
| *Menyanthes trifoliata* | 1 | 1 | 1 | | | 1 | 2 | | | | | | | | | | | | | | | | | | | |
| *Pogonia ophioglossoides* | 1 | 1 | 1 | | | 1 | | + | | | | | | | | | | | | | | | | | | |
| *Iris versicolor* | + | | | | | | | + | r | 1 | + | | | | | | | | | | | | | | | |
| *Drosera anglica* | 1 | 1 | 1 | | | | 1 | | | | | | | | | | | | | | | | | | | |
| *Smilacina trifolia* | + | + | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| *Potentilla palustris* | + | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Unknown #48* | | | | | | + | | | | | | | | | | | | | | | | | | | | |
| *Trientalis borealis* | | | | | | | | | + | | | | | | + | + | + | 1 | | + | | | + | | | |
| *Lysimachia terrestris* | | | | | | | | | | + | | | | | | | | | | | | | | | | |
| *Eriocaulon septangulare* | | | | | | | | | | + | | | | | | | | | | | | | | | | |
| *Oenothera biennis* | | | | | | | | | | + | | | | | | | | | | | | + | | | | |
| *Potentilla norregica* | | | | | | | | | | + | | | | | | | | | | | | | | | | |
| *Osmunda cinnamomea* | | | | | | | | | 1 | | | | | | 3 | + | | | | | | | | | | |
| *Pteridium aquilinum* | | | | | | | | | | | | | | + | 1 | 1 | 2 | 4 | 1 | 4 | | | | | | |
| *Maianthemum canadense* | | | | | | | | | | | | | | | + | | 1 | 1 | + | + | | | + | | | |
| *Melampyrum lineare* | | | | | | | | | | | | | | | | | 1 | 1 | 1 | + | | | 1 | | | |
| *Cornus canadensis* | | | | | | | | | | | | | | | + | + | + | 1 | 1 | | | | | | | |
| *Epigea repens* | | | | | | | | | | | | | | | + | | 1 | 1 | 1 | + | | | | | | |
| *Clintonia borealis* | | | | | | | | | | | | | | | + | + | 1 | | 1 | | | | | | | |
| *Rubus allegheniensis* | | | | | | | | | | | | | | + | + | | | | | | | | | | + | |
| *Lycopodium annotinum* | | | | | | | | | | | | | | | | | 1 | + | r | | | | | | | |
| *Linnaea borealis* | | | | | | | | | | | | | | | | | + | + | 1 | | | | | | | |
| *Cypripedium acaule* | | | | | | | | | | | | | | | | | | + | + | + | | + | | | | |
| *Lycopodium obscurum* | | | | | | | | | | | | | | + | | | + | | | | | | | | | |
| *Lycopodium clavatum* | | | | | | | | | | | | | | | | | 1 | + | | | | | | | | |
| *Cornandra umbellata* | | | | | | | | | | | | | | | | | | + | | | | | 2 | | | |
| *Habenaria clarellata* | | | | | | | | | | | | | | | | | | + | + | | | | 2 | | | |
| *Aralia hispida* | | | | | | | | | | | | | | | | | | | | | | | r | | | |
| *Coptis trifolia* | | | | | | | | | | | | | | | | | + | | | | | | | | | |
| *Aralia nudicaulis* | | | | | | | | | | | | | | | | | | 1 | | | | | | | | |
| *Oxalis Acetosella* | | | | | | | | | | | | | | | | | | + | | | | | | | | |
| *Goodyera pubescens* | | | | | | | | | | | | | | | | | | | 1 | | | | | | | |
| *Mitchella repens* | | | | | | | | | | | | | | | | | | | + | | | | | | | |
| *Monatropa uniflora* | | | | | | | | | | | | | | | | | | | r | | | | | | | |
| *Lathyrus maritima* | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| *Epilobium angustifolium* | | | | | | | | | | | | | | | | | | | | | | | r | | | |
| *Rumex Acetosella* | | | | | | | | | | | | | | | | | | | | | | | r | | | |
| *Hudsonia tomentosa* | | | | | | | | | | | | | | | | | | | | | | | | 1 | + | |

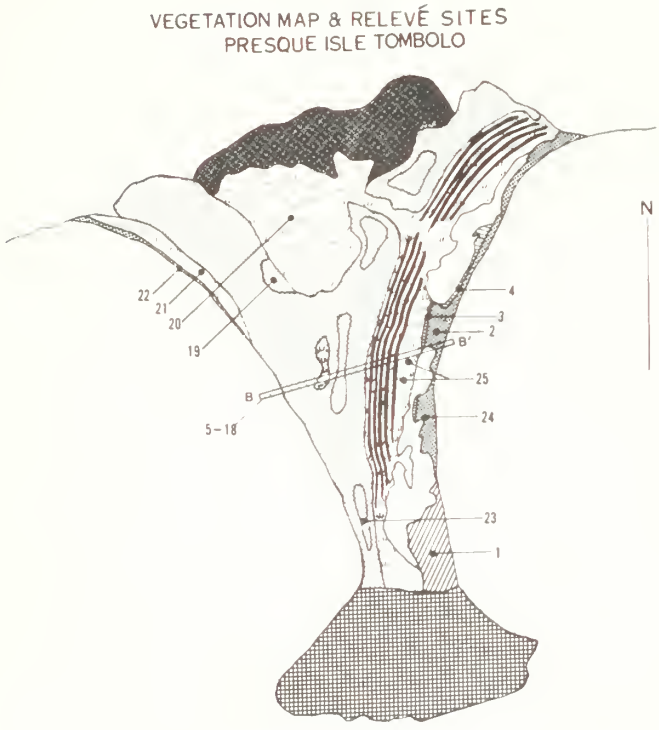



FIGURE 8. Map showing location of releves on the Presque Isle tombolo. The size of the plant community represented by the releve is indicated by the extent of the pattern surrounding the releve site.

TABLE 2C. Summary chart of species present in herb layer (graminoids and seedlings) and ground layer in 25 releves on Presque Isle tombolo.

SUMMARY TABLE FOR RELEVÉS

| | HYDRIC (poorly drained) | | | | | | | | | | MESIC | | | | | | | | | | XERIC (well drained) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Relevé number | 25 | 20 | 17 | 15 | 13 | 21 | 11 | 6 | 9 | 24 | 18 | 16 | 14 | 12 | 10 | 8 | 23 | 5 | 19 | | 7 | 4 | 3 | 1 | 22 | 2 |
| total no. of species | 24 | 21 | 18 | 8 | 20 | 16 | 15 | 13 | 24 | | 9 | 14 | 14 | 15 | 19 | 16 | 23 | 30 | 22 | | 21 | 10 | 11 | 24 | 8 | 9 |
| HERB LAYER Cont. | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Graminoids | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Carex oligosperma* | 3 | 2 | 2 | 4 | 2 | 2 | 4 | 3 | | | 1 | 1 | 1 | | | | | | | | | | | | | |
| *Cladium mariscoides* | 2 | 2 | 2 | | 2 | | | | 2 | | + | | | | | | | | | | | | | | | |
| *Rhynchospora alba* | 1 | 2 | 2 | | 2 | 1 | | | | | | | | | | | | | | | | | | | | |
| *Carex rostrata* | 2 | 2 | | | | 2 | | 3 | | | | | | | | | | | | | | | | | | |
| *Carex muricata* | + | | + | | | | 1 | | + | | | | | | | | | | | | | | | | | |
| *Eriophorum virginicum* | 1 | | 2 | | + | 1 | | | | | | | | | | | | | | | | | | | | |
| *Scheuchzeria palustris* | | + | + | | + | + | | | | | | | | | | | | | | | | | | | | |
| *Rhynchospora fusca* | 2 | | | | 2 | | | | 1 | | | | | | | | | | | | | | | | | |
| *Carex Michauxiana* | 2 | | 2 | | | | | | | | | | | | | | | | | | | | | | | |
| *Carex lasiocarpa* | 1 | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Carex exilis* | 1 | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Carex brunnescens* | + | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Unknown #45* | | | | | | | | + | | | | | | | | | | | | | | | | | | |
| *Carex trisperma* | | | | | | | | + | | | | + | | + | + | | | | | | | | | | | |
| *Carex limosa* | | | | | + | 1 | | | + | | | | | | | | | | | | | | | | | |
| *Scirpus cyperinus* | | | | | | + | | | 1 | | | | | | | | | | | | | | | | | |
| *Glyceria canadensis* | | | | | | + | | | | | | | | | | | | | | | | | | | | |
| *Juncus canadensis* | | | | | | 1 | | | | | | | | | | | | | | | | | | | | |
| *Carex paupercula* | | | | | | 1 | | | | | | | | | | | | | | | | | | | | |
| *Juncus pelocarpus* | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| *Carex viridula* | | | | | | | | | + | | | | | | | | | | | | | | | | | |
| *Carex lenticularis* | | | | | | | | | + | | | | | | | | | | | | | | | | | |
| *Unknown #32* | | | | | | | | | + | | | | | | | | | | | | | | | | | |
| *Unknown #42* | | | | | | | | | + | | | | | | | | | | | | | | | | | |
| *Unknown #43* | | | | | | | | | + | | | | | | | | | | | | | | | | | |
| *Unknown #44* | | | | | | | | | | | | | + | | | | | | | | | | | | | |
| *Unknown #46* | | | | | | | | | | | | | | | | + | + | | | | | | | | | |
| *Armophila breviligulata* | | | | | | | | | | | | | | | | | | | | | + | + | 1 | 1 | | |
| *Carex arctata* | | | | | | | | | | | | | | | | | + | | | | | | | | | |
| *Carex pensylvanica* | | | | | | | | | | | | | | | | | | | | | 2 | | | | | |
| *Carex scoparia* | | | | | | | | | | | | | | | | | | | | | 1 | | | | | |
| *Unknown #40* | | | | | | | | | | | | | | | | | | | | | + | | | | | |
| *Unknown #41* | | | | | | | | | | | | | | | | | | | | | + | | | | | |
| *Unknown #47* | | | | | | | | | | | | | | | | | | | | | + | | | | | |
| Seedlings | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pinus Strobus* | | | | | | | | | | | | + | + | + | | 1 | 1 | | | | + | | | + | | |
| *Betula papyrifera* | | | | | | | | | | | | + | + | + | + | + | + | | | | | | | | | |
| *Picia mariana* | | + | | | | | | | | | | | | + | | | + | | | | | | | | | |
| *Pinus resinosa* | | | | | | | | | | | | + | | | | + | 1 | | | | + | + | | | | |
| *Acer rubrum* | | | | | | | | + | | | | | | | + | 2 | + | 1 | | | + | | | | | |
| *Abies balsamea* | | | | | | | | | | | | | | | | | + | 1 | | | | | | | | |
| *Tsuga canadensis* | | | | | | | | | | | | | | | | | | + | | | | | | | | |
| *Larix laricina* | 1 | | | | | | | | | | | | | | | | | | | | | | | | | |
| GROUND LAYER | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Moss | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Sphagnum sp.* | 3 | 5 | 4 | 4 | 4 | 5 | 4 | 4 | | | | | | | | | | | | | | | | | | |
| conspicuous mosses | 1 | | | | | | | | | | | + | | | 1 | | 1 | | | | + | 1 | | 1 | | |
| Lichens | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Cladonia sp.* | | | | | | | | | | | | | | | | | | | | | 1 | | | | | |
| conspicuous lichens | | | | | | | | | | | | | | | | | 1 | | | | | + | | 2 | | |

TABLE 3. Chart showing the relationship between topography, vegetation, and some environmental factors.

| Topographic Zone | Vegetation Type | Plant Community | Dominant Species | Representative Relevés | Dominant Growth Form | Moisture Status | Exposure to Wind |
|---|---|---|---|---|---|---|---|
| Active dunes | lake dunes | Dunegrass | *Ammophila breviligulata* | 2 | graminoid | xeric | extreme |
| Interdune hollows | lake dunes | Sedge Hollow | *Cladium/Juncus* | 24 | graminoid | hydric | high. |
| Stabilized dunes/beach ridges | lake dunes | Beach Heather | *Hudsonia/Pinus* | 1,22 | woody/forbs | xeric | extreme |
| | northern conifer forest | Pine-Blueberry | *Pinus/Vaccinium* | 4 | woody | dry-mesic | high |
| | | Pine-Bracken | *Pinus/Pteridium* | 5 | woody/forbs | dry-mesic | moderate |
| | | Black Spruce | *Picea mariana* | 8,10 | woody | wet-mesic | moderate |
| | northern mixed forest | Pine-Birch-lichen | *Pinus/Betula/ Cladonia* | 7 | woody | dry-mesic | low moderate |
| | | Pine-Maple | *Pinus/Acer* | 23 | woody/forbs | dry-mesic | moderate |
| | | Hemlock-Birch | *Tsuga/ Betula* | 19 | woody | mesic | low moderate |
| | shrub carr | Leatherleaf-Pine | *Chamaedaphne/ Pinus* | 12,14,16, 18,3 | woody | wet-mesic | high |
| Inter-ridge troughs/ filled lake basins | open bog | Sedge-Sphagnum | *Carex/Sphagnum* | 25,17,15,13, 21,11 | graminoid | hydric | high |
| | | Ericaceous shrubs-Sedge-Sphagnum | *Chamaedaphne/ Carex/ Sphagnum* | 20,9,6 | woody/ graminoid | hydric | moderate |

Water level is believed to have stabilized, because of a halt in erosion at the Port Huron outlet between 3200 and 2500 B.P. (Lewis 1969). This stage has been designated the Algoma state. During this period of stability, at 184 m (596 ft) MSL, the final barrier beach ($S_d$ of Fig. 2 & 5), which forms the northeast shore of the tombolo, was probably developed. The subsequent drop to the Sault stage, 181 m (586 ft) MSL, undoubtedly aided the development of this final Algoma beach, exposing more beach material to wind action. Because of the short duration of the Sault stage and its distance below present lake level, it is reasonable to conclude that no shorelines from this stage remain visible today. Although the present lake level is only about 2 m (80 in) below the presumed lake level at the time of the tombolo's inception, the present writer feels that dune deposition is responsible for initially raising the altitude of the formation sufficiently above lake level so that rising water levels of the past 2200 years have not totally submerged the tombolo.

Additional evidence was sought to verify the historical lake-level interpretation of the tombolo's origin. Extensive coring was conducted in the large triangular-shaped bog. It was ascertained that the bog graded from one meter in depth on the edges to eight meters near the center. Sediments extracted from the central basin contained 1.5 m of lake sediments at the base of the core, overlain by 6.5 m of organic sediments. Loss of ignition was recorded for representative samples taken from the eight meters of sediment. Results (Fig. 6) show that the lake sediments contain less than 40% organic matter, and that the past sediments contain more than 80% organics. Lenses of sand were found in many cores, possibly the result of overwash during high winds, when the enclosing ridges were poorly developed. It is concluded that a small triangular lake existed, enclosed by sand ridges, until the lake-level in adjacent Lake Superior dropped, causing a comparable drop in level of the enclosed lake. At this time the lake may have been quite shallow, and the development of a bog environment was probably initiated (Fig. 5). As the lake level began to rise, due to uplift at the St. Mary's River outlet, an increasingly deeper bog mat would have developed.

The history of the bog inferred from the sediment stratigraphy, although not conclusive evidence, does fit the falling and rising sequence of lake level during the past 5500 years. Samples 6.54 m below the surface of the bog, near the contact of the basal clay with highly organic sediment, were dated by radiocarbon analysis as 4990 ± 170 years old (GX-4552). Lake sediments lying below the carbon-dated layer were deposited before that in an enclosed or partially enclosed lake formed by the developing spits ($S_a$, $S_b$ of Fig. 5). The 1.5 m of lake sediments were probably deposited within a relatively short time following separation of the small lake from the Lake Superior basin. At this time, it is impossible to identify an absolute date for the beginning of lake deposition. Evidence supports a beginning date that coincides with the extension of the spits, that enclosed the lake and formed the Presque Isle tombolo. The radiocarbon date from the base of the organic sediments, and the inclusion of additional time for the deposition of lake sediments, puts the inception of Presque Isle tombolo within the Nipissing time period of 5500 B.P. described by Lewis (1969) and Saarnisto (1975).

## PLANT ECOLOGY

The methods utilized in mapping the distribution of plant species and describing the vegetation assume that a plant community can be distinguished as a discrete unit of vegetation. According to Mueller-Dumbois and Ellenberg (1974), a plant community is a combination of plants interacting with one another in an environment they modify and depend upon. Thus, a plant community as defined for this study refers to an aggregation of organisms sharing a common habitat type and having a characteristic species composition.

Structural, compositional, and environmental criteria were utilized as uniformly as possible in identifying and classifying plant communities. Boundaries of these communities were located primarily by visible differences in structure of vegetation and species composition and differences in topography. Analysis of aerial photographs provide a basis for identification of major boundaries, and reconnaissance on foot verified the reliability of the boundaries assigned. Structural and compositional differences were recognized according to height and relative importance (percent cover) of the dominant species (Table 1). Topographic boundaries were clearly evident because of difference in elevation.

Secondarily, environmental criteria, such as exposure to wind and moisture condition, were estimated. Exposure was considered on a scale from low (protected) to extreme (unprotected). Moisture conditions were estimated by combining information on exposure, height above water table, and known ecological requirements of species present within the habitat. Single plots in each unit were analyzed according to the Braun-Blanquet relevé method. The relevé plot was large in relation to relief so that slope and aspect were of lesser significance than height above water table and exposure to wind action. Each relevé was rated on a scale from hydric to xeric according to status of available moisture.

The twenty-five relevés were arranged and rearranged according to presence or absence of the species (Table 2). This is a numerical method, carried out by visual inspection of the species lists, placing together those relevés with the greatest number of species in common. The relevés can be divided rather readily into three major groups: hydric, mesic, and xeric. The compilation of data in this manner show a positive correlation between species presence and available moisture. The gradient along which species align runs consistently from the top left of the tables to the bottom right. Species present in hydric communities gradually or in some cases sharply drop in importance as more xeric conditions prevail.

The pattern is consistently visible in all canopy layers: trees, saplings, seedlings, shrubs, and herbs. As an example, in the shrub I layer, (Table 2) *Chamaedaphne calyculata, Myrica gale, Andromeda glaucophylla,* and *Kalmia poliofolia* dominate the hydric communities but rarely occur in the xeric communities. As those species drop in importance, *Ledum groenlandicum, Gaylussaccia baccata, Vaccinium angustifolium,* and *Vaccinium myrtilloides* appear as dominants in the mesic communities. The trend continues with different species present and dominant in the xeric communities: *Juniperus communis, Spirea alba, Prunus pumila,* and *Arctostaphylos uva-ursi.*

A positive correlation also exists between topography and the mosaic of plant communities found on Presque Isle tombolo. Similar patterns have been established in coastal systems by Oosting and Billings (1942), Martin (1959), and Au (1974). Martin's classic work on the vegetation of Island Beach State Park, New Jersey, is a comprehensive study of the interrelationships among vegetation, topography, and environment in a marine coastal dune system. On Presque Isle tombolo the same interrelationships exist on an inland-lake coastal-dune system, where salt spray is not a factor. The conclusions reached in both studies are striking in their similarities. In both cases the existing zoned mosaic of vegetation corresponds with the zoned mosaic of topography. The major difference in the two systems is the salt versus fresh-water influence. Species composition and distribution correlates with species level of salt tolerance in the marine dune system. This factor, though absent in the inland-lake dune system, does not alter the similarity in distribution of life-form types. The similar patterns found in both marine and inland-lake dune systems demonstrate the existence of an analogous combination of environmental and physical processes.

According to Martin (1959), topography occupies a central and diagnostic position in the analysis of a complex environment, because it controls the intensity of limiting factors but does not act upon the plants directly. Topography serves as an indicator of plant distribution and habitat type on the Presque Isle tombolo. Four distinct topographic zones exist (Fig. 7): active dune, interdune hollow, stabilized dune/beach ridge, and inter-ridge trough or filled lake basin. The zones vary significantly in configuration, position of exposure, and elevation, even though relief of the tombolo is never greater than seven meters.

The active dunes are low (Relevé #2) combining with the beach to form the mid-section of the northeast shoreline of the tombolo. The low relief of this section, directly exposed to northeast winds, is maintained by overwash during major storms (Godfrey 1974). The interdune hollow zone (Relevé #24), is located in this same area in wet depressions behind and between the active dunes. The stabilized dunes can be separated into four distinct regions by location on the tombolo and by vegetation cover. (1) One area lies south of and adjacent to the active dunes, bordering the northeast shore (Relevé #1). A distinct rise in elevation separates these stabilized dunes from the overwash active-dune area. The greater deposit of sand in this area is explained by its position on the tombolo in relation to longshore currents and angle of exposure to wave and wind actions. These dunes are stabilized by a xeric population of low herbaceous and shrubby plants. (2) A ridge of stabilized dunes (Relevé #3) lies directly behind most of the active dunes, except where they have been obliterated by overwash. It is a narrow ridge stabilized predominantly by the ericaceous shrub *Chamaedaphne calyculata* (Leather leaf) and by a single line of scattered trees. It is bordered on its back side by open water of the flooded lagoons. (3) The third area (Relevés #12, 14, 16 & 18) is much like the second in vegetation cover but distinct in form. These ridges are small, parallel, sand ridges (4 to 10 m wide) exhibiting no dune development. (4) The fourth area of stabilized dunes, adjacent to and southwest of the parallel sand ridges, are the broad "Nipissing" dune ridges (Relevés #5 & 7), forested by confier and mixed northern hardwoods. The inter-ridge troughs (Relevés #11, 13, 15, 17, 21) 5-10 m strips of sphagnum bog, separate the parallel sand ridges. The filled lake basin (Relevé #20), now a 16 ha triangular-shaped bog, is enclosed by the "Nipissing" dune ridges.

The relationship between topography and plant-community distribution is demonstrated on a profile (Fig. 7, located on Fig. 8 B-B'). Dominant species present along the transect are symbolically illustrated on the topographic profile so that representative communities of most habitats were included within the transect. The profile clearly demonstrates that the occurrence of a specific vegetation type is associated with a given topographic unit. Tabel 3, compiled with information from both the profile and relevé data, defines twelve distinct communities, each characterized by a unique combination of physiographic parameters and dominant vegetation.

*Successional Relationships*. -- In the absence of longterm data on successional patterns on Presque Isle tombolo, clues to the probable successional relationships must be gathered from the existing vegetation. On a broad scale, succession on the tombolo does not correspond with the age of the substrate. Trees of the oldest age class (approximately 100 years old) presently exist on the oldest "Nipissing" dune ridges and also on the youngest "Algoma" dune ridge. Thus, the existing vegetation cover does not indicate the age of the landform but is a product of dynamic environmental, biotic, and physical processes.

It appears that succession on the tombolo is particularly dependent on the status of water level. As water level drops, new surfaces are exposed for colonization by pioneer species. The newly exposed surfaces provide protection to areas that previously bordered the lake edge. In this manner, active dunes can develop into stabilized dunes, and a traditional pattern of dune succession (dune-builders to jack pine, or white pine to black oak-white oak, Olson 1958a) might evolve.

However, the trend of rising water levels over the past 2000 years causes a reversal from traditional patterns of succession. This is evident on the southwest edge of the forested dunes. Exposure to wind and wave action has in localized areas created small mobile dunes (populated with species characteristic of the active dunes), midst the stable forested dunes. The dead trees on the outer beach ridges are another example. The flooding condition caused by the rising water table requires the establishment of species more tolerant of a hydric environment.

The dynamics of equilibrium and patterns of successional development can be followed on a smaller scale in each of the different topographic zones. The active dunes are currently stable within a cycle of sand deposition, stabilization by pioneer species (predominantly *Ammophila breviligulata*), and overwash and destruction of the dunes. The stabilized dunes (Beach Heather community) are potentially an intermediate stage between active dunes and

forested dunes. The establishment of equilibrium on these dunes is maintained by the interaction between vegetation involved in stabilization and physical forces, *i.e.*, wind action (blowouts), active in the destruction of the stability.

The forested dune ridges appear to be quite stable, dominated by species capable of reproducing beneath their own kind. Olson's study of rates of succession and soil change on the Lake Michigan sand dunes shows that soil maturation occurs within the first 1000 years after stabilization. He found that little improvement in soil fertility occurs after this length of time. The condition of low fertility favors vegetation with low nutrient requirements. In this environment, there is little likelihood of improving nutrient conditions as these species are unable to return nutrients to the soil. Thus, except in isolated locations, according to Olson (1958a), it is unlikely that succession on dune surfaces reaches the climax mesophytic forest that Cowles (1899) spoke of in his model of sand-dune succession in the Lake Michigan dunes. The dune-ridge forests of Presque Isle tombolo are predominantly forests composed of species with low nutrient requirements, *Pinus resinosa, Pteridium aquilinum,* and *Vaccinium angustifolium*. The fire history, evidenced by fire scars and historical record, is an additional factor determining the dominance and continuance of the Pine forest on the dune ridges.

Successional development on Presque Isle tombolo is controlled by physical and environmental forces unrelated to the age of the substrate. The existence of active dunes, dunes stabilized by low shrubby growth, and dunes stabilized by forest growth does not necessarily represent seral stages in autogenic succession. Succession is primarily an interzonal phenomena, characterized by cyclical rather than linear patterns of development.

## CONCLUSIONS

The complex pattern of plant communities, within such close proximity, is the object of speculation. What was the geologic history that gave rise to such a diverse landform? What effects have climate, winds, currents, and storms had on the development of the existing topography? Plant zonation functions as a keen indicator of the subtle continuum of change, as ridges grade into troughs, and troughs into ridges. The interrelationship of biotic and physical factors involved in the development of Presque Isle tombolo demonstrates the diversity found in vegetation and topography which are dynamically interacting.

According to Wright (1966): "The accuracy of any historical reconstruction depends on the abundance of the primary data, and on how well data can be interpreted. If the record is landforms or physical sediments, one should understand the nature of the geomorphic and geologic process." The synthesis of information from geomorphic and geologic history, interpretation of existing topographic features on the tombolo, and the results from sediment and radiocarbon analyses, provide the basis for the development of an hypothesis.

The origin of the ridges and troughs that form Presque Isle tombolo are related to water-level fluctuations, wind, and currents. The inception of the tombolo began approximately 5500 years ago, as the lake level began to retreat from the high period of the Nipissing lake stage, 188 m (608 ft) MSL. A series of parallel ridges, culminating with a final barrier beach formed on the northeast shore of the tombolo, are evidence of the continued retreat of the lake level. The outer beach is identified as an Algoma beach, formed between 3200 and 2500 B.P. History of the bog (B of Fig. 2), inferred from the sediment analyses, fits the falling and rising sequence of lake levels in the Lake Superior basin during the past 5500 years. A radiocarbon date 4990 ± 170 years B.P., from the deepest organic sediments in this bog and the conclusions from the sediment analyses together support the lake-level interpretation of the origin of Presque Isle tombolo.

Billings (1952) acknowledges that "the complexity of the interrelationships between the plant and its environment is almost enough to discourage any attempts at a complete analysis and synthesis". In the study of Presque Isle tombolo, a preliminary attempt has been made to interpret the floristic patterns in terms of the geomorphic processes active in the formation of the existing topography. A total understanding of the ecological processes interacting on the Presque Isle tombolo awaits more specific investigation of additional biotic and abiotic parameters.

Boundaries between adjacent plant communities are visibly distinct. When organized into the summary table (Tabel 2), certain species are found to possess sufficient physiologic adaptability to enable them to occur in more than one community, so that a nearly continuous gradient seems to exist from hydric to xeric. By measure of structure and composition, five different vegetation types are recognized within this gradient: lake dunes, northern conifer forest, northern mixed forest, shrub carr, and open bog. Four different topographic zones are identified: active dunes, interdune hollows, stabilized dune/beach ridges, and inter-ridge troughs or filled lake basin. A combination of the following parameters: topographic zone, vegetation type, moisture status, degree of exposure to wind action, and dominant species define twelve separate plant communities (Table 3).

It is difficult to evaluate accurately the relative importance of the parameters studied. However, Presque Isle tombolo clearly demonstrates the interrelationship and interdependence of topography, environment, and vegetation. A rich flora exists because of the abundance of diverse habitats. Any number of variables combine to define the uniqueness of a given site. One or more variables may express their dominance at a given location, for example: extreme wind conditions (a limiting factor to the stature and available moisture for vegetation in the Beach Heather community), exposure to wave action and over-wash (a limiting factor to the development of dune vegetation), nutrient-poor soil (a limiting factor to species composition in forest flora), moisture conditions (a limiting factor in bog development), and sand-stabilizing vegetation (a limiting factor to dune mobility).

The interwoven relationship of geomorphic processes and topography have created a landform that combines with environmental factors in many distinct combinations. The habitat that results requires plants capable of adapting and co-existing in the ecosystem they comprise. The environmental factors, the topography, and the

geomorphic processes are reciprocally modified by the vegetation existing in the habitats. The Presque Isle tombolo emerges as a dynamic system demonstrating the vital interrelationships among physical and biotic processes.

## LITERATURE CITED


ANONYMOUS. 1974. Stockton Island Survey: An ecological survey and environmental impact study of Stockton Island, Apostle Islands National Lakeshore. Northland College, Ashland, Wisc. 71 pp.

AU, SHU-FUN. 1974. Vegetation and Ecological processes on Shackleford Bank, North Carolina. Nat. Park Service Scientific Monograph Series. No. 6. 86 pp.

BEALS, E. W. and G. COTTAM. 1960. The forest vegetation of the Apostle Island, Wisconsin. Ecology. 41(4):743-751.

BILLINGS, W. D. 1952. The environmental complex in relation to plant growth and distribution. Quart. Rev. Biol. 27:251-165.

COLLIE, GEORGE. 1901. Wisconsin shore of Lake Superior. Geol. Soc. Amer. Bull. 12:197-216.

CONWAY, V. M. 1949. The bogs of Central Minnesota. Ecol. Monogr. 19:173-206.

COOPER, W. S. 1958. Coastal Sand Dunes of Oregon and Washington. Geological Society of America. Memoir 72. 169 pp.

_____. 1967. Coastal Dunes of California. Geological Society of America. Memoir 104. 131 pp.

COWLES, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Bot. Gas 27:95-117, 167-202, 281-308, 361-391.

CURTIS, J. T. 1959. The vegetation of Wisconsin. An ordination of plant communities. Univ. Wisconsin Press, Madison, Wisc. 657 pp.

CUSHING, E. J. and H. E. WRIGHT, JR. 1965. Piston corers for lake sediments. Ecology 46: 380-384.

ENGSTROM, W. 1972. Spatial patterns in beach morphology and sedimentation in the Apostle Islands of northern Wisconsin. Ph.D. Dissert. Univ. of Wisc., Madison. 236 pp.

EVANS, O. F. 1972. The Origin of Spits, Bars, and Related Structures. p. 52-72. *In*: Spits and Bars. Schwartz, M. L. (ed.), Dowden, Hutchinson, and Ross. Stroudsburg, Penn. 452 pp.

FARQUHAR, O. C. 1972. Stages in Island Linking. p. 307-330. *In*: Spits and Bars. Schwartz, M. L. (ed.), Dowden, Hutchinson, & Ross. Stroudsburg, Penn. 452 pp.

FARRAND, W. R. 1960. Former shorelines in western and northern Lake Superior Basin. Ph.D. Dissert. Univ. of Michigan, Ann Arbor. 226 pp.

_____. 1969. The quaternary history of Lake Superior. 12th Conf. Great Lakes Research Proceedings: 181-197.

GATES, F. C. 1942. The bogs of Northern lower Michigan. Ecol. Monogr. 12:213-254.

GLEASON, H. A. and A. CRONQUIST. 1963. Manual of vasuclar plants of northeastern United United States and adjacent Canada. D. Van Nostrand Co., New York. 810 pp.

GODFREY, P. J. and M. M. GODFREY. 1974. The role of overwash and inlet dynamics in the formation of salt marshes on North Carolina Barrier Islands. P. 407-428. *In* Ecology of Halophytes. Reinold, R. J. and W. H. Queen, (eds.), Academic Press, New York. 605 pp.

GULLIVER, F. P. 1899. Shoreline topography. Proc. Amer. Acad. Arts and Sciences. 34:151-258.

HEINSELMAN, M. L. 1970. Landscape evolution, peatland types, and the environment in the Lake Agassiz peatlands natural area, Minnesota. Ecol. Monogr. 40:235-261.

HOUGH, J. L. 1958. Geology of the Great Lakes. University of Illinois Press, Urbana, Illinois. 313 pp.

JOHNSON, D. W. 1919. Shore processes and shoreline development. Wiley, New York. 524 pp.

KING, C. A. M. 1959. Beaches and Coasts. .. Edward Arnold, Ltd., London. 403 pp.

KUCHLER, A. W. 1964. Potential Natural Vegetation of the conterminous United States. American Geographic Society, New York. 116 pp.

LAING, C. C. 1958. Studies in the ecology of *Ammophila breviligulata* L. seedling survival and its relation to population increase and dispersal. Bot. Gaz. 119:208-216.

LEVERETT, FRANK. 1929. Moraines and Shorelines of the Lake Superior Basin. U.S. Geol. Survey Prof. Paper. 154-A:1-72.

LEWIS, C. F. M. 1969. Late Quaternary history of lake levels in the Huron and Erie basins. Proc. 12th Conf. Great Lakes Res. Int. Assoc: 250-270.

LEWIS, W. V. 1931. The effect of wave incidence on the configuration of a single beach. Geog. Jour. 78:129-143.

_____. 1932. The formation of Dungeness Foreland. Geog. Jour. 80:309-325.

LOY, W. G. 1962. The Coastal geomorphology of western Lake Superior. Univ. of Chicago M.S. thesis. Chicago, Illinois. 85 pp.

MARSHALL, ERNEST. 1967. Lake Superior ice characteristics. 10th Conf. Great Lakes Research Proceedings:200-214.

MARTIN, W. E. 1959. The vegetation of Island Beach State Park, New Jersey. Ecol. Monogr. 29(1):1-46.

MUELLER-DOMBOIS, D. and H. ELLENBERG. 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons. New York. 547 pp.

OLSON, J. S. 1958a. Rates of succession and soil changes on southern Lake Michigan Sand Dunes. Bot. Gaz. 119(3):125-169.

_____. 1958b. Lake Michigan dune development. I. Wind velocity profiles. Jour. Geol. 66:254-263.

_____. 1958c. Lake Michigan dune development. II. Plants as agents and tools of geomorphology. Jour. Geol. 66:345-351.

_____. 1958d. Lake Michigan dune development. III. Lake-level, beach, and dune oscillation. Jour. Geol. 66:473-483.

OOSTING, H. J. and W. D. BILLINGS. 1942. Factors effecting vegetational zonation on coastal dunes. Ecology 23:131-142.

SAARNISTO, MATTI. 1975. Stratigraphical studies on the shoreline displacement of Lake Superior. 12:300-319.

SCOTT, IRVING. 1926. Ice push on lake shores. Mich. Acad. Sci. Arts. Letters Papers. 7:107-122.

SHARP, R. P. 1953. Shorelines of the glacial Great Lakes in Cook County, Minnesota. Amer. Jour. of Science. 251:109-139.

TANS, W. E. and R. H. READ. 1975. Recent Wisconsinrecords for some interesting vascular plants in the western Great Lakes Region. The Michigan Botanis. 14:131-143.

TAYLOR, F. B. 1894. A reconnaissance of the abandoned shorelines of the south coast of Lake Superior. Amer. Geol. 8:365-383.

THWAITES, FREDIRK. 1912. Sandstones of the Wisconsin coast of Lake Superior. Wis. Geol. and Natural Hist. Survey Bull. No. 25. 117 pp.

TURNOCK, W. and D. B. LAWRENCE. 1953. Measurement of the level of the ground water at the Cedar Creek Natural History Area, central Minnesota. University of Minnesota, Dept. of Botany Report. 11 pp.

USDC. 1974a. Wisconsin. p. 450-452. *In*: Climates of the states. Vol. I., Water Info. Center, Inc., Washington, D.C., 480 pp.

USDC. 1974b. Duluth, Minnesota. Local Climatological Data. Annual Summary with Comparative Data. National Oceanic and Atmospher. Admin. Environm. Data Serv. Nat. Climatic Center, Asheville, N.C.

USDC. 1976. Great Lakes Pilot. Nat. Oceanic and Atmospheric Adm., Washington, D.C. 637 pp.

WRIGHT, H. E., JR., 1966. Stratigraphy of lake sediments and the precision of the paleoclimatic record. p. 157-172. *In*: Proceedings of the International Symposium on World Climate. Royal Meteorological Society, London. 324 pp.

WRIGHT, H. E., JR., D. A. LIVINGSTONE, and E. J. CUSHING. 1965. Coring devices for lake sediments. p. 494-520. *In:* Handbook of paleontological techniques. Kummel, B., and D. M. Raup, (eds.), W. H. Freeman Co., San Francisco. 852 pp.

WRIGHT, H. E., JR. and W. A. WATTS. (with contributions by S. Jerlgersma, J. C. B. Waddington, T. C. Winter, and J. Ogawa). 1969. Glacial and vegetational history of northeastern Minnesota. Minnesota Geol. Surv. Spec. Publ. 11:1-59.

# THE *SEQUOIADENDRON GIGANTEUM* EXHIBIT AT THE WORLD'S COLUMBIAN EXPOSITION IN CHICAGO, 1893[1]

Donald J. McGraw[2]

## PROLOGUE

Nearly one-half a millenium after Christopher Columbus first landed in the New World, the citizens of America made preparations to celebrate the four hundredth birthday of the discovery. It was the intention of ardent men across the land to assemble a great exposition to demonstrate the achievements of America. The year of the great fair was to be 1891-92. As is often the case with such gargantuan adventures, the sheer weight of the machinery bogged down into the morass of good intentions and it was not until October 1892 that Chicago hosted the World's Columbian Exposition, the "Chicago World's Fair."

A call went out across the country from the fair committee to states, regions, and counties to prepare exhibitions of local successes to better demonstrate to the world the agricultural, industrial, and cultural achievements of America. In a few counties, and in one in particular, the response to Chicago was unique. The County of Tulare in east-central California chose to send a section of Giant Sequoia, *Sequoiadendron giganteum* (Lindl.) Buchholz, 1939, as its exhibit.[3]

It was not the first time such an exhibit traveled east from California. Indeed, the matter of convincing fair-goers that such tree sections of the immensity common to the Giant Sequoia were real was no mean task. At the centennial fair of America's founding in Philadelphia in 1875, a sequoia section so shoddily cut and reassembled as to be unconvincing was labeled a "California Hoax." That demeaning appellation did not, however, fall upon the Tulare exhibit 18 years later in Chicago. It is one of the threefold purposes of this paper to indicate why the American populace accorded these two apparently similar exhibits with such differing receptions.

The story of the 1893 Tulare section has been recounted upon several occasions in rather disparate publications, but in each only highlights have been given and often only a modicum of historical accuracy is present. It is the second and main purpose of this study to present a fuller and, hopefully, more accurate history of the subject and, in so doing, to elaborate further upon already published, but abbreviated, accounts elsewhere. A variety of previously unpublished materials has come to light and assists in producing a fuller history.

The cutting operation of the tree was brilliantly recorded by a pioneer photographer, C. C. Curtis, and is a vivid account of the methods of preparation of the exhibit. Although a number of the scenes of the operation have been published, others have never been made available. It is the third purpose of the current paper to make the photographic history available in print.

The research on this subject was begun in 1970 during the author's first summer season as an interpreter on the staff of the General Grant Grove area of Sequoia and Kings Canyon National Parks.

## THE PROPER EXHIBIT

In historic Kern County, California, efforts had for some time been underway to select exhibition material for the Exposition. In a plan formulated in meetings between Kern and Fresno counties, it had been decided to ask Tulare County to join in a three-county central California exhibit consortium. A communication sent to the interested commission already extant in Visalia, Tulare County, was received favorably and its secretary responded that it would accept the tri-county invitation.[4] The commission then quickly approached the County Board of Supervisors to request an appropriation of $5000 in order to prepare a fitting exhibit. The Board took the matter under advisement with a promise to respond within a day or two. Apparently that did not happen, for on June 11 the *Visalia Daily Times* indicated that it had reminded the Board and others who read the newspaper that "the matter [of the appropriation] must not be dropped and all persons who have the welfare of the county at heart should give the matter their aid and attention."[5] The editors went on to suggest a petition be circulated to urge action on the part of the Board.

Several petitions were circulated--all in opposition to the appropriation. The *Times* editors remarked that the matter "seems to have settled itself down to a one-sided question."[6] Yet, inexplicably the matter was reversed by late July and early August when a long series of newspaper articles, not only in the *Times*, but in other Central Valley (California) dailies, began discussions on the Giant Sequoia that had been selected for the exhibit. Other evidence indicates that not $5000 but $15,000 actually was appropriated.[7] We are left with a gap in the historical record which would enlighten us on how this interesting reversal took place.

The *Times* first introduced to the county residents a tree cut on the land of Mrs. M. C. K. Shuey in Tulare County which it claimed had been selected as the exhibit.[8] In fact, this tree was apparently never intended for the Columbian Exposition. The most authoritative discussion of all *Sequoiadendron giganteum* trees cut for any exhibition purposes at any time occurs in the *Historical Bulletin* of the Tulare County Historical Society.[9] No explanation of the "Shuey tree" has been forthcoming regarding its final disposition. The *Times* went on, however, some day later to provide correct information on the actual exhibit tree, the General Noble.[10]

The Noble Tree was selected as the one to represent Tulare County in Chicago. It is an interesting aside that the tree itself was not actually within the confines of the county boundary lines of Tulare, but slightly to the north in that of Fresno. Evidently this never led to any acrimony or disagreements.

The name General Noble, like the names of so many other famous Giant Sequoias, recognized a military leader from the period of the War Between the States (but see below). The Noble was apparently the namesake of John Willock Noble (1831-1912), soldier, lawyer, and finally Secretary of the Interior. A native of Lancaster, Ohio, there is no evidence he ever saw the tree in its native environs. Whether he ever saw it or even knew of its existence as an exhibit at the fair is equally

unknown. However, the exhibit section held the most prominent place in the most notable building at the fair, the United States Government Building. Therefore, it would not seem surprising to surmise that Noble saw it, or was, at least, aware of the section. The official history written on the fair calls the tree section the John W. Noble tree,[11] and it is a fact that Noble, as Interior Secretary, strongly supported the American Forestry Association in regard to land law revisions in 1891.[12] Who named the tree for him and when is not known, if we depend upon Gray's small volume on named sequoias.[13]

Most trees named for generals were so named by men who fought under them during the War Between the States and who later came west often seeking adventure and fortune in the Sierra Nevadan lumbering enterprises. But no other tree within several miles of the Noble was named after a general in the 1860's to 1880's. It is the author's impression that the Noble was so christened only shortly before the cutting. It is believed that it was not by appreciative war veterans but by local lumbermen appreciative of Secretary Noble's favorable forestry stance.

The story of the Noble really begins with its cutting and it is that period about which most is known.

## FELLING A GIANT

On August 12, 1892, the first of three crosscuts was made into the General Noble and its existence as an exhibit for the next 39 years was established.[14] Its existence as a living thing, however, came to a halt.

An anonymous author in the *Historical Bulletin* of the Tulare County Historical Society said that

> *At first they* [exhibits of sequoia] *were greeted with skepticism but gradually the reports of eyewitnesses and the general distribution of photographs overcame doubts and California's Big Trees were accepted as facts.*[15]

It is true than many more people had seen the great tree in situ by the 1890's than by 1876 when the centennial "Hoax" was seen. Further, the photographic evidence provided by Curtis was undeniable. But a third factor was undoubtedly responsible for the belief that the exhibit of 1893 was not a hoax. The reason was that the Noble section was very carefully prepared as compared to the Centennial Tree.[16] The significant role of photographic evidence is considered in the next section, but the actual cutting operation must first be detailed here.

The General Noble grew on a piece of land just about three airline miles north of what was then General Grant National Park in a magnificent Sequoia grove known as the Converse Basin. The land was owned by the U.S. Government and was a forest reserve. A contract for sequoia cutting operations was held for that area by the Smith and Moore Company, and hence, they owned the Noble.

The Smith and Moore Company had purchased thousands of acres of land and, by 1888, had incorporated. Austin D. Moore, the company's president, was an extravagant character with a showplace home in San Francisco. The more practical partner, Hiram C. Smith, the vice president, was actually the woods boss and assumed direct charge of the Kings River operation which included the Converse Basin.[17]

The World's Fair commission of Visalia, with its $15,000 in hand, purchased the Noble (for $5,000) from Smith and Moore, who opened contract bids to cut and haul the sections. The successful bidder was a Mr. Burr Mitchell of the nearby village of Miramonte.[18]

Very few roads existed, even by 1892, in that heavily lumbered basin. For that reason, a contract to build a wagon road to haul out the sections was granted Mr. R. Ball of LeGrand, California, by Smith and Moore.[19] The road cost $1,500.[20] When the road was completed, it was possible to haul the sections to the valley hamlet of Monson, which was the railhead.

The first cut made that mid-August was 52 feet above the level of the ground, according to most reports.[21] That figure is probably correct in that a surveyor, Fred Beraria, had made extensive studies of the tree.[22] The diameter, at 52 feet, was 19 feet 6 inches, according to Beraria.

Although sequoias are routinely cut some distance above the ground to avoid the so-called "butt swell" at their bases, the matter of 52 feet might seem excessive. The reason for choosing that height was to allow for considerable quality material for exhibition below that level and above the swell.

Although a number of men were present during the cutting (they are named in the legend to Fig. 1), only five were actually involved in felling the tree. Gray notes that Burr Mitchell, Will Irwin, Dayton Dickey, and Jesse Pattee were involved. But Pattee (d. 1951), about whom most is known, has indicated that "Captain" Jamison[23] was the foreman.[24] The story of the cutting, which took 13 days, has been given in uneven sketches in Gray, the *Historical Bulletin* and in a variety of contemporary newspaper articles, as well as some more recent publications.[25] Not previously available in its entirety, however, is the text of a wire-recorded interview of Jesse Pattee done some years ago.[26] A similar interview with C. C. Curtis is also enlightening.[27] Blending these sources, the story becomes more vivid, but no less factual.

Jamison himself did not actually handle any cutting tools; only Pattee and his colleagues did. "Two Scotsmen, riggers from San Francisco, helped with scaffolds and ropework," Pattee remembered. Their names are unrecorded, but they may be among those pictured in Figure 1. As the main portion of the tree toppled from the first cut at 52 feet, it was expected to clear the tall stump with no difficulties. Indeed, a considerable number of falling wedges were inserted (by Mitchell) in the saw cut to assure a clean fall. But such a fall did not occur. The massive bulk of the tree slipped back upon the stump and smashed the scaffolding, leaving no escape route for Pattee and his partner at that dangerous moment. As the tree fell, the two men jumped onto the tall stump as their only avenue of escape. They lay there, face down, arms and legs spread, for a period of 20 minutes. It took that long for vibrations to cease before they could stand upright! The uneven fall broke off a large portion of bark and sapwood from the intended exhibit material below the cut. Curtis recorded on film that splintered piece, but the photograph is presumed no longer extant. He noted that the crew decided to "patch" on the splinter and said, "No one seemed to notice [the patch] at Chicago or anywhere else."[28] The repair must be laid as a tribute to the lumberjacks, for it was just such patching of even the properly cut parts on the 1875 tree that were so shoddy as to leave the impression of a hoax.

The next step was to remove staves of bark and sapwood each 14 feet in length The interior

(heartwood) of the stump was hollowed out and, according to Pattee, discarded. Figures 8-11 show this very well. Pattee indicated that the sections were marked, not with paint or something similar, but by a coded (?) pattern of nails driven into each section. That facilitated reassembly in Chicago, which was not done with any of the cutting crew present so far as can be determined.

After the staves were removed, a fresh stump surface 38 feet above the ground existed. A 2-foot-thick wheel section was removed in pie-wedge sections. This became the floor for the upper "room" of the final two-story high exhibit. Another 14 feet of staves were removed. This yielded two "rooms," one above the other and each with 14-foot high walls. The upper "room" had a 2-foot thick floor. The lower "room," then, had a ceiling, but the upper "room" was without one.

Ball (builder of the wagon road) hauled the carefully labeled and crated sections from the Converse Basin to the rail line at Monson. There the boxes were shipped to Chicago. No shipping date is known, but it must have been about August 25 or within a few days after that.

The entire operation was recorded masterfully by Curtis, whose story in regard to this entire project is a poignant one.

*Charles C. Curtis and His Photographs*

A native of Marshalltown, Iowa, Curtis (dates believed to be 1862-1955) first came to California in 1881.[29] He joined a studio in Hanford, California, in 1884 with a partner named Tandy who had advertised for an apprentice to learn the photographic trade. Shortly thereafter, he joined the now-famous Kaweah Colony, one of several well-known experiments in communism in the United States during the 19th century. Headquartered at Visalia, the colony sought to cut timber, including Giant Sequoias, in the area of Giant Forest in what soon came to be known as Sequoia National Park. The federal proclamation creating the Park in 1890 forestalled the cutting plans. The Colony dissolved not long afterward.[30]

Thereafter, all 11 summer seasons, Curtis did photographic work in the sequoia forests of the High Sierra in and near Kings Canyon and Sequoia National Parks. Additionally, he engaged in such work in a variety of nearby central valley communities.

Just prior to the cutting of the Noble, Curtis made an agreement with Smith and Moore to photograph the entire process. It was "no firm deal," he said.[31] Nevertheless, the loose contract ensured him funds to develop and print "thousands of [photographic] prints."

Upon completion of the field work and preparation of prints, he went to the fairgrounds in Chicago with the intention of selling copies to fair visitors. His discovery that only one Chicago-based firm (The Werner Company) had sole photographic concession rights came as a rude shock. It was possible, though, to obtain sales-licensing from that company for $250 per sales booth and 25% of the gross receipt.[32] The amount was beyond his means and so he telegraphed Smith and Moore at their corporate headquarters in San Francisco. He received no reply for several days. In a Chicago newspaper he recalled reading the saddening news that Smith and Moore Company had failed.[33] However a corporate biographer of Smith and Moore, Hank Johnston, does not provide evidence to support Curtis' recollection.[34] The company was in financial distress in 1892-94, however, but did not fail outright. What actually happened between Curits and Smith and Moore over his funding request remains unanswered.

In desperation Curtis turned to the Werner Company, holders of the exclusive concession rights, and sold "two or three thousand prints" to them.[35] By this time his ready cash had ebbed to the point that he sought from a distant relative living in Chicago (?) a loan sufficient only to get him back to California.[36]

Soon after his return, he read a newspaper article concerning a great warehouse fire in Chicago. It was the Werner warehouse wherein all his prints (though not negatives) were stored. The company had no insurance. About that time someone offered Curtis $3000 for the Noble negatives, but on the basis of the loose contract with Smith and Moore, Smith disallowed the sale.[37]

The demoralized Curtis moved to the Kettleman Plains on the west side of California's great Central Valley where he had 160 acres of land. The land had been purchased right after the Kaweah Colony failed near Sequoia National Park, when it had sought to move elsewhere. Although the Colony never moved, Curtis and some others privately purchased several 160-acre tracts.[38] He photographed the grain harvests, but lost what little money he had and his health, as well.

He moved northward to San Jose and took a laborer's position in a spice mill there in 1899. He hid a great number of photographic negatives under some floor boards in the mill building. Soon thereafter he moved to nearby San Francisco. In that city he worked at the J. A. Folger Company, coffee importers. He was credited with being one of the four men who helped save the Folger mill from burning during the great earthquake and fire of 1906. Shortly after the holocaust he learned that the spice mill was to be razed. He was able to recover the negatives without incident, however.[39]

Curtis passed the remainder of his life in first Berkeley, and then later Pasadena, California. Little more has been published on his life than that related above. His position in the history of western Americana and in photography remains to be assessed.

The camera he employed was a monstrosity of 45 pounds and used glass negatives of 8 by 10 inch dimensions. To develop the negatives Curtis awaited nightfall and worked under a red lantern. The prints were made on albumin paper which had been sensitized by silver nitrate solution.[40]

The series of photographs accompanying this paper are, to the author's knowledge, all of the pictures still extant taken by Curtis of the Noble cutting. Each picture is described separately in the figure legends. Andrews has indicated that all pictures of the cutting operation are published in his work (1958). This is not the case. Curtis has said that he took 18 pictures of the operation.[41] Andrews shows much fewer. The present work is not complete either, but is believed to be as complete as is now possible. Curtis had indicated implicitly that he provided Harold Schutt of the Tulare County Historical Society with copies of all remaining views.[42]

Other photographs accompany this narrative. Their origin is given in the figure legends and thanks for permission to reproduce them is given in the first footnote.

*At the Fair*

A German-American, Dr. T. W. Zaremba, made a



FIGURE 1. The cutting crew and others at the base of the Noble Tree. The men are l. to r. Sam Turk, Will Gwin, Dayton Dickey, Jesse Pattee, Capt. Jamison, Burr Mitchell, John Bodkins, Tom Gibson, Creed Archer. Identification after *Historical Bulletin,* 6:1950, Tulare County Historical Society. Schutt Collection.



FIGURE 2. Another view of the gathered men and their supplies at the base of the Noble. Some can be identified from Figure 1, others are unknown. Schutt Collection.



FIGURE 3. Capt. Jamison and Burr Mitchell at the base of the Noble. Schutt Collection.



FIGURE 4. Initial scaffolding prior to first cut. Platform is at 25 feet above ground level. The men in the scene are not identified. It is possible the woman is Charles C. Curtis' wife. Schutt Collection.



FIGURE 5. First cut at 52 feet and accomplished by double-bladed axe. It appears that the saw-cutting from opposite the axe is about ready to begin. Schutt Collection.



FIGURE 6. The actual fall of the Noble. Although this reproduction is not of great quality, it is apparent that the original photo was very well done. To catch a tree in the act of falling without blur on the older, slow-speed films was the mark of a first-rate photographer. Schutt Collection.



FIGURE 7. A view of the upper portion of the Noble as it lay on the ground (lower left). The great split later to be "patched" can be seen on the left side of the tall stump (right of center). Schutt Collection.



FIGURE 8. Hollowing and sectioning the "upper room." Note careful handling of exhibit section on end of winch line. Schutt Collection.



FIGURE 9. Time out for a bear hunt. Note slain American Black Bear, lower center. The men are not identified, but hunter (with rifle) may be Creed Archer. Schutt Collection.



FIGURE 10. The wheel section ("floor" of "upper room") has been removed. The platform is in the third, or lowest, position preparatory to cutting sections of the "lower room: of the exhibit. This picture, printed backwards, shows the split on the right side of the trunk above one man's head. Schutt Collection.



FIGURE 11. Hollowing and sectioning the "lower room." Schutt Collection.



FIGURE 12. A view of unloading marked sections to a waiting wagon. This scene was repeated many times throughout the cutting operation. Schutt Collection.



FIGURE 13. The last wagon leaves with exhibit sections and the cutting is complete. Schutt Collection.



FIGURE 14. Wagons with sections move down the specially constructed road on the way to the railhead. Reprinted from Andrews' *Redwood Classic*, with permission.



FIGURE 15. The Noble exhibit as it appeared in the rotunda of the U.S. Government Building at the World's Columbian Exposition, 1893. After a German-language Fair guide publication of unknown origin.

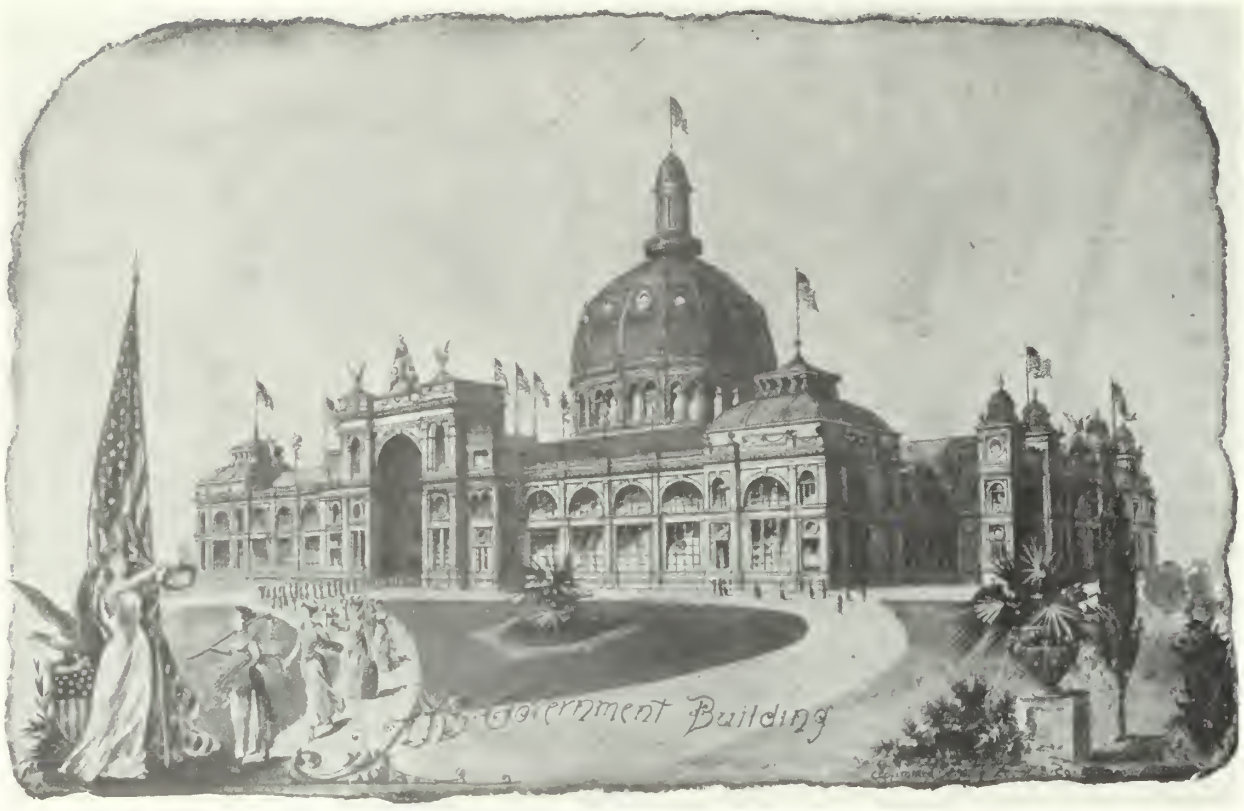



FIGURE 16. The U.S. Government Building. After Truman, *History of the World's Fair.*



FIGURE 17. The Noble exhibit as it appeared while on the Mall in Washington, D.C. Note the cupola-bearing roof which at first protected visitors to its interior and later the stored lawn-care tools. The photo was taken by Harry Shannon, a newspaperman, in 1915. Note a portion of one of the original buildings of the Department of Agric ulture (built 1867) in the left background. Collection of the Columbia Historical Society.



FIGURE 18. A picture of Jesse Pattee as he looked in 1950 shortly before his death. Taken by Harold Schutt, the Noble Tree, known to modern visitors as the "Chicago Stump," is in the background. Schutt Collection.



FIGURE 19. The Noble tree stump ("Chicago Stump") in 1950 with Jesse Pattee in foreground. Note that the bark has almost completely sloughed off. A holocaust fire which swept the area in 1955 destroyed the ladder which was never replaced. Schutt Collection.



FIGURE 20. Charles C. Curtis. Reprinted from Andrews' *Redwood Classic*, with permission.



FIGURE 21. The home of Charles C. Curtis and his family while recording the Noble cutting. The house is built upon a sequoia stump. Curtis is looking out the window with a daughter (Cecile?) by his side. Reprinted from Andrews' *Redwood Classic*, with permission.

pronounced effort in June of 1884 to assemble a World's fair to commemorate the 400th anniversary of Columbus' discovery. The event was to be held in Mexico, but soon thereafter, Chicago was decided upon. The history of the Worlds' Columbian Exposition has been best treated in Truman and the interested reader is referred to this rather rare volume.[43]

The *Visalia Daily Times* began a 2-year long series on happenings at the "World's Fair" on July 2, 1892. Great excitement then and throughout the reports the *Times* carried was in evidence, for Tulare County was to be well-represented. Not only would a great many exhibits be in the California Building, but the Noble section would have the distinction of standing in the great rotunda of the United States Government Building, surely a great honor.

The agricultural prowess of Tulare County would be well-represented for

> *it is only necessary that our* [agricultural] *advantages be known abroad to attract an enterprising class of settlers and hasten development in which all are interested.*[44]

Finally on October 20, 1892, nearly a year later than originally planned, "an immense parade" of more than 50,000 participants opened the World's Columbian Exposition.

The newspaper accounts in Tulare County indicated that considerable excitement had been generated by the Fair. Local merchants capitalized on the event in a variety of ways. Merchants S. Sweet and Company in Visalia even offered hardbound books (*The Columbian Worlds Fair Atlas*, a guidebook) to their customers free of charge.[45]

Tulare County residents were exhorted to see the Fair and their county exhibit in person by purchasing a ticket on the Santa Fe Route:

> *Ho For Chicago!*
> *How to get to the World's Fair is the question*
> *The railroads want $100*
> *for the round trip ticket*
> *and there are many people*
> *in Tulare County who will*
> *have to stay at home. This*
> *will be too bad for everything*
> *worth seeing in the civilized*
> *world will be on exhibition*
> *in the windy city . . ..*

Therefore, one only had to contact the *Visalia Daily Times* office to find out how, for three weeks' labor (doing what was not specified), one could earn enough money for the trip or

> *. . . to secure a $75 sewing machine, or a paid-up scholarship for six months in the Chestnutwood Business College at Santa Cruz* [California].[46]

So it was in Visalia and across the country, Go to Chicago. How many Visalia residents or visitors in general ever saw the Noble remains unknown.

In addition to the 8,000 half-pound boxes of raisins given out by Fresno County exhibitors during the Fair, they also displayed a mysterious statuette. Carved by "a young Italian" in the likeness of Mercury, the statue was said to have been from wood taken from the Noble. A picture of such a sequoia-wood statuette exists in the files of Grant Grove, Kings Canyon National Park (and in the authors collection), but its origin is unknown. As well, the identity of the "young Italian" remains mysterious. The whole matter is discussed in only one source and is not referred to elsewhere.[47]

The Fair passed into American history and the exhibits went back to their respective states in most instances. The Noble section, however, was destined for another, rather bizarre fate.

### *Washington, D.C., and the Mysterious End of the Noble*

At the close of the Fair in 1893. the Noble was moved (by whom, by whose orders, or when exactly, are unknown) to Washington, D.C. There, on a concrete slab poured for the purpose, stood the Noble Tree section from 1893 until 1932. With a cupola roof (see Fig. 17) it hosted visitors for many years. But, sometime prior to 1932, the spiral staircase was condemned and the whole exhibit closed to public use.

For several more years the "structure" held lawn-care tools used by federal employees in their lawn-work near the old Department of Agriculture Building (erected in 1867). The Noble stood near the northwest corner of Independence Avenue and Twelfth Street, southwest, on a mall proper. Various guidebooks of the day note it.[48]

"The Rambler" (columnist Harry Shannon) in the October 31, 1915, issue of the Washington *Sunday Star* said,

> *The old redwood tree trunk which has stood in the* [Agriculture] *grounds since mature men and women of Washington were boys and girls, has taken on a mantle of ivy. Few persons pass this old relic without stopping to examine it and at least to pay it the tribute of a glance, and this long dead tree is one of the most frequently photographed objects in the Capital.*

Several years later it was a central picture in the artgravure of the *Washington Post*.[49]

In 1932, it was dismantled and placed in storage in that condition in a steel shed at the United States Department of Agriculture Experiment Farm in Arlington, Virginia. It is not known why.

In 1952, a manager of the Pacific Lumber Company of San Francisco wrote the National Park Service. He was inquiring about the disposition of the section which he surmised was of a tree cut in 1854. The NPS seemed uninformed in 1952 about the Noble and directed the letter to David Lynn, then Architect of the Capitol. He seemed as poorly informed but believed the Noble was moved to Beltsville, Maryland, when the Experiment Farm land was transferred to the Army for war use. This has never been substantiated.[50]

With all the revived interest generated by this author in determining the final disposition of the Noble section, no more information than was available in 1956 has been forthcoming. In that year W. D. McClellan, originally of Tulare County and employed at United States Department of Agriculture in Washington, stated

> *I have talked with several men at Beltsville who were acquainted with the Sequoia tree . . . Jimmy Taylor, our greenhouse foreman, Joe Rhodes and Johnny Alexander, our two fieldmen, were all familiar with it. They said they used it for tool storage . . .. After removal from* [the Mall] *to Arlington Farm it was enclosed in sheet metal. None of these men know of any*

*order for moving it when* [the Farm] *was taken over by the Armed Forces for* [construction of] *the Pentagon, Rhodes and Alexander were the last two men to move material from Arlington Farm to Beltsville.*

*Just by chance I did talk with a man at Beltsville who had just previously been told of the final disposition of the tree. It seems that the Colonel* [in charge of the move] *called someone at Beltsville* [at USDA] *asking what they wanted done with the tree. This Colonel was told to forget he had asked the question and to use his own judgement. What he did I don't know but the tree may be buried under the Pentagon to be unearthed by some future archeologists who will speculate on the finding of a* Sequoia Gigantia [sic] *at that location!*[51]

It seems an inglorious end for such a noble tree. The record of misuse of these magnificent trees is astounding, however. Yet the Noble served an important educational purpose in its American odyssey, even though it would probably be alive today had there been no World's Columbian Exposition.

FOOTNOTES

1. For their many efforts the author wishes to thank Harold Schutt, Tulare County Historical Society; Robert Truax, Columbia Historical Society; Doris Randall and Marge Hamlin, Tulare County Library; the staff of Sequoia and Kings Canyon National Parks; authors Hank Johnston, Ralph W. Andrews, Kramer Adams; Elbert Little, U.S.D.A.-F.S.; Helena M. Weiss, D. H. Nicolson and Conrad V. Morton, National Museum of Natural History-Smithsonian Institution; Lllewelyn Williams, U.S.D.A.-Agricultural Research Service; Paul Spivey, U.S.D.A.-F.S.; David Mendengall, *Chicago Tribune*; Sylvia Arrigoni, Chicago Public Library; Kenneth B. Pomeroy, American Forestry Association; Larry L. Meyer, *Westways* magazine; Records History, U.S. Army; Lee S. Motteler, Rand-McNally and Company.
2. Biology Department, Franklin College, Franklin, Indiana 46131.
3. The binomial used here is that currently deemed most correct by R. J. Hartesveldt et al., in *The Giant Sequoia of the Sierra Nevada*, Washington, D.C., Government Printing Office, 1975, page 24.
4. Article, *Visalia Daily Times*, June 7, 1892, p. 2.
5. Article, *Visalia Daily Times*, June 11, 1892, p. 1.
6. Article, *Visalia Daily Times*, July 25, 1892, p. 2.
7. Fern Gray, *And the Giants Were Named* (Three Rivers, California: Sequoia National History Association, n.d.), p. 12.
8. Article, *Visalia Daily Times*, date undeterminable, but ca. August, 1892.
9. *Historical Bulletin* (Visalia, California: Tulare County Historical Society, October, 1950), No. 6.
10. Article, *Visalia Daily Times*, August 13, 1892, p. 1.
11. Maj. Ben C. Truman, *History of the World's Fair* (Chicago: Monarch Book Co., 1893).
12. Dumas Malone, ed., *The Dictionary of American Biography* (New York: Scribners, 1934), p. 539ff.
13. Gray, *And the Giants Were Named.*
14. The date of Aug. 12 has never been published elsewhere but is established by an article in the *Visalia Daily Times*, Aug. 13, 1892, p.1.
15. *Bulletin*, p. 1.
16. *Ibid.*, p. 1-6.
17. Hank Johnston, *They Felled the Redwoods* (Los Angeles: Trans-Anglo Books, 1966). p. 24.
18. Gray, and *Bulletin*, p. 1.
19. *Ibid.*
20. Article, *Visalia Daily Times*, Aug. 13, 1892, p. 1.
21. Gray, and *Fresno Weekly Republican*, Aug. 19, 1892, p. 8. However, others set the height at 50 feet. See *Bulletin*, p. 1.
22. Gray.
23. The U.S. Army has no records of a Captain Jason and no other sources discuss him. His identity has remained a mystery. All others mentioned above in the figures were local lumberjacks or, in Mitchell's case, a local landowner-lumberjack.
24. Harold Schutt, transcript of a wire-recorder interview with Jesse Pattee, Feb. 17, 1947. Xerographic copy of transcript in author's files.
25. For example, in Ralph W. Andrews, *Redwood Classic* (New York: Bonanza, 1958), p. 109.
26. Schutt, transcript.
27. The transcript of an interview with C. C. Curtis done by J. R. Challacombe, no date, a popular expositor on sequoia lore, was provided the author by Harold Schutt. Xerographic copy in the author's files.
28. Challacombe, transcript.
29. In *Redwood Classic*, Andrews states (p. 109) that Curtis came to California prior to 1880. This is apparently derived from an interview with one of Curtis's daughters conducted by Andrews. This seems in error as Curtis himself has stated, at least twice, that the year was 1881. The corroboration is in the interview with Curtis by Challacombe and in a letter from Curtis to Schutt in 1950. Neither of these sources was available to Andrews.
30. The history of the colony has been treated in several publications, but see Douglas Hillman Strong *Trees or Timber* (Three Rivers, California: Sequoia Natural History Association, n.d.), p. 22ff.
31. Challacombe, transcript.
32. *Ibid.*
33. *Ibid.*
34. Johnston, *They Felled*, p. 25.
35. Challacombe, transcript.
36. *Ibid.*
37. *Ibid.*
38. Andrews *Classic*, p. 109, and Challacombe transcript.
39. Andrews, *Classic*, p. 109.
40. *Ibid.*
41. Schutt, 1950 letter, and Challacombe, transcript.
42. Schutt, 1950 letter.
43. Truman, *History.*
44. Article, *Visalia Daily Times*, July 16, 1892, p. 1.
45. Advertisement and copperplate, *Visalia Daily Times*, Jan. 12, etc., 1893, p. 3.
46. Advertisement and copperplate, *Visalia Daily Times*, Aug. 2, etc., 1893, p 3.
47. *Report of the World's Fair Commission*(San Francisco: State of California, 1893), p. 43
48. For example, a variety of Rand-McNally Guidebooks of the Capitol mention it, viz., "A tower in the garden, composed of slabs with their foot-thick bark from one of the giant trees (Sequoia) of California, should not be neglected, for it represents the exact size of the huge tree, General Noble, from which the pieces were cut" (1900 edition; same wording for next 15 yearly editions). Also, it is shown in map form in *What There is to See in the United States Department of Agriculture* (Washington, D. C.: U.S.D.A., ca. 1922), p. 6

and map (unnumbered pg.), a guidebook.

49. Article and photograph, *Washington Post*, Mar. 13, 1921, artgravure section.

50. Edric C. Brown, letter to Director NPS, Jan. 11, 1952; and David Lynn, letter to Edrec C. Brown, Nov. 6, 1952. Xerographic copies in author's files from originals in files of Columbia Historical Society, Washington, D.C.

51. W. D. McClellan, in a letter from him quoted in *Los Tulares* (successor to the *Historical Bulletin*), *Quarterly Bulletin of the Tulare County Historical Society*, No. 26, Mar. 1, 1956, p. 2.

# PALEOECOLOGY OF HOLOCENE AND PLEISTOCENE LACUSTRINE SEDIMENTS FROM ZION NATIONAL PARK, UTAH

Richard H. Hevly[1]

Naturally formed lakes are relatively rare phenomena among the wind and water sculptured plateaus, mesas, and canyons of the lower elevation and relatively more arid portions of southern Utah and adjoining northern Arizona. Not infrequently, however, one encounters geological evidence of the former existence of lakes in such areas. The lakes have been formed in a variety of ways, but often they have been the result of damming of streams by lava flows and landslides. The sediments accumulated behind such dams often include fossils indicative of environmental conditions at the time of sedimentation. While accumulation of *lacustrine* sediments in such basins varies with climatically and edaphically controlled runoff, sedimentation could potentially occur during intervals characterized by non-sedimentation or even erosion in *alluvial* environments. Hence, analysis of the fossil content of such lacustrine sediments affords not only the opportunity to reconstruct the environment of deposition but also obtain paleoecological data on temporal intervals often lacking in nearby alluvial records.

Recently an opportunity became available to examine sediments of five lakes in Zion National Park, Sentinal Slide Lake, Paria Lake (= Taylor Creek Slide Lake), Beatty Lake (= Taylor Creek Bog), Trail Canyon Lake, and Coalpits Lake (Fig.1). These localities may be characterized as occurring between 4200 and 6300 feet elevation in Pinyon-Juniper Woodland with bordering pine-oak-fir forest in adjoining coves and Chaparral on adjoining exposed south-facing slopes. Near streams which border the sample localities abundant riparian deciduous trees occur, including such taxa as willow *(Salix)*, cottonwood *(Populus)*, ash *(Fraxinus)*, alder *(Alnus)*, hackberry *(Celtis)*, walnut *(Juglans)*, birch *(Betula)*, and maple *(Acer)*. Further details concerning location and geology are given in Hamilton (1977).

All of these lakes except Beatty Lake have breached their dams and erosion has exposed the lacustrine sediments in the banks of small washes. The sediments have been deposited in successive layers of coarse to fine grained texture with intervening layers of darker colored more organic sediments. Fossils sought included microfossil invertebrates, algal relicts and the spores and pollen of various plants as well as macrofossils such as invertebrates (*e.g.* snails and various arthropods), bones of vertebrates, and various plant fragments such as seed. Macrofossils were recovered by screening of the sediment and microfossils were recovered by chemical digestion of sediment samples. The sediment samples were usually obtained in a manner typical for arroyos: *e.g.* removal of 100 g samples from the principal strata in the cleaned face of a profile. At Beatty Lake, an extant landslide lake, a 2½ inch livingston piston corer was used to obtain a 1.35m core subsequently divided into 5cm intervals.

Samples were extracted by routine HCL-HF procedures for disaggregation and solution of carbonatesand silicates followed by acetolysis and KOH treatment for solution of soluble organics. A drop of acid-resistant residue from each sample was mounted on individual slides and covered by a #1, 22 x 40 mm coverslip. These preparations were scanned with a Leitz research microscope at a magnification of 450x. Macro- and microfossils were identified using standard references. Pollen proportions were determined and graphed. Selected proportions were graphed as departures from standardized means reducing the significance of variation in local vegetation for interpretation.

Macrofossils (except mollusks in some localities) were scarce and poorly perserved as noted for landslide lakes in Northern Arizona by Lance (m.s.). Vertebrate bones (*Bison, Thomomus*, fish and bird) were recovered from Pleistocene Lake Trail Canyon (Hamilton, in press). Tracks of Camel and a variety of invertebrates including horsehair worm, ant, beetle, and aquatic insect larva as well as impressions of aquatic plants and a mussel were found in sediments of Coalpits Lake (Hamilton in press). Mollusks were found in all lakes and carbonized roots and stems of plants were encountered in some horizons particularly in the Holocene landslide lakes. From a total of 204 mollusks obtained from the Holocene landslide lakes (Table 1), only three shells of aquatic snails *(Gyraulus* and *Physa)* and one valve of a clam *(Sphaerium)* were recovered. The Pleistocene lava lakes have thus far yielded 98 mollusks of which 87 are aquatic species (Table 1).

Microfossil remains were more abundant and more consistently recovered than previously studied landslide lakes, including pollen of seed plants, spore of Bryophytes *(mosses* and *liverworts)* and Pteridophytes (ferns and fern allies, *e.g. Selaginella,* spike moss, and *Equisetum,* horsetail or scouring rush). The sediments proved to be largely devoid of microscopic aquatic invertebrates and algal remains but a few Diatoms were found and they were limnophilous periphytic species which thrive in water of high pH and conductivity suggesting shallow environments of high evaporatic potential (Table 2). Only the pollen of seed plants were recovered in sufficient quantity from the relatively more fine textured and organic strata to determine the relative abundance of major types (presence only of other microfossils is indicated below; Fig. 2). Where possible, a pollen count was made of the first 200 grains encountered in contiguous non-overlapping rows. Percentages of the pollen counted in each sample were determined and are shown graphically below (Fig. 2), arranged according to provenience and stratigraphic relationship.

The pollen record can basically be divided into two major categories: arboreal (AP) or tree pollen and non-arboreal (NAP) or shrub, herb and grass pollen, The arboreal pollen includes such types as pine *(Pinus)*, juniper *(Juniperus)*, oak *(Quercus)*, PAP *(Picea, Abies, Pseudotsuga)* and RAP (riparian tree pollen). Pine pollen was further categorized as to size, the smaller grains being mostly referable to pinyon pine, while the larger grains are mostly referable to yellow and

[1]Department of Biological Sciences, Northern Arizona University.

white pines. Non-arboreal pollen included numerous pollen types such as Cheno-Ams (Chenopodiaceae, gossfoot or lamb's quarter family + *Amaranthus* or pigweed), Compositae (sunflower family, including Artemisia or sagebrush), Gramineae (grass family). Pollen of various aquatic herbs such as the Cyperaceae (Sedge family), Umbeliferae (Carrot family), Cruciferae (Mustard family), *Potamogeton* (knotweed), *Typha* (cattail), *Lemna* (duckweed), and *Myriophyllum* (water milfoil), was counted. The pollen sum included only terrestrial plants excluding the pollen of aquatic plants whose proportions were based on the total pollen count (Fig. 2).

*Beatty Lake and Paria Lake:* These lakes constitute a series of slide lakes on the same tributary in the northwest corner of Zion National Park. Beatty Lake (pollen series A) is an extant pond situated in a narrow canyon vegetated by pinyon-juniper-oak woodland (ponderosa pine and fir in coves) at an elevation of 6300 feet. This pond is very shallow, weed filled, and bordered by riparian trees. The sediments were found to consist of more or less inorganic red clay to a depth of 130 cm. Pollen was obtained only from the relatively more organic strata at depths of 0, 10-15, 20-25, 35-40, and 100-105 cm. Except for occasional fragments of the leaves and stems of aquatic herbs, no other macrofossils were found. The pollen record of the upper 40 cm. is relatively homogenous and may provide legitimate modern comparative samples for fossil samples from Taylor Creek. For that reason it will be described in detail below.

The modern ephemeral weed-choked pond yields a pollen record with only 2 to 3.5% aquatic herb pollen. Although it is bordered by riparian trees, these pollen types constitute only 3.5 to 7.5% of the pollen record. The total arboreal pollen, including the riparian tree pollen, ranges from 46 to 53% of the pollen recovered from terrestrial plants. The most abundant arboreal pollen types are pine and juniper, averaging 26 and 15% respectively (P/S ratio = 60% pine) and reflecting more or less the local vegetation type. Two-thirds or more of the pine is composed of small pollen grains probably referable to pinyon pine, thus also reflecting the local occurrence of that species. Although locally abundant near the lake, Oak (*Quercus*) pollen constitutes only 3.0 to 7.5% of the pollen form terrestrial plants, a pattern typical of western oaks. Nearby cove forests contain ponderosa pine, Douglas Fir (*Pseudotsuga*), and White Fir (*Abies*). Large pine pollen grains, probably largely referable to ponderosa pine, constitute about one-third of the pine pollen observed, and pollen from other conifers of the cove forests contribute 1.5 to 3.0% of the total pollen recovered. The remaining 36 to 54% of the pollen record is non-arboreal pollen composed predominately of Cheno-Ams, Compositae, and Gramineae, averaging 11.5, 17.0 and 9.0% respectively.

Tree-ring studies of a very old ponderosa pine which was partially buried by the rock-fall dam creating Beatty Lake indicate that this damming probably occurred about A.D. 1469 (Laing and Stockton, 1976). Approximately 25 meters of alluvium have accumulated behind this dam suggesting an average sedimentation rate of 5 cm per year, closely agreeing with modern rates of 4.5 cm per year, based on observations of sediment transport by Hamilton (in press). Therefore, the pollen record probably does not represent more than 30 years of record. The deepest sediments of Beatty Lake have not as yet been sampled, but those which have been sampled are sandier than the upper ones and contain a pollen record characterized by arboreal pollen percentages ranging from 56 to 60%. Pine pollen is more abundant and juniper less abundant than in the upper 40 cm of pond sediments. Pollen of riparian trees and aquatic herbs is more rare and the pollen of Compositae more abundant than in the upper sediments. Thus, at least one undated, drier, cooler episode is recorded in the sediments of Beatty Lake.

The entire 13-meter section of Paria Lake (area = .04 mile$^2$; Hamilton, in press; pollen series C and B) differs from the stratigraphically superimposed Beatty Lake in the predominance of sandy to gravelly sediments containing a variety of fossils, including organic lenses of herbaceous plant hash, stumps and limbs of trees, gastropods, and a number of different kinds of microfossils such as pollen of seed plants, bryophyte and pteridophyte spores, and algal relicts (e.g. diatoms). The sediments of this lake are dated by $C_{14}$ dates of 2880 ± 200 and 3610 + 300 B.P. near the top and bottom of this section respectively (Eardly 1966; Hamilton, in press).

The upper sediments of the Paria Lake are particularly characterized by the occurrence of numerous lenses of plant hash approximately 2.5 to 7.5 cm. in thickness alternating with much thicker lenses of sand. This zone proved to be particularly productive of pollen unlike the majority of slide lake sediments sampled here and elsewhere in the Southwest (Lance, n.d.). The pollen record of the section, which was obtained almost exclusively from the organic seams, exhibited variation of composition and proportion of arboreal pollen both less and greater than that observed in the upper 40 cm of Beatty Lake. The surface sediments of Paria Lake are very sandy and gravelly and extremely eroded, but one sample (C-1) from very near the top of the section has yielded enough pollen for a 100-grain count. This sample is remarkable because of the great reduction of AP (8%) and increased relative abundance of NAP (89%), particularly of Compositae and Poaceae (55 and 21% respectively). The inferred environment based on modern AP pollen proportions from northern Arizona would suggest a warmer, drier environment than presently found in the study area; however, one that provided adequate moisture for the persistence of both aquatic herbs and riparian trees (3%). Although the AP record is very limited, the slightly greater relative abundance of juniper than pine may possibly indicate an open woodland or savanna with local over-representation of Compositae and Gramineae in the pine behind the lower dam.

The uppermost sample from Paria Lake differs strikingly from the next lower sample (B-1) which has high proportions of arboreal pollen (53.5%), particularly of juniper and PAP. Pollen of the Gramineae, Cyperaceae and Typhaceae are also more abundant than in the upper levels of Beatty Lake. Samples B-2 through B-8 are all remarkable because they contain less arboreal pollen than in the upper levels of Beatty Lake, while samples B-13, B-14 and B-17 contain more arboreal pollen than the surface or near-surface samples of the pond.

The implications of these AP proportions when compared to studies of modern pollen recovered from various plant communities of northern Arizona is that the environment surrounding Paria Lake has undergone change from woodland to savanna and back again to woodland on several occasions. Such apparent changes of AP proportions could, however, be strongly influenced by NAP production.

Studies of the modern pollen rain in northern Arizona have shown that analysis of AP composition (Pine-Juniper ratios and Pine-size ratios) can provide a technique of reconstructing environmental change independent of the influence of over-representation of local NAP (Hevly, 1968). When examined in this way (Fig. 3) only the 100-105 cm sample from Beatty Lake exhibits more pine in its pine-juniper ratio than found in the woodland vegetation of the Colorado Plateau; however, most samples from Paria Lake exhibit less pine and more juniper than found in the modern woodland pine-juniper ratios of the study area or on the Colorado Plateau. Samples with high AP and high pine proportions resemble near pine canopy situations in woodland, while the samples with high AP and high juniper resemble near juniper canopy situations in woodland. Samples characterized by low AP and with low pine and high juniper proportions probably reflect Juniper-Savanna (samples B-2 through B-8). Thus, the analysis of arboreal pollen generally supports the inferences developed on the AP/NAP ratios alone.

Pollen, spore, algal relicts (including several diatom types) and occasional shells of aquatic snails definitely indicate that at least the organic sediments of Paria Lake represent lacustrine depositional environments. At no time does this pond appear to have been deep, since plants tolerating only shallow water are present throughout the record and intervening sandier lenses contain only shells of land snails. Regionally at least two periods more xeric than at present. Plants very much like those occurring locally appear to have been present throughout the several thousand years spanned by this very fragmentary record.

*Sentinal Slide Lake:* Sentinal Slide Lake (Area = .772 mile$^2$; Grater, 1945; Hamilton, in press) is located in the south fork of the Virgin River at an elevation of about 4,300 feet and is surrounded by pinyon-juniper-oak woodland and chaparral with a riparian woodland the adjoining upland from which water and sediments are denied contain ponderosa pine, white and Douglas Fir and Aspen bordering the permanent stream. Sediments of Sentinal Slide Lake like those of Paria Lake contain abundant sands; however, in the Emerald Pool (--D--series) and to a more limited extent in the Birch Creek (--E--series) exposures of this lake, greenish or grayish clays and silts are common and often contain organic residues. At the Birch Creek locality a red silt near the top of the section (E-4) has been $C_{14}$ dated at 3600 ± 400 (W3371 Hamilton, in press).

In Sentinal Slide Lake only the organic clays and silts contain pollen, suggesting that pollen deposition and preservation occurred only in the depositional environments with low sediment transport capability. Pollen samples from Sentinal Slide Lake generally exhibit increasing relative abundance of pine and PAP with depth and increasing proportion of large pine pollen relative to small. Pollen of *Juniperus*, *Quercus*, RAP, *Ephedra*, Cheno-Ams, and Compositae generally diminish with increasing depth. The only departure from this general trend thus far detected occurs in sample E-4 where pine values drop to 6%, some 14% less than in modern samples. Compositae and and Gramineae pollen increase in relative abundance 27 and 6% respectively over modern values. Pollen of Cyperaceae, *Typha*, *Potamogeton*, *Lemna*, *Myriophyllum*, and *Equisetum*, *Selaginella*, ferns, bryophytes, and algal relicts also increase during this interval. The sediments of this horizon are brown silts including carbon films of aquatic plants while underlying and overlying this are thick strata of sand.

Pollen, spore, and algal relict and aquatic clam shells definitely indicate that the finer textured sediments of Sentinal Slide Lake represent lacustrine depositional environments. Beginning about 3600 + 400 B.P., the regional environment as reflected by the terrestrial pollen types became increasingly more mesic progressing backward in time to at least 4000 B.P. which Hamilton (1977) estimates to be the initiation date of Paria Lake.

The fluctuating presence and absence of pollen, spores, and algal relicts along with the variation of sediment texture suggest considerable instability in Paria and Sentinal Slide Lakes. That is, there appear to have been pulses of deposition characterized by fine-textured sediments, fossils, and apparently sufficient persistence of moisture that aquatic plants become established and accumulated more rapidly than they decayed. The periods characterized by coarser textured sediments and absence of fossils may represent relative brief periods of rapid deposition perhaps under conditions of flooding or at least conditions which were generally unsuitable for preservation of organic materials. Flushing of land snails form nearby surfaces probably occurred under such conditions. These lakes seem rarely to have had appreciable depth as pollen of deep water tolerant species was recovered abundantly in only a few strata of Sentinel Lake; however the alternating lacustrine and non-lacustrine depositional record may parallel in part the changing water level detected in other Post-Pleistocene Southwestern lakes (Hevly, 1964; 1974). These lakes provide a Post-Pleistocene record often missing in alluvial sections because of erosion. At least twice during the Post-Pleistocene, environment conditions as indicated by the above pollen data have undergone significant fluctuation suggestive of the Post-Pleistocene environmental changes widely documented in western North America (Adam, 1975; Hevly 1974; Madsen, 1972; Mehringer and Warren, 1976; Phillips and Van Devender, 1974; Sercelj and Adam, 1975.)

*Trail Canyon and Coalpits Lakes:* These lakes were formed by lava damming during the Pleistocene and the two samples described here provide an excellent comparative sample for Pleistocene palynology and paleoecology. The provenience of these lakes is different from that of Sentinal Slide Lake on the nearby North Fork of the Virgin River, since their watersheds at present contain no fir and little Ponderosa Pine. Modern samples obtained recently contain about 1% PAP, 20% pine (over half of which is composed of small sized grains), 16% juniper, 10% oak, 8% Cheno-Ams, 20% Compositae, and 13% Gramineae. The Pleistocene samples contain about 11% PAP, 76% pine pollen (over half of which is composed of large sized grains) and 8% grass pollen. The tremendous difference revealed by this comparison of pollen percentages clearly indicates the magnitude of environmental change that had occurred at lower elevations in Zion National Park since the retreat of the last continental ice sheets. The pollen record of these lakes indicates changes of magnitude and direction comparable to these found in nearby areas of Nevada and Northern Arizona as indicated by both macroscopic and microscopic data (Hevly and Karlstrom, 1974; Martin et. al., 1961; Mehringer, 1967; Van Devender and King, 1971; Spaulding, 1977; Wells and Berger, 1967).

TABLE 1. Fossil mollusks recovered by Hamilton (in press) from Holocene and Pleistocene Lakes, Zion National Park. Ecological data from Bequaert and Miller (1973).

| Terrestrial Gastropods | Southwestern Ecology | Trail Canyon & Coalpits | Fossil Occurrence Paria L. | Sentinel L. |
|---|---|---|---|---|
| Cochlicopa lubrica (Muller) | 4,500-9,000 feet in drift in seasonally most canyons | - | | - |
| Discus cronkhitei (Newcomb) | 2,750-12,000 feet in humid to moist conditions under rock or wood or in litter | - | 51 | 9 |
| Discus shimekii (Pilsbry) | 7,200-12,100 " " " " " " | - | 21 | |
| Euconulus fulvus (Muller) | 5,000-10,500 " " " " " " | - | 11 | 1 |
| Microphysula ingersollii (Bland) | 7,000-11,000 " " " " " " | | - | 2 |
| Oreohelix strigosa (Pilsbry) | 3,000-8,000 " " " " " " | | 1 | |
| Succinea avara (Say) | 3,500-7,200 " " " " " " | 6 + 1 | 95 | 5 |
| Vallonia perspectiva (Sterki) | 3,500-8,700 " " " " " " | | 13 | |
| **Aquatic Clams** | | | | |
| Pisidium sp. | Species not known but genus common in Southwest ranging from 3,500 to 9,500 feet in streams, and lakes and small ponds. | 5 | | |
| Sphaerium (Musculium) partumeium | Species not listed for Southwest. Other species range in elevation from 3,000 to 5,000 in creeks and ponds. | | | 1 |

| Aquatic Snails | Southwestern Ecology | Trail Canyon & Coalpits | Fossil Occurrence Paria L. | Sentinal L. |
|---|---|---|---|---|
| Physa sp. | Species not known but genus common in Southwest, ranging from 1,000 to 8,700 feet in small flowing streams and stagnant water. | | 1 | |
| Lymnae (Stagnicola) bulimoides | Subspecies not listed for Southwest. Other sub sp. range in elevation from 4,850 to 6,900 feet in springs, small pools, and other moist habitats. | 1 | | |
| Helisoma tenue (Dunker) = Planorbella tenuis | Ponds & lakes usually below 6,000 feet but ranging up to 8,700. | 1 + 4 | | |
| Gyraulus parvus (Say) | Springs, ponds & lakes between 3,000 and 8,250 feet | 17 + 54 | | 2 |

TABLE 2. Diatoms from Paria and Beatty Lakes. Identifications by David Czarnecki, Dept. Bio. Sci. N. Ariz. Univ., Flagstaff. Ecological inferences based on Lowe (1974).

| Taxa | Ecological Inferences | Fossil Occurrence Beatty L. | Paria L. |
|---|---|---|---|
| Cymbella cistula (Hemp.) Grun. | Alkaliphilous (opt. pH 8)<br>Oligosaprobic<br>Limnophilous to limnobiontic<br>Periphytic<br>Cosmopolitan | + (Loc.B) | |
| Epithemia turgida (Ehr.) Kutz | Alkaliphilous (opt. pH 8)<br>Saproxenous to beta mesosaprobic<br>Limnophilous<br>Periphytic<br>Common Southwest sp. | + Core A | — |
| Fragilaria vaucheriae (Kuts.)Pet. | Alkaliphilous (opt. pH 6.5-9.0) grows best in waters of high conductivity<br>Beta-mesosaprobic<br>Limnophilous to Rheophilous<br>Periphytic<br>Common Southwest sp. | — | +(Loc. B) |
| Navicula sp. | Too poorly preserved for identification Species of this genus usually inhabit standing water but a few occur in flowing water as well. Many species are periphytic becoming common in the summer and fall. | — | +(Loc.C) |

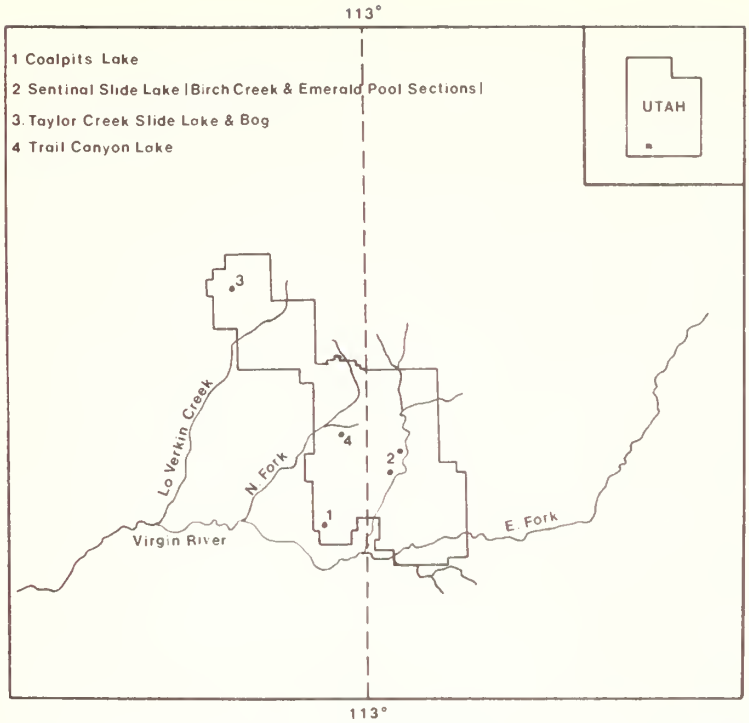



FIGURE 1. Map of Zion National Park showing the locations of five Holocene or Pleistocene Lakes: Beatty Lake (=Taylor Creek Bog), Paria Lake (= Taylor Creek Slide Lake), Sentinal Slide Lake, Trail Canyon Lake and Coalpits Lake.

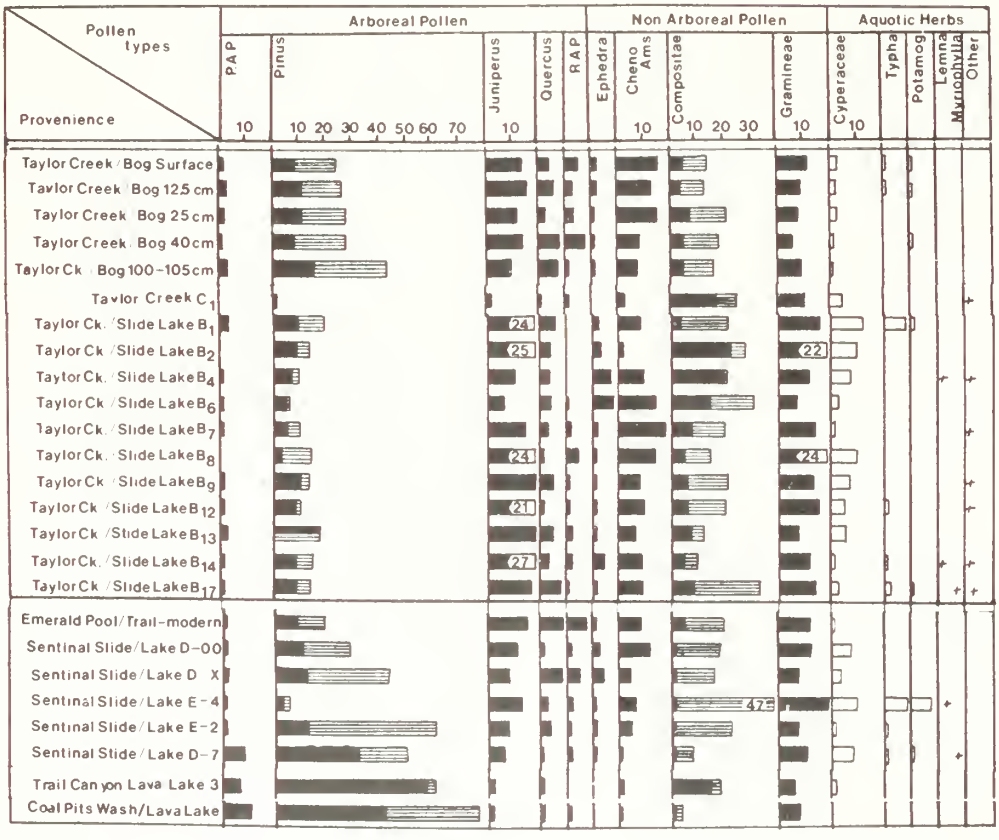



FIGURE 2. Pollen diagram of Beatty Lake (=Taylor Creek Bog), Paria Lake (=Taylor Creek slide Lake), Sentinal Slide Lake, Trail Canyon lava Lake and Coalpits lava Lake. The near equivalency of AP/NAP and AP composition ratios of Holocene Sentinal Lake sample D-7 and those from the Pleistocene Lakes seemingly suggests profound environmental change during the Neoglacial in Zion National Park exceeding that observed elsewhere in the Southwest. Alternatively the data may reflect redeposition of arboreal pollen from the Kolob Plateau with increased runoff water during particularly mesic interval since Martin (1963) has observed pine pollen to be transported in froth of summer flood water in southern Arizona. Such transport is not a universal phenomenon, however, since pine pollen was not recovered in summer flood froth in northern Arizona (Hevly, 1970) perhaps as a result of in flood fragmentation or oxidation prior to, during or after flooding or even removal by earlier floods. Therefore the data may reflect both expanded pine forest and an unknown amount of exaggeration due to redeposition since the records exceed other Southwestern records.

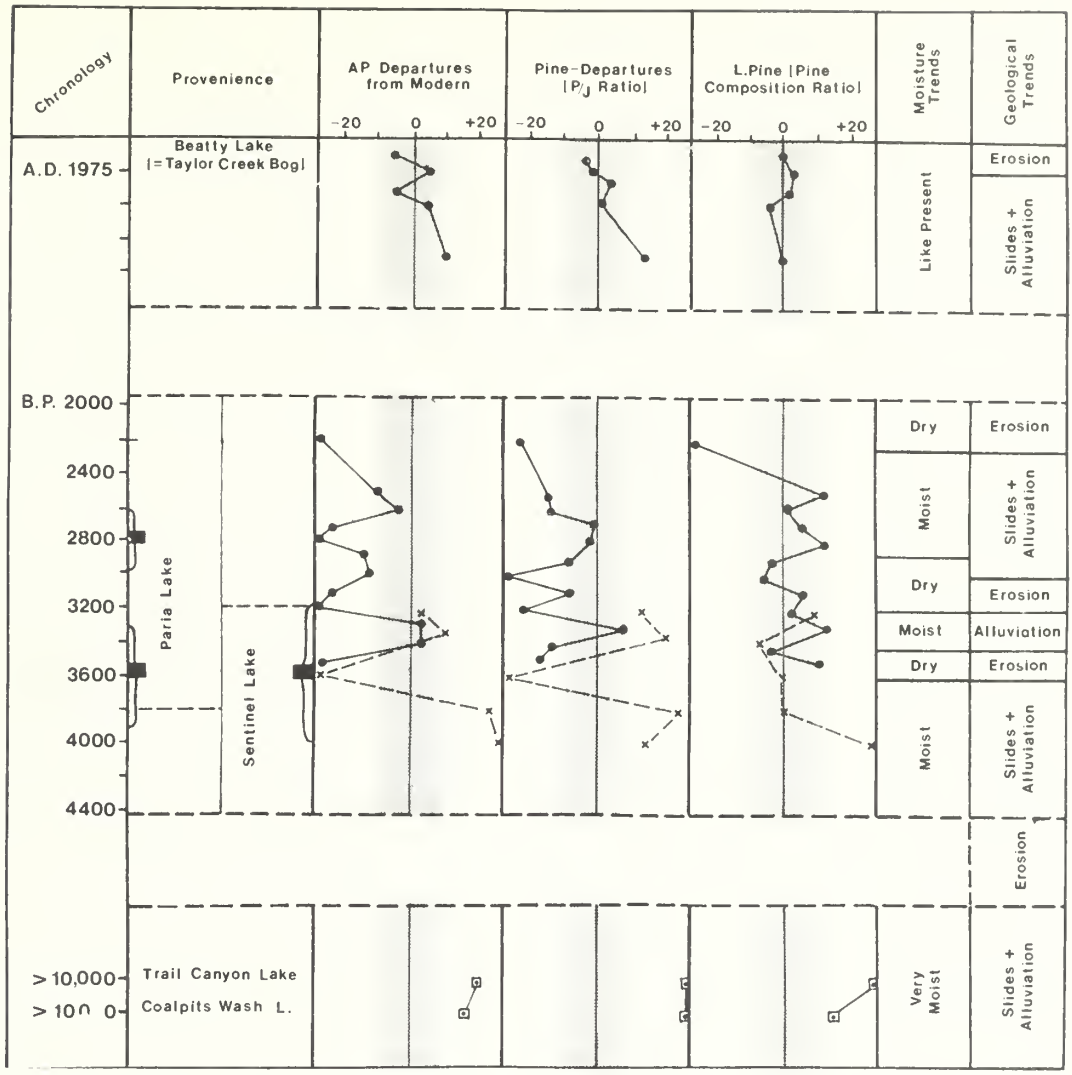



FIGURE 3. Summary diagram of major palynological data relating to moisture and geological trends. The palynological data are plotted as departures from mean pollen proportions of modern woodlands in northern Arizona and southern Utah, the stippled bars representing two standard deviations of pollen proportions from the mean values (percentages which exceed the stippled areas are significant at the 5% level). Both Paria and Sentinal Lakes leave breached their dams and have been eroded. Studies of growth in a tree whose roots were exposed by erosion of sediments of Paria Lake indicate that breaching of that lake occurred by A.D. 1740 (Laing and Stockan, 1976). A channel 130 meters deep has been cut in 230 years indicating an erosion rate of these unconsolidated sediments of about 6.3 cm per year. Carbon-14 dates indicate that this lake took at least 730 years to fill with sediment. More likely the duration of time to fill is several hundred years greater since the very youngest sediments to accumulate have been eroded away.

## SUMMARY AND CONCLUSIONS

The Holocene lakes of Zion National Park were formed by landslides during relatively more cool-moist intervals. Sedimentation in the resulting basins was primarily attributable to accumulation of fine to coarse grained sediments washed into the basin during periods of run-off from summer storms and melting snow. Differential sedimentation of the particles has resulted in successive layers of sand, silt and clay. The basins continued to accumulate sediments during intermittent periods of relatively more warm-dry intervals and alternating cool-moist intervals until the sediments filled the basins and the dams were breached. The duration of these lakes has been estimated to be generally less than a millenium.

The Holocene lakes appear never to have had appreciable depth as indicated by the scarcity of pollen of aquatic plants tolerant of deep water and the abundant pollen of aquatic plants tolerant of shallow water. As indicated by the ecological requirements of the scarce fossil diatoms, the water of the lakes appears to have been alkaline (pH 8-9) and of high conductivity further suggesting shallow environments of high evaporative potential. These lakes were also generally ephemeral as indicated by the scarcity of fossil snails requiring permanent moisture and the abundance of terrestial snails. Nevertheless there were some intervals during which standing water existed in these basins since diatoms, aquatic snails, and pollen of aquatic plants accumulated in darker colored, more organic seams among the alternating sands, silt, and clay layers.

Analysis of the sediments from these Holocene lakes has yielded for the first time a record of conditions during non-depositional intervals recognized in alluvial sections elsewhere in the Southwest. Environmental conditions changed significantly during the deposition of sediment in these basins, erosion, or non-deposition outside and sometimes inside the basins apparently corresponding to intervals characterized palynologically by diminished arboreal pollen while periods of alluviation and landslides were characterized by increased arboreal pollen. By comparison to modern pollen samples obtained from a variety of modern plant communities diminishing arboreal proportions should reflect increasing aridity while the opposite would be true of increasing arboreal proportions (Fig. 3). The interpretation so derived is in agreement with trends noted elsewhere in the Southwest.

The Pleistocene lakes are strikingly different from the Holocene lakes. The Pleistocene lakes formed behind lava dams rather than landslides. The snails are more abundant and many more of them are species requiring permanent moisture, suggesting greater permanence to these Pleistocene lakes than the Holocene lakes. Thicker accumulation of sediments also suggest greater duration for these lakes prior to breaching of the dams.

## ACKNOWLEDGEMENTS

Appreciation for financial support to undertake this study is expressed to the Zion National History Association and to Northern Arizona University for released time for analysis, interpretation and travel. The author has greatly benefited from the field and laboratory assistance of J. Ward and W. Hamilton who both contributed through discussion to the better understanding of the data presented herein. Partial results of this study were presented at the First Conference on Research in National Parks (A.I.B.S.) - New Orleans, LA, Nov., 1976 and the Arizona Academy of Science - Las Vegas, Nev., April, 1977.

## LITERATURE CITED

ADAM, D. P. 1975. A late Holocene pollen record from Pearson's Pond, Weeks Creek landslide, San Francisco Peninsula, California. J. Res. U. S. Geol. Survey. 2(6):721-731.

BEQUAERT, J. C. and W. B. MILLER. 1973. The Mollusks of the Arid Southwest. Univ. Ariz. Tucson. 271 p.

EARDLY, A. J. 1966. Rates of denudation in the high plateaus of southwestern Utah. Geo. Soc. Amer. Bull. 77:777-780.

GRATER, R. K. 1945. Landslide in Zion Canyon, Zion National Park, Utah J. Geo. 50(20):116-124.

HAMILTON, W. L. in press. Holocene and Pleistocene Lakes in Zion National Park. Proceedings of First Conference on Research in National Parks. (A.I.B.S.)

HEVLY, R. H. 1964. Paleoecology of Laguna Salada. *In*: P. S. Martin et al., Chapters in the prehistory of Eastern Arizona, II. Fieldiana (Anth.) 55:1-261.

_____. 1968. Modern pollen rain in Northern Arizona. J. Ariz. Acad. Sci. 5(2):116-127.

_____. 1970. Botanical Studies of a Strange Jar Cached at Grand Falls Arizona Plateau.

_____. 1974. Recent Paleoenvironments and Geological History at Montezuma Well. J. Ariz. Acad. Sco. 9(2):66-75.

HEVLY, R. H. and T. N. V. JARLSTROM. 1974. Southsest Paleoclimate and Continental Correlations. *In*: Geology of Northern Arizona. (T.N.V. Karlstrom and others, editors). Geological Soc. Amer. (Rky. Mt. Sect.) Field Guide 2:257-295. Flagstaff.

LAING, D. and C. W. STOCKTON. 1976. Riparian dendrochronology; a method for determining flood histones of ungaged watersheds. final report OWRT Project # A-058-An3. by laboratory of tree-ring Research, University of Arizona.

LANCE, J. F. n.d. Lake and Moqui Canyons. Unpublished manuscript.

LOWE, R. L. 1974. Environmental Requirements and Pollution Tolerances of Freshwater diatoms. EPA - 670/4-74-005. Cincinnati, 334 pp.

MADSEN, D. B. 1972. Paleoecological investigations in Meadow Valley Wash, Nevada. *In*: D. D. Fowler (ed.), Great Basin Cultural Ecology: A symposium Desert Research Institute Publications in Social Sciences. 8:57-65.

MARTIN, P. S. 1963. The Last 10,000 Years. Univ. of Ariz Press Tucson 87 pp.

MARTIN, P. S., B. E. SABELS and D. SHUTLER, JR. 1961. Rampart cave coprolite and ecology of the Shasta Ground Sloth. Am. J. Sci. 259:102-127.

MEHRINGER, P. J. JR. 1967. Pollen analysis of the Tule Springs Site, Nevada. *In*: Pleistocene Studies in Southern Nevada. H. M. Wormington and D. Ellis (eds.) Nevada State Museum Anth. Pap. No. 13:129-200

MEHRINGER, P. J., JR. and CLAUDE N. WARREN. 1976. Marsh, dune and Archaeological Chronologies, Ash Meadows, Amargosa Desert, Nevada. Nevada Archeo. Survey Research Report 6.

PHILLIPS, A. M. III and T. R. VAN DEVENDER. 1974. Pleistocene packrat middens from the Lower Grand Canyon of Arizona. J. Ariz. Acad. Sci. 9(3):112-119.

SERCELJ, A. and D. P. ADAM. 1975. A late Holocene pollen diagram from near Lake Tahoe, El Derado County, California. J. Res. U.S.G.S. 3(6):737-745.

SPAULDING, G. 1977. Late Quaternary vegetational change in the Sheep Range, Southern Nevada. J. Ariz. Acad, Sci. 6(4):240-244.

VAN DEVENDER, and J. E. KING. 1971. Late Pleistocene vegetational records in western Arizona. J. Ariz. Acad. Sci. 6(4):240-244.

WELLS, P. V. and R. BERGER. 1967. Late Pleistocene History of Coniferous Woodland in the Mohave Desert. Sciences. 155:1640-1647.

# PALYNOLOGY OF THE GALLATIN MOUNTAIN "FOSSIL FORESTS" OF YELLOWSTONE NATIONAL PARK, MONTANA: PRELIMINARY REPORT[1]

Phillip L. DeBord[2]

## INTRODUCTION

Thousands of people visit Yellowstone each year to see its geysers, travertine terraces and associated mineral pools, animal life, plant life, and the beauty of its terrain. Many backpack to experience Yellowstone's beauty in a deeper way.

However, few people ever see one of the most unique sights in all of the world-the "Fossil Forests" in Yellowstone.

Holmes' (1878) diagram (Figure 1) illustrates quite well the suggested sequence of events that produced the petrified forests. A forest was growing in a broad valley. A volcano erupted. The heavy ash covered the leaves and limbs of the trees, choking out life and causing them to fall off the main trunk. Breccia from the volcano caused the local streams to overflow their banks, inundating the forest. The slow-moving subariel or subaqueous breccias delivered the death blow to the forest, surrounding the trunks of the standing trees and preserving them in their position of growth. After approximately 200 years conditions were conducive for reforestation. A new forest grows to maturity and the sequence is repeated. Therefore, what is preserved for us is a series of forests (as many as 50) one on top of the other.

A number of studies of modern pollen (Lichti-Federovich and Ritchi 1968, Tinsley and Smith 1974, Webb III 1974) illustrate that there is a relationship between the pollen spectra and the vegetation of an area. Webb III (1974) states, "Maps of the relative abundances of pollen data, therefore, provide direct information about maps of the relative abundances of vegetational data."

The purpose of this study is to apply Webb's hypothesis to the unique setting of the Gallatin "Fossil Forests" in an effort to reconstruct the paleoclimatology, paleoecology, and depositional history of these forests.

## DESCRIPTION OF AREA

The study area is located approximately three miles from Specimen Creek bridge (which crosses U.S. Highway 191) on the southernmost flank of Big Horn Peak.

The stratigraphy of the area as described here is the result of the work of Smedes and Prostka (1972). A 335' vertical section with twenty-two forests has been described. The section starts at the contact between the Fortress Mountain Member and the Daly Creek Member of the Sepulcher Formation and descends to the tree line and associated ground cover. The section was started at the contact because of the visual distinctness between the two members. The Fortress Mountain Member is a light bluish gray color while the Daly Creek Member is a dark reddish brown to gray. Thus, any subsequent investigator can readily find the beginning of the section. The age of the section is late early Eocene to early middle Eocene, i.e., late Wasatchian to early Bridgerian provincial stage.

Petrologically, the Daly Creek Member in this section is composed of volcanic andesitic conglomerate in a pumice and ash matrix of alluvial origin (Smedes and Prostka 1972). Interbedded with the conglomerate are stratified lenses of tuffs containing organic material.

## METHODS

### *Field Techniques*

The section was described by the following procedure: 1) using a Brunton Compass and starting at the contact between the two members of the formation, I descended to the first organic zone; 2) this organic zone contained a vertical trunk with its base in the organic zone and therefore was designated unit 1 or forest 1; 3) the vertical depth of the unit was recorded; 4) the organic zone was traced across the slope and described in relation to thickness, organic content and any "unusual" characteristics, i.e., disappearance and reappearance, evidence of water deposition, and splitting into two or more zones; 5) vertical trunks were typed with a hand lens as being pine, sequoia, or deciduous, if field identification was not possible, wood samples were taken and identified from thin sections in the laboratory; 6) it was noted whether vertical trunks possessed roots and if so the condition of the roots; 7) the diameter of all vertical trunks, horizonal logs and diagonal logs was recorded as well as the intervening distance; 8) palynology samples were taken from the organic zone; 9) the distance between samples and the type tree near the collection site was recorded and 10) the grading, bedding, and sorting of the unit was recorded. The lateral extent of each forest was from the approximate area of the fault on the west end of the section around the corner on the east end to the tree line unless the breccia promontories were too precipitous (lower part of the section).

This study is concerned with units 1, 5, 6, 9, and 10 because they contain an adequate number of trees and discrete forest types.

### *Laboratory Techniques*

Because of the quality of preservation only thirty-one of the ninety palynology samples collected could be used for making pollen counts. Only six of the thirty-one samples had outstanding preservation quality; however, the rest could be utilized by assigning the pollen or spore to a major category. Three hundred grains, pollen or spores, were counted from each sample placing the entity into one of the following categories: 1) clubmoss or fern, 2) bisaccate, 3) taxodiaceous type, 4) angiosperm, and 5) indeterminable.

[1]This work was done at the Department of Biology, Loma Linda University, and was supported by a grant from Geoscience Research Institute, Berrien Springs, Michigan. I wish to thank Glen F. Cole, Supervisory Research Biologist, for his cooperation, Marilyn Emtage for making the thin sections and keying out the wood that could not be field-identified, Bill Hughes for his help with the photography, and Dr. A. J. Roddy and Kathy Ching for their help with the manuscript.

[2]Department of Biology, Loma Linda University, Loma Linda, California 92354.

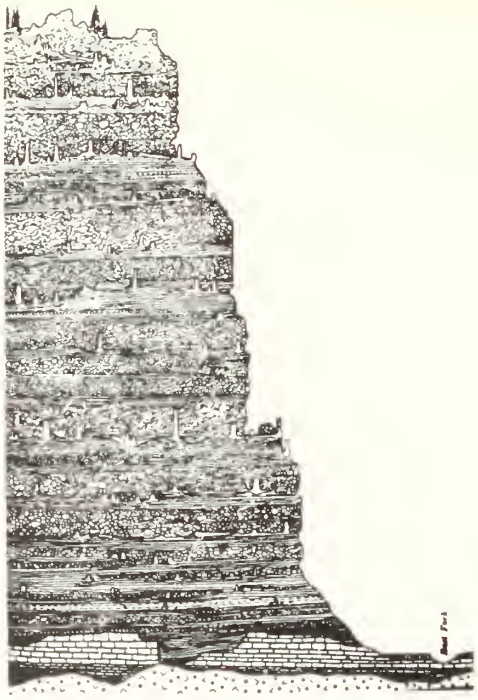


FIGURE 1. W. H. Holmes' diagram of a section of the Amethyst Mountain "Fossil Forest." Reproduced from Holmes (1878).

TABLE 1. Tree composition (vertical and horizontal).

| | Unit 1 | Unit 5 | Unit 6 | Unit 9 | Unit 10 | Total |
|---|---|---|---|---|---|---|
| Sequoia | 8 | 8 | 6 | 1 | 4 | 27 |
| Pine | 5 | 0 | 0 | 19 | 26 | 50 |
| Deciduous | 10 | 18 | 8 | 0 | 9 | 45 |
| Total | 23 | 26 | 14 | 20 | 39 | 122 |

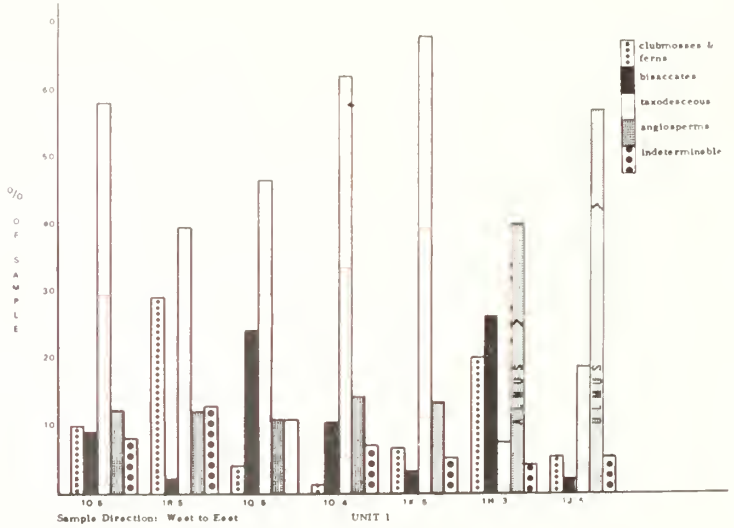



FIGURE 2. Composite histogram of unit 1.

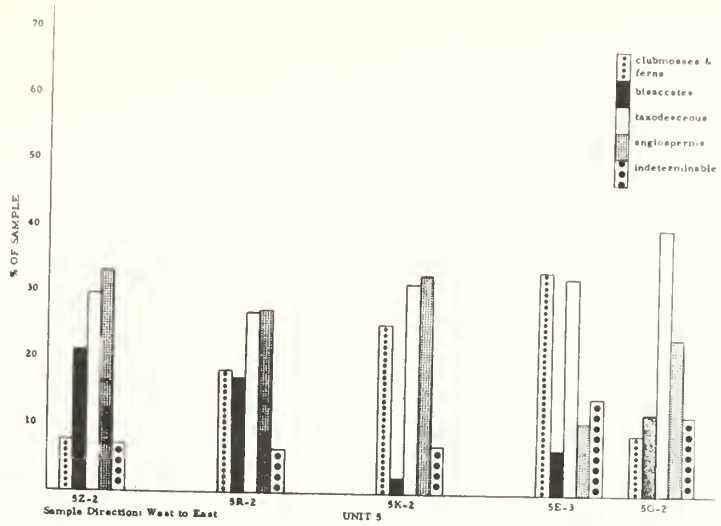



FIGURE 3. Composite histogram of unit 5.

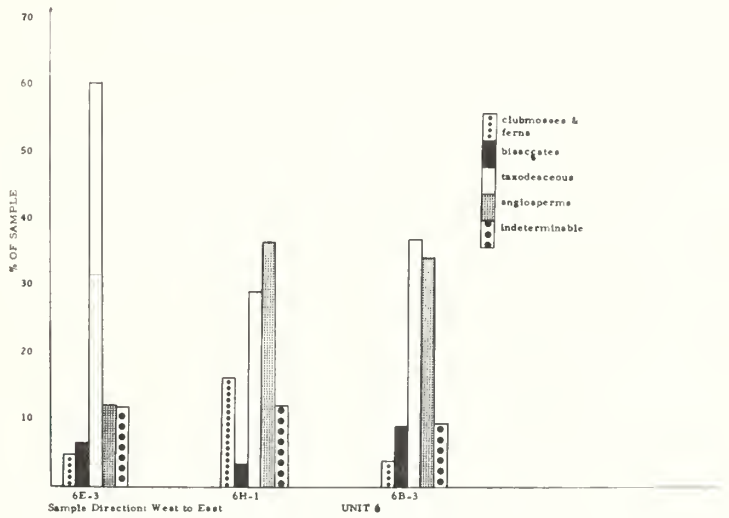



FIGURE 4. Composite histogram of unit 6.

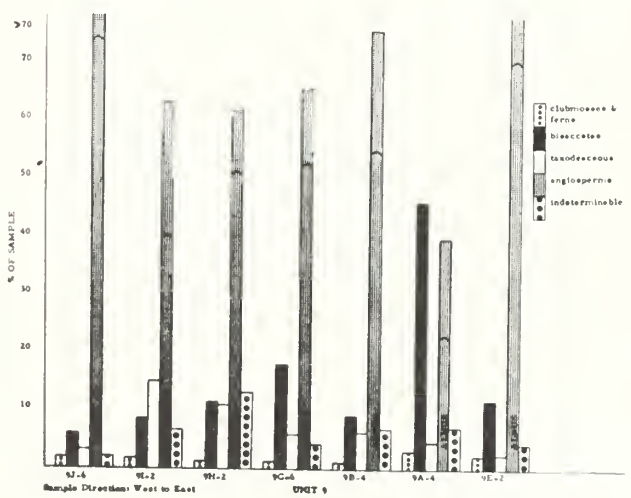



FIGURE 5. Composite histogram of unit 9.

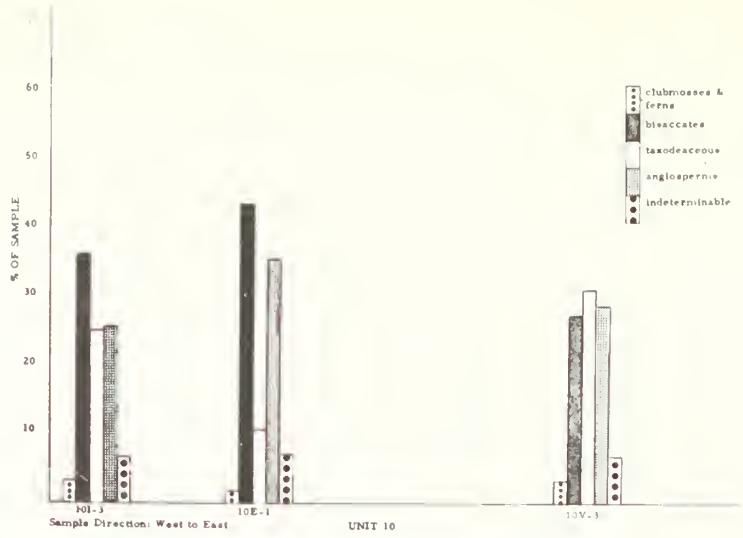



FIGURE 6. Composite histogram of unit 10.

TABLE 2. Percent trees vs. percent pollen.

| | Unit 1 | Unit 5 | Unit 6 | Unit 9 | Unit 10 |
|---|---|---|---|---|---|
| Sequoia trees | 35 | 31 | 43 | 5 | 10 |
| Taxodeaceous pollen | 45 | 32 | 43 | 7 | 23 |
| Pine trees | 22 | 0 | 0 | 95 | 67 |
| Bisaccate pollen | 11 | 12 | 7 | 16 | 36 |
| Deciduous trees | 43 | 69 | 57 | 0 | 23 |
| Angiosperm pollen | 23 | 26 | 28 | 67 | 30 |

*Photography*

All specimens illustrated in this study were photographed with the Polaroid attachment of a Zeiss Ultraphot II binocular research microscope. All photomicrographs were taken on Type 55 positive/negative Polaroid film. These photographs were taken with an oil immersion (100X) planachromat objective using Nomarski interference contrast to emphasize the surface ornamentation. Enlargements were made on Kodak Polycontrast rapid RC paper and prints were developed in Kodak Dektol developer. All photographs other than palynomorphs were copied from 35mm Ilford FP4 film and developed as above.

All figured specimens are shown on the plates at a standard magnification of 1000X to illustrate the relative size differences.

## RESULTS AND DISCUSSION

At this time there are over 130 forms in the palynoflora. As with other Eocene palynofloras (Fisk and DeBord 1974, Leopold 1974) it indicates a flora with great ecological and taxonomic diversity (Plates 1-3). Taxonomic study of the palynoflora is still in progress.

A composite histogram of each unit was constructed from the relative abundance of each category in each sample. Therefore, any category can be traced across the unit.

Unit 1 or forest 1 is a mixed forest containing twenty-three trees (Table 1). Looking at the angiosperm category (Figure 2) and tracing it from the west end of the unit to the east end it appears to be quite consistent from sample to sample except for samples 1H-3 (unit 1, sample H, slide # 3) and 1J-5. These two samples are from a split area in the organic zone. 1H-3 is from the lower zone and 1J-5 is from the middle zone just above 1H-3. There is a dramatic change in the angiosperm component from a mixture to a dominance of *Alnus* in the lower zone and *Ulmus* in the middle zone. At the present time I have no explanation for this phenomenon. Overall the other categories in this unit appear to be quite consistent from sample to sample. It should be noted that no statistical tests have been applied to any of the preliminary data presented in this paper.

Unit 5 (Figure 3) is a forest consisting of only sequoia and deciduous trees and no pines (Table 1). Each category is fairly consistent across the unit with several categories showing greater concentrations between samples, but overall the spectra is quite consistent. The presence of pine pollen (bisaccate category) in this unit could possibly be explained by wind transport from forests growing at a higher elevations.

Unit 6 (Figure 4) is another forest with only sequoia and deciduous trees (Table 1). Although preservation in this unit was extremely poor, there were three samples that could be utilized, which gave a spread across the unit. Although sample 6E-3 does have an abundance of taxodeaceous type pollen, all categories are consistent across the unit.

The palynoflora of unit 9 (Figure 5) indicates a forest dominated by *Alnus*. But this is a pine forest (Table 1). Because of the prolific nature of pine the pollen profile should be extremely high in this forest, i.e., 60-70% of the

palynoflora (McAndrews and Wright, Jr. 1969). Only one sample shows a percentage that indicates deposition beyond the forest edge.

Unit 10 (Figure 6) is another mixed forest (Table 1). Of all of the units this one is the most consistent from sample to sample. It is interesting to note that this unit having seven more pine trees than unit 9 has considerably more pine type pollen.

Table 2 shows the comparison between the relative abundance of tree type and pollen type. Units 1, 5, 6 and 10 show a close correlation. Units 1 and 10 show an underrepresentation of pine type pollen. Unit 9 is quite anomalous, overrepresented in deciduous type pollen, especially in *Alnus*, and extremely underrepresented in pine type pollen.

## CONCLUSIONS

The preliminary data from units 1, 5, 6, and 10 are in general agreement with the results from studies of modern forests. However, unit 9 cannot be explained by any modern analog and represents a striking anomaly. Further study may resolve this problem.

## LITERATURE CITED


FISK, L. H. and P. L. DEBORD. 1974. Plant microfossils from the Yellowstone fossil forests: preliminary report. Geol. Soc. Am. Absts. with Programs 6(5):441-442 (Abst.).

HOLMES, W. H. 1878. Report on the geology of the Yellowstone National Park. U.S. Geological Survey of the Territories, Annual Report no. 12, pt. 2, pp. 1-57.

LEOPOLD, E. G. 1974. Pollen and spores of the Kisinger Lakes fossil leaf locality. pp. 49-66. *In*: An early middle Eocene flora from the Yellowstone-Absaroka volcanic province, northwestern Wind River Basin, Wyoming. H. D. MacGinitie. University of California Publications in Geological Sciences 108. 103 pp.

LICHTI-FEDEROVICH, S. and J. C. RITCHIE. 1968. Recent pollen assemblages from western interior of Canada. Rev. Palaeobot. Palyn. 7:297-344.

MCANDREWS, J. H. and H. E. WRIGHT, JR. 1969. Modern pollen rain across the Wyoming basins and the Northern Great Plains (U.S.A.). Rev. Paleobot. Palyn. 9:17-43.

SMEDES, H. W. and H. J. PROSTKA. 1972. Stratigraphic framework of the Absaroka volcanic supergroup in the Yellowstone National Park region. U. S. Geol. Surv. Prof. Paper 729-C. 33 pp.

TINSLEY, H. M. and R. T. SMITH. 1974. Surface pollen studies across a woodland/heath transition and their application to the interpretation of pollen diagrams. New Phytol. 73:547-565.




PLATE 1. Clubmosses and ferns. (All figures 1000X.) 1-*Cardio angulina* 2-*Selaginella* 3-*Deltoidospora* 4-*Undulatisporites* 5-Unknown trilete 6-Unknown trilete 7-?*Cicatricosisporites* 8-*Verrucatosporites* 9-*Laevigatosporites ovatus* 10-?*Schizaea*.

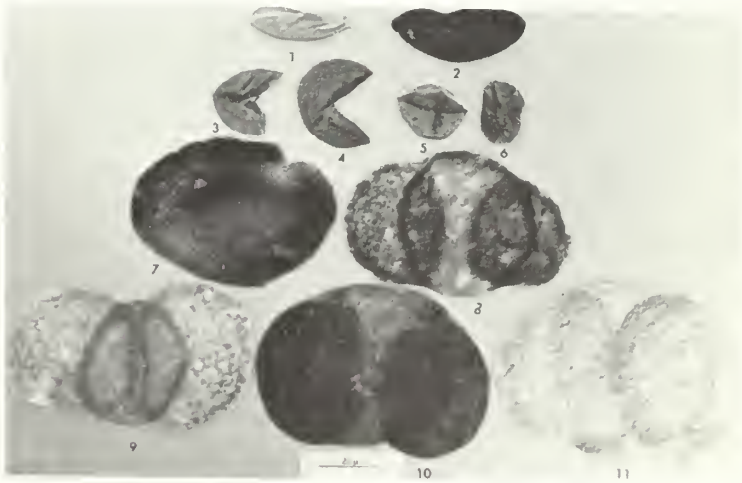


PLATE 2. Gymnosperms. (All figures 1000X.) 1-*Cycadopites* 2-Unknown monosulcate 3-*Taxodium hiatipites* 4-*Taxodiaceae-pollenites hiatus* 5-*Sequoia lapillipites* 6-?*Thuja* or *Juniperus*.

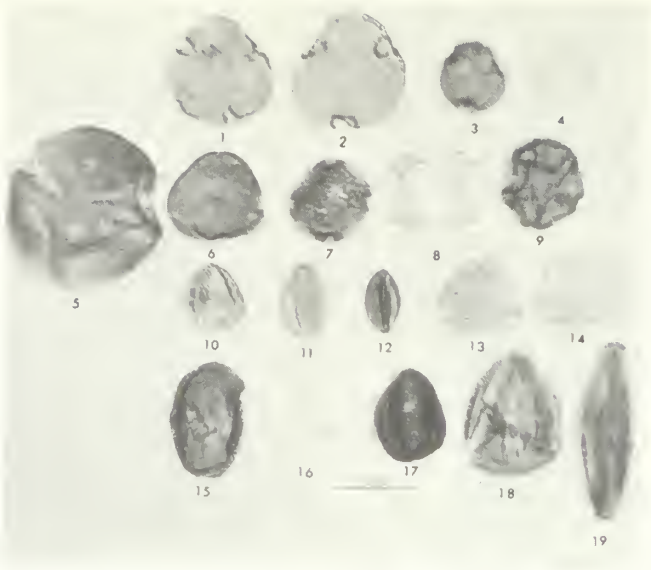



PLATE 3. Angiosperms. (All figures 1000X.) 1-*Fremontia* 2 and 3-*Tilia* 4-*Momipites coryloides* 5-*Nyssa* 6-*Carya* 7-*Ulmus-Zelkova* 8-*Planera* 9-*Alnus* 10-*Acer* 11-*Salix* 12-*Liliacadites* 13-Unknown 14-Unknown 15-? *Populus* 16-*Ilex* 17-Unknown 18-*Rhus* 19-Unknown.

# THE ECOLOGY OF SAWGRASS IN THE EVERGLADES OF SOUTHERN FLORIDA[1]

Ronald H. Hofstetter and Frances Parsons[2]

## INTRODUCTION

This study was undertaken to assess the current status of sawgrass: its growth characteristics, vigor and distribution, and the environmental factors affecting it, in the Florida Everglades.

## EVERGLADES

The Everglades is the largest contiguous peatland in the continental United States, occupying about 10,000km$^2$ or roughly one-third the area of southern Florida (Davis 1943, Egler 1952, Craighead 1971). Historically it extended from the southern end of Lake Okeechobee southward to the mangrove fringe. Lying in an elongated shallow basin, it is bordered on the east by the Atlantic Coastal Ridge and on the west by the Immokalee Rise and the Big Cypress.

Sawgrass, *Cladium jamaicense* Crantz, is the dominant plant of the Everglades, accounting for up to 70% of the vegetative cover (Loveless 1959). Sawgrass occurs as a monoculture; or mixed with other gaminoids, herbs and aquatics, and it can be found in virtually every community in southern Florida.

The Everglades has a "Tropical Savanna" climate, in the sense of Köppen (Hela 1952), with alternating wet and dry seasons, a mean January temperature of 20°C and a mean July temperature of 28°C.

The mean annual precipitation ranges from 110 to 165cm, varying with location. Between 60 and 80% of the annual precipitation occurs during the wet season from May to October (Thomas 1970). Rainfall is associated mostly with convective activity, is highly variable in quantity and distribution, and is frequently accompanied by gustiness and lightning. Precipitation in the dry season occurs mostly as light steady rains associated with the passing of cold fronts, and lightning is rare.

The Everglades basin is the lower part of the Kissimee River-Lake Okeechobee - Everglades drainage system (Parker et al. 1955). The average slope of the Everglades is 2.8cm per kilometer (Hartwell 1970), so there is a general tendency for water to flow southward as a slow, broad sheet during the wet season when most of the area is flooded. Local heavy precipitation, however, may temporarily alter local flow patterns. This fresh-water head and seaward flow prevents intrusion of salt and brackish water up the estuaries into the Everglades. During the dry season the water table drops and surface water appears only in the deepest sloughs and gator holes. At the peak of the dry season, some surface sediments may become dusty dry. The decreased fresh-water head and flow permit brackish water to move inland of the mangrove fringe.

The Everglades is underlain by limestone of Pleistocene and Miocene age (White 1970). The sediment of part of the Everglades is muck and peat, derived mostly from sawgrass. It is deepest at the north end and shallower southward. This Histosol is classified as Typic Medihemist and Medisaprist (McCollum et al. 1976). In the southernmost part of the Everglades, muck exists only in the deepest sloughs and most of the surface sediment is calcareous marl, deposited through the action of algae and bacteria. Marl forms an impervious seal over the limestone bedrock.

Fire has been a natural force affecting all of the ecological communities of southern Florida, promoting the graminoid communities and pinelands, preventing invasion by mangroves and hardwoods (Robertson 1953). As most of the natural fires are of lightning origin, they are common in the wet season, when sediment and plant roots are protected by moisture, and uncommon for most of the dry season (ibid).

Man has interfered extensively with the natural processes of hydrology and fire in the Everglades to the extent that destructive, man-caused, dry-season fires occur almost annually in this important natural area.

## SAWGRASS

Sawgrass is a coarse sedge consisting of a firm stock, from which roots and rhizomes, leaves and inflorescences grow. The apical meristem lies at the top of the stock, continuing to produce the leaves, which are "V"-shaped in cross-section and are serrated along the edges and the underside midrib (Yates 1974). Vegetative growth continues year-round, but slows somewhat during the dry season (Fisher 1971, Forthman 1973). In flowering the primary meristem is carried upward at the apex of the developing inflorescence. Following fruiting in July-August, the culm dies, but tillers arising vegetatively from rhizomes continue to develop. Density of inflorescences varies greatly from one area to another and from one year to the next, (Alexander 1971) and controlling factors are unknown. Large numbers of seeds may be produced, but viability is usually low (ibid) and varies from year to year. Vegetative reproduction is common and seedlings are uncommon within established sawgrass communities (ibid).

The leaves have a high proportion of aerenchyma, which in mature green leaves and standing dead leaves may be involved with gas exchange between the submerged plant parts and the atmosphere.

[1]We are grateful to the National Park Service for financial support from 1971 to 1975 in the form of contract EVER-N-48 as part of its contribution to the South Florida Environmental Project. Gratitude is also expressed to USDA-Forest Service for a Research Agreement to continue the work on sawgrass, particularly the spot sampling in 1975-76. Numerous people have contributed, but special thanks are due to Dr. T. R. Alexander, University of Miami, and Mr. L. Bancroft, Management Biologist, Everglades National Park.

[2]Department of Biology, University of Miami, Coral Gables, Florida 33124.

Conway (1938) demonstrated that *Cladium mariscus*, a related species, oxygenates its roots by diffusion through the aerenchyma of its leaves. Parsons (in prep.) has evidence that there is also some aeration of the rhizosphere of *C. jamaicense*.

Where flooding is continuous sawgrass forms tussocks and the meristem may develop above the sediment surface (Alexander 1971, Yates 1974).

## METHODS

There is considerable heterogeneity in species composition and in sawgrass vigor even within individual communities. This fact, along with the high cost of reaching remote areas by helicopter, required modification of methods commonly used in vegetation studies.

To supplement the information gained from reanalyses of permanent transects begun in 1971 and reported in part by Forthman (1973) and Hofstetter and Parsons (1975), one-time, meter-square samples were taken in sawgrass communities at 26 sites throughout the Everglades (see Fig. 1 for locations). Water depth, cover of plant components, and density of inflorescences were recorded, and square meter quadrats were clipped at the sediment surface. In the laboratory plant components were separated, and the total number of leaves, and the length and width of the longest leaf in each sawgrass culm were determined. The brown and green leaves of sawgrass and individuals of other species were separated, dried at 105°C, and weighed.

## RESULTS AND DISCUSSION

### *Sawgrass Characteristics*

Values for the selected characteristics of sawgrass from the meter-square sampling sites are presented in Table 1. The maximum values from transects studies between September 1971 and October 1976 are: length of longest leaf: 317cm, site 15; width of longest leaf; 21mm, site 16; leaves per culm: 10.1, site 16; density: 67 culms $\cdot$ $m^{-2}$, site 23. Individual values for each transect at several times are recorded elsewhere (Forthman 1973, Hofstetter and Parsons 1975).

The largest value for standing crop (at site 8) is the result of high values of both green and standing dead material. This sample was selected from a small stand that had an unusually high density (55 culms $\cdot$ $m^{-2}$) or robust culms (average values of 283cm and 20mm for length and width respectively of longest leaves and 10.2 leaves per culm). These values are much higher than those typical of sawgrass in that area. Several sites (5, 11, 14, 16) had similar values for aboveground green biomass. At site 5 the individual culms were small, but their density was high, whereas at site 16 there was lower culm density, but the culms were robust with more numerous and more robust leaves. The culm density at site 14 was more than double that at site 16, and the length and width of the longest leaves were comparable, but there were fewer leaves per culm at site 14. This indicates, then, that measurement of no one or two characteristics of sawgrass will serve to predict standing crop of green matter.

The plot of width against length of longest sawgrass leaf (Fig. 2), however, reveals a linear relationship with a correlation coefficient of 0.942. Biomass of standing litter reflects both the rate of green matter production and of litter production, seasonality, and is greatly affected by time since burning.

The above-ground biomass at site 8 contains 31,000kcal $\cdot$ $m^{-2}$ ash-free, dry weight of living and standing dead sawgrass (Hofstetter and Parsons 1975). The ash content of this matter is between 3.0 and 7.4% of dry weight (ibid).

The values of sawgrass characteristics recorded in Table 1 should not be used alone as an indication of the overall quality of sawgrass in those areas sampled or in the entire Everglades. Many more samples and determinations of the percentage area occupied by the different communities and of the vigor of the vegetation within each community would be necessary.

Insufficient time has passed to determine annual growth patterns for individual sawgrass culms, but some possible trends are developing. One culm had 6 leaves and an average leaf length of 78cm in February, and in October it had 10 leaves with an average leaf length of 185cm. During that period this culm produced 2400cm of total leaf length. If the leaves are between 10 and 13mm wide, this represents a production of 64 to 92g dry weight and 335 to 440 kcal. of energy. In that period 920cm (length) of green leaves died and 860cm (length) of standing brown leaves, including 7 entire leaves, became litter.

### *Decline of Sawgrass*

Our observations over the past 8 years indicate that sawgrass is continuing to decrease in distribution and in stature throughout the entire Everglades system. There are insufficient data on past conditions, however, to quantify these observations.

The causes of sawgrass change appear to be a combination of natural and man-caused phenomena, although these are not yet fully understood. The primary controlling factor apparently is hydroperiod (Robertson 1953, Loveless 1959): the depth, timing, and duration of flooding. The canals, levees, 3,500$km^2$ of Water Conservation Areas, and water management practices influence all of the Everglades (Fig. 1). In the southern (downstream) ends of the Conservation Areas the depth of surface water and/or period of flooding has increased. Here sawgrass is being replaced by cattail (*Typha*) and other hydrophytes (Loveless 1959, Alexander 1971, McPherson 1973, Alexander and Crook 1975). In much of the historical Everglades the depth and period of flooding has decreased and the surface sediments are excessively dry and/or dry for unusually long periods. This problem has been intensified by several unusually dry years between 1970 and 1975. In these drier areas sawgrass is being displaced by more mesophytic species, for example, *Panicum hemitomum, Andropogon* spp. and especially by woody plants, such as *Myrica cerifera*, and *Baccharus* spp. (Robertson 1953, Loveless 1959, McPherson 1973, Alexander and Crook 1975).

Sawgrass has also increased in stature and area in some locales. In the wetter parts of the Conservation Areas where sawgrass has been displaced by more hydric species, it has replaced more mesic species on somewhat higher ground. Where the hydroperiod has been shortened sawgrass has displaced more hydric species in the sloughs (McPherson 1973, Alexander and Crook 1975). Overall, however, sawgrass has experienced a net loss (Robertson 1953, Loveless 1959, Hofstetter and Parsons 1975).

As a consequence to the reduced hydroperiod,

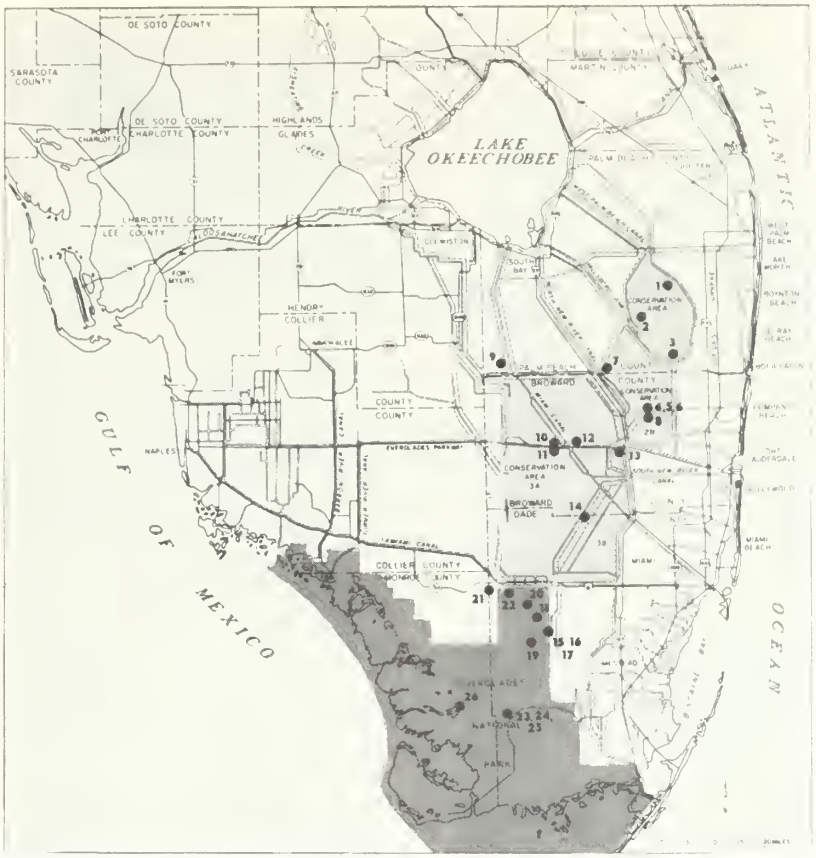



FIGURE 1. Map of southern FLorida showing major natural and anthropogenic features, and locations of meter-square sampling sites.

TABLE 1. Average values (and standard deviation) of sawgrass characteristics at selected sites throughout the Everglades.

| Map # | Site I.D. | Longest Leaf Length (cm) | Longest Leaf Width (mm) | Leaves / culm | Culms / $m^2$ | Inflor. # / $m^2$ | Inflor. % | D.M. # / $m^2$ | D.M. % | O.D. Biomass (g) Green | Litter | Total | Cover (%) Green | Litter | Sampling Date |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | CA-1 | | | | | | | | | | | | | | |
| 1 | TA-4 | 199 (37) | 14 (3) | 6.8 (1.6) | 37 | 0 | 0 | 3 | 8 | 1420 | 1420 | 2840 | 75 | 90 | 4-III-76 |
| 2 | TA-6 | 218 (47) | 13 (4) | 7.9 (2.6) | 48 | 0 | 0 | 2 | 4 | 1590 | 2720 | 3310 | 30 | 95 | 4-III-76 |
| 3 | TA-8 | 159 (120) | 17 (8) | 8.5 (3.3) | 72 | 2 | 3 | 2 | 3 | 2150 | 2780 | 4930 | 50 | 60 | 4-III-76 |
| | CA-2A | | | | | | | | | | | | | | |
| 4 | N. Trans. | 167 (67) | 15 (6) | 6.1 (2.8) | 19 | 0 | 0 | 4 | 21 | 310 | 230 | 540 | 20 | 10 | 2-III-76 |
| 5 | Site 2-3 | 137 (82) | 13 (7) | 6.7 (3.8) | 51 | 2 | 4 | 0 | 0 | 1080 | 880 | 1960 | - | - | 2-III-76 |
| 6 | Site 10 | 142 (82) | 12 (6) | 5.8 (2.7) | 39 | 0 | 0 | 1 | 5 | 960 | 680 | 1640 | - | - | 2-III-76 |
| 7 | NW a)tillers exc. | 218 (67) | 17 (5) | 8.7 (2.5) | 27 | 7 | 13 | - | - | - | - | - | - | - | 14- IV-76 |
| | b)tillers inc. | 169 (83) | 14 (6) | 7.0 (2.6) | 54 | - | - | 0 | 0 | 2010 | 2750 | 4760 | 70 | 80 | 14- IV-76 |
| | CA-2B | | | | | | | | | | | | | | |
| 8 | Site 1 | 283 (83) | 20 (6) | 10.2 (3.7) | 55 | 2 | 4 | 1 | 2 | 2720 | 3690 | 6410 | 93 | 25 | 2-III-76 |
| | CA-3A | | | | | | | | | | | | | | |
| 9 | RP | 239 (53) | 16 (5) | 8.7 (2.0) | 47 | 6 | 13 | 0 | 0 | 1620 | 1080 | 2700 | 95 | 95 | 7- IV-76 |
| 10 | TA-7 | 177 (54) | 14 (3) | 9.9 ( - ) | 47 | 10 | 21 | 2 | 4 | 790 | 990 | 1780 | 70 | 17 | 10-III-76 |
| 11 | TA-25 | 169 (61) | 13 (4) | 10.6 (2.9) | 48 | 10 | 21 | 0 | 0 | 1080 | 540 | 1620 | 35 | 10 | 10-III-76 |
| 12 | TA-44 | 139 (49) | 11 (4) | 8.0 (2.1) | 57 | 0 | 0 | 2 | 4 | 540 | 790 | 1330 | 30 | 25 | 10-III-76 |
| 13 | Br-2W a) Cladium | 106 (89) | 13 (7) | 8.3 (4.8) | 15 | 1 | 7 | 4 | 27 | 350 | 370 | 720 | - | - | 10-III-76 |
| | b) Typha | 264 (104) | 13 (4) | 5.9 (2.2) | 8 | - | - | - | - | 350 | 770 | 1120 | - | - | 10-III-76 |
| | CA-3B | | | | | | | | | | | | | | |
| 14 | Site 1 | 201 (77) | 16 (5) | 7.2 (2.0) | 53 | 0 | 0 | 1 | 2 | 1050 | 1220 | 2270 | 80 | 100 | 14- IV-76 |
| | ENP | | | | | | | | | | | | | | |
| 15 | L67B-N | 216 (71) | 13 (4) | 8.4 (2.4) | 40 | 0 | 0 | 2 | 5 | 1020 | 3090 | 4110 | 52 | 98 | 16- II-76 |
| 16 | L67B-S | 205 (81) | 16 (6) | 10.1 (3.8) | 24 | 0 | 0 | 0 | 0 | 1080 | 2300 | 3380 | 57 | 98 | 16- II-76 |
| 17 | L67B Typha | 226 (37) | 13 (3) | 6.8 (1.9) | 26 | - | - | - | - | 850 | 1280 | 2130 | - | - | 12-III-76 |
| 18 | SV-3 | 170 (52) | 10 (3) | 6.4 (1.8) | 66 | 0 | 0 | 6 | 9 | 710 | 1960 | 2670 | - | - | 31-III-76 |
| 19 | SV-2 | 176 (73) | 10 (4) | 6.8 (2.1) | 41 | 0 | 0 | 0 | 0 | 510 | 1990 | 2500 | - | - | 24-III-76 |
| 20 | SVR | 234 (64) | 15 (4) | 8.8 ( - ) | 35 | 0 | 0 | 0 | 0 | 960 | 2550 | 3510 | 20 | 49 | 9- II-76 |
| 21 | TR-3C | 165 (56) | 11 (4) | 7.5 (2.5) | 117 | 4 | 3 | 14 | 12 | 1220 | 1050 | 2270 | 90 | 13 | 1-III-76 |
| 22 | TR-2 | 153 (90) | 13 (5) | 8.4 (3.1) | 109 | 29 | 27 | 2 | 2 | 1900 | 910 | 2810 | 90 | 13 | 1-III-76 |
| 23 | PHO-Trans. 1 | 197 (33) | 11 (3) | 6.3 (1.8) | 22 | 0 | 0 | 1 | 5 | - | - | - | 13 | 77 | 8-XII-75 |
| 24 | PHO-Trans. 2 | 177 (18) | 12 (2) | 6.1 (2.1) | 51 | 0.8 | 2 | 7 | 14 | - | - | - | 7 | 27 | 8-XII-75 |
| 25 | PHO-Trans. 3 | 168 (54) | 10 (4) | 6.8 (2.4) | 18 | 0.3 | 2 | 5 | 31 | 200 | 2330 | 2530 | 12 | 78 | 8-XII-75 |
| 26 | Lostman R. | 149 (33) | 8 (3) | 7.5 (1.9) | 44 | 0 | 0 | 0 | 0 | 310 | 2720 | 3030 | 80 | 100 | 16- IV-78 |

D.M. = dead middle, i.e. culms whose interior leavee ere brown while some of the exterior leaves are still green

O.D. = oven-dried at 105°C

See text for further explanetions

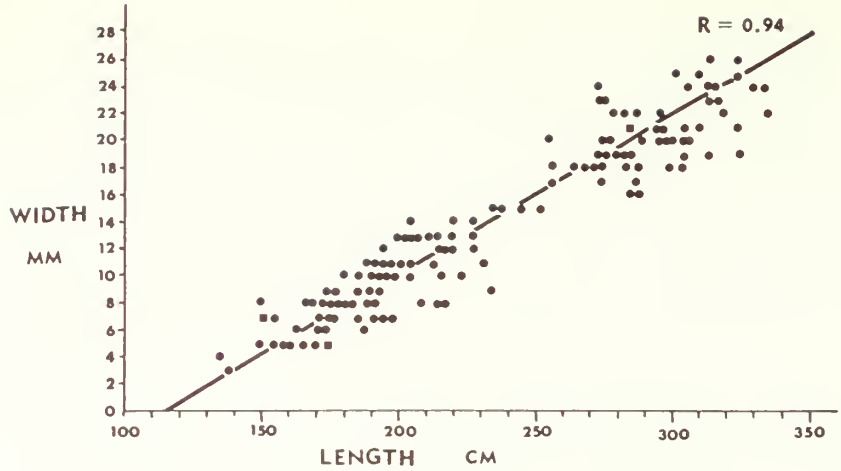



FIGURE 2. Relationship of length to width of the longest sawgrass leaf per culm.

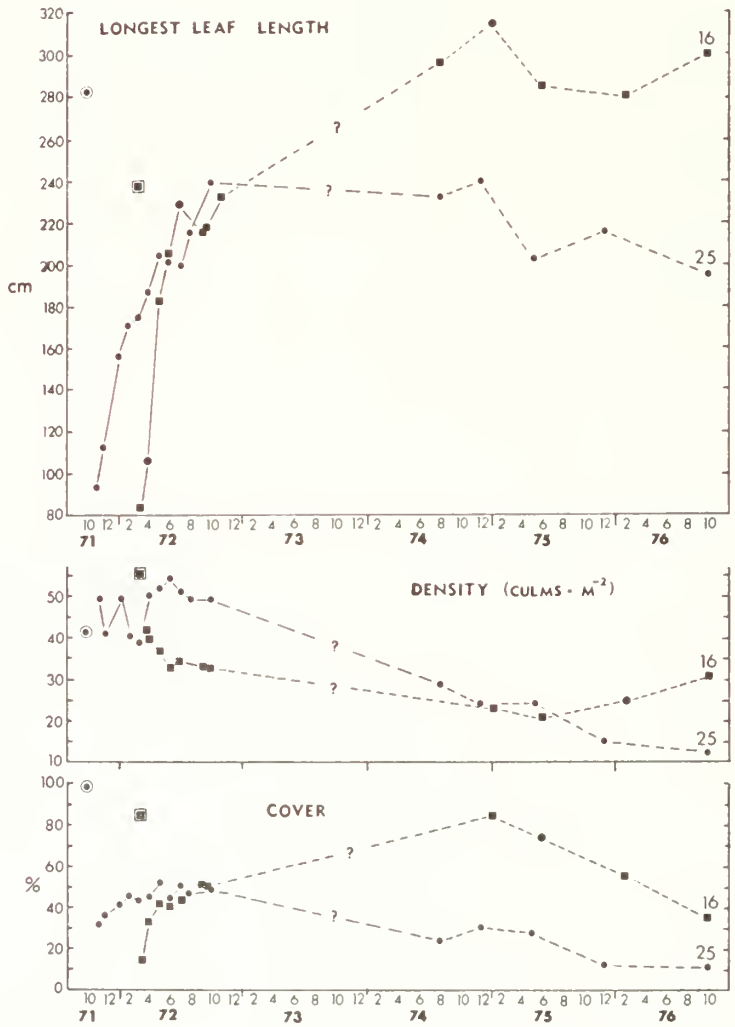



FIGURE 3. Changes in length of longest leaf, density, and cover of sawgrass with time at two sites in Everglades Natinonal Park.

the extension and duration of brackish water has increased in the lower ends of the fresh-water wetlands, and sawgrass is being replaced by salt marsh species (Robertson 1953, Alexander and Crook 1975). Another serious consequence of reduced hydroperiod is the increased frequency and severity of fires, especially ground fires (Robertson 1953, Loveless 1959, Hofstetter and Parsons 1975). These are primarily incendiary (arson), dry-season fires that kill sawgrass and other species that normally benefit from surface fires when they are protected by moisture during the wet season.

Another problem has been the invasion and displacement of sawgrass and other native species by exotic plants, especially cajeput (*Melaleuca quinquenervia*) (Alexander and Crook 1975, Hofstetter and Parsons 1975). This woody species is rapidly colonizing mesic sites and natural sawgrass communities (when the sediment is adequately exposed). *Melaleuca* tolerates burning, has semiserotinous fruit, and is generally promoted by fires. Dense forests of this eucalypt are forming, mostly along the eastern edge of the Everglades. All of the Everglades system is threatened and will succumb eventually if preventive action is not taken soon.

Besides being replaced by other species sawgrass has been dying in excess of normal, particularly in the interior of the densest stands. This condition, called decadent sawgrass (Hofstetter 1973), was first observed in winter 1970, by Alexander and Hofstetter and has been spreading rapidly throughout the Everglades. In some of the still-living culms the leaves are unusually short and chlorotic. This appears to be a nutritional problem that is not yet understood. More commonly seen, however, are normal culms with dead innermost leaves. In some cases death of the youngest leaves and meristem appears to result from fungal infection. In some instances normal elongation of the innermost leaves is hindered and the leaves impact accordian style for unknown reasons. Most commonly, however, death appears to result from the action of a boring larva, tentatively identified as *Scirpophaga perstrialis* (Hofstetter and Parsons 1975). At one study site 31% of the culms, and at another site 14 culms $\cdot m^{-2}$ (12% of culms present) were so killed.

Figure 3 shows the changes that have occurred in two of the study sites (16 = L67-S, 25 = Pa-Hay-Okee Transect 3) since 1971. The values from 1971 to 1972 are from Forthman (1973) who studied post-burn growth responses. Since the decadent condition began to appear these transects have been re-examined (Hofstetter and Parsons 1975). With decadence, while some of the culms may remain robust, most culms decline in length and width of leaves, culm density, and sawgrass cover. Sawgrass at L67 now appears to be recovering, with values of leaf length and culm density increasing.

### *Prescribed Burning*

Prescribed burning is now common practice in southern Florida, mostly in the early to middle part of the dry season to reduce fuels for fire control (Hofstetter and Parsons 1975). Before the decadent sawgrass condition becomes advanced, burning appears to delay its onset, but does not appear to prevent or to reverse the developing condition.

Prescribed burning must be avoided when damage to the meristem is likely and especially when the muck (peat) is dry enough to burn. Burning must be avoided when the water table is rising as submerging the fire-pruned culm will result in its death (Alexander 1971, Forthman 1973). Burning of the developing inflorescence will result in loss of these seeds and death of the culm. H. Werner of Everglades National Park (Pers. comm.) recommends burning sawgrass in January and February with 10 to 15cm of surface water. The long-term effect of annual burning or of time of burning has not yet been determined.

### *Hydroperiod Management*

Sawgrass appears to require an annual period of dry down (Loveless 1959), but the return of the hydroperiod to a natural situation is unlikely and probably impossible for much of the Everglades system. Nevertheless some efforts are being made or (at least) are being planned to improve this situation.

## CONCLUSIONS

Length and width of the longest leaf per culm, numbers of leaves per culm, culm density and standing crop of sawgrass vary greatly throughout the Everglades and within individual communities. There appears to be a linear relationship between the width and length of the longest leaves that holds for sawgrass over much of its range. Standing crop of sawgrass can not be accurately determined except by clipping and drying.

Sawgrass appears to be declining in general distribution, dominance, and vigor within the Everglades. Some of this change can be attributed, at least in part, to altered hydroperiod, to excessively hot dry-season fires, to displacement by cajeput, to insect damage, and possibly to nutrient conditions. Studies on all of these factors are continuing.

There is little reason to suspect that the vegetational changes in the Everglades will not continue, and consequences of a continued decline in sawgrass are not known because the role this plant plays in the Everglades is not fully understood.

## LITERATURE CITED


ALEXANDER, T. R. 1967. Effect of Hurricane Betsy on the southeastern Everglades. Quart. Jour. Fla. Acad. Sci. 30(1):10-24.

ALEXANDER, T. R. 1971. Sawgrass biology related to the future of the Everglades ecosystem. Soil and Crop Sci. Soc. Florida Proc., 31:72-74.

ALEXANDER, T. R., and CROOK, A. G. 1975. Recent and longterm vegetation changes and patterns in South Florida. Part II. Final Report. Mimeo. Report to Dept. of Interior, National Park Service. May 1975.

CONWAY, V. M. 1937. Studies in the autecology of *Cladium mariscus* R. Br. III. The aeration of the subterranean parts of the plant. The New Phytologist. 36:64-96.

CRAIGHEAD, F. C. 1971. The trees of South Florida. Vol. 1. The natural environments and their succession. Univ. Miami Press, Coral Gables, Fl. 212 p.

DAVIS, J. H. 1943. The natural features of southern Florida. Florida Geol. Surv. Bull. 25. 311 p.

DINEEN, J. W. 1972. Life in the tenacious Everglades. In Depth Report. 5(1). Central and Southern Florida Flood Control District.

EGLER, F. E. 1952. Southeast saline everglades vegetation, Florida and its management. Vegetatio 3(4-8):213-265.

FISHER, J. B. 1971. Inverted vascular bundles in the leaf of *Cladium* (Cyperaceae). Bot. Jour. Linnean Soc. 64(3):277-293.

FORTHMAN, C. A. 1973. The effect of prescribed burning on sawgrass, *Cladium jamaicense* Crantz, in South Florida. Masters Thesis. University of Miami, Coral Gables, Florida.

HARTWELL, J. H. 1970. Some aspects of the availability of water from the Everglades to the Everglades National Park, Florida. Open File Report 70007, U.S. Geol. Survey, Tallahassee, Fl. 36 p.

HELA, I. 1952. Remarks on the climate of South Florida. Bull. Marine Sco. of Gulf of Mexico and Carribbean Sea. 2(2):438-447.

HOFSTETTER, R. H. 1973. Effects of fire in the ecosystem - an ecological study of the effects of fire on the wet prairie, sawgrass glades, and pineland communities of South Florida. Report EVER-N-48 to U. S. Dept. Interior, National Park Service. NTIS Accession No. PB-231940/AS.

HOFSTETTER, R. H. and PARSONS, F. 1975. Effects of fire in the ecosystem. An ecological study of the effects of fire on the wet prairie, sawgrass glades, and pineland communities of South Florida. Part II. Final Report EVER-N-48, Department of Interior, National Park Service, May 1975.

LOVELESS, C. M. 1959. A study of the vegetation of the Florida Everglades. Ecol. 40(1):1-9.

MCCOLLUM, S. H., CARLISLE, V. W., and VOLK, B. G. 1976. Historical anc current classification of organic soils in the Florida Everglades. Soil and Crop Sci. Soc. Florida Proc. 35:173-177.

MCPHERSON, B. F. Vegetation in relation to water depth in Conservation Area 3, Florida. U. S. Geol. Survey, Open-file Report 73025, Tallahassee, Fl.

PARKER, C. G., FERGUSON, G. E., LOVE, S. K., et al. 1955. Water resources of South Eastern Florida with special reference to geology and ground water of the Miami Area. U. S. Geol. Surv. Water Supply Paper 1255.

ROBERTSON, W. B. 1953. A survey of the effects of fire in Everglades National Park. U. S. Dept. Interior, National Park Service. Mimeo Report. Homestead, Fl. 169 p.

THOMAS, T. M. 1970. A detailed analysis of climatological and hydrological records of South Florida with reference to man's influence upon ecosystem evolution. Tech. Report 70-2. Rosenstiel School of Marine and Atmospheric Science, Univ. Miami, Miami, Fl.

WHITE, W. A. 1970. The geomorphology of the Florida peninsula. Florida Bur. Geol., Geol. Bull. No. 51.

YATES, S. A. 1974. An autecological study of sawgrass, *Cladium jamaicense*, in southern Florida. Masters Thesis, Univ. of Miami, Coral Gables, Fl.

# SEASONAL DIFFERENCES IN NITROGEN AND PHOSPHORUS CONCENTRATIONS IN SAWGRASS IN SOUTHERN FLORIDA

Frances Parsons[1]

## INTRODUCTION

Phosphorus and nitrogen are essential macronutrients in plants. Phosphorus is believed to be often a limiting factor in freshwater ecosystems. The chemical forms in which nitrogen exists and is taken up by plants growing in waterlogged organic sediments is not completely understood. As sawgrass, *Cladium jamaicense* Crantz, occurs in virtual monoculture in many large areas of the Everglades of southern Florida, it is important to study possible influences on sawgrass of changes in these vital nutrients caused by seasonal climatic changes.

Phosphorus has been shown to have a short residence time and a rapid turnover rate in some freshwater bodies (Hutchinson and Bowen 1950, Rigler 1956, Pomeroy 1960). Pomeroy (1960) pointed out that the turnover rate of phosphate is probably more important to community well-being in freshwater ecosystems than in the concentration of phosphorus.

In natural plant communities, usable forms of nitrogen result from microbial transformations of organic nitrogen compounds of plant and animal origin and from nitrogen fixation. Usable forms of nitrogen to plants are nitrate, an anion, and ammonium, a cation. Nitrite, an intermediate state in the geochemical cycle of nitrogen, is of interest because it is toxic to plants under certain conditions (Bingham et al. 1954, Court et al. 1962). Climatic changes through the seasons affect the size, composition, and activity of the microbial populations responsible for these changes (Viets 1965, Davy and Taylor 1974). Climatic changes also affect the nature and quantity of the organic material upon which the microorganisms live. The annually alternating submergence and exposure of the sediments that occur over much of the Everglades would be expected to have an effect on the chemical forms that nitrogen takes in the sediment. When Everglades sediments are drained for agricultural crops, nitrification proceeds rapidly (Neller 1944). The widespread drainage of the sawgrass Everglades lengthens the time during the year that these sediments are above water and could be expected to have an effect on the timing of occurrence of these different chemical forms of nitrogen. If conditions are adverse to some of the nitrifying bacteria, toxic levels of nitrite could accumulate.

Tusneem and Patrick (1971) described nitrogen transformations in waterlogged soils used for growing rice in Louisiana. These conditions superficially resemble those where sawgrass grows naturally in the Everglades of southern Florida, but the soils are different in composition and condition, the plants may well have different metabolic processes, and the climate is different. The rice soil that Tusneem and Patrick (1971) described, for example, was Crowley silt loam with a total nitrogen content of 770ppm. Everglades muck contains from 3.0 to 3.8% total nitrogen (Miller 1918, Hammer 1929). Rice utilizes ammonium more efficiently than nitrate in all stages of growth (Bonner 1946); the nitrogen form required by sawgrass is unknown. The climate of Crowley, Louisiana, which lies at 30°11' north latitude, is somewhat more temperate than that of the southern Everglades at 25°45' north latitude.

The climate of southern Florida has been called "tropical savannah" (Hela 1952). In general, it consists of a warm wet season that extends from May through September and a cool dry season that extends from October through April. Four seasons, however, can be identified as shown in Table 1. Winter, which lasts about three months from the first of December to about the end of February, is typified by mild temperatures, very little rainfall, falling water table, and minimum radiation due to low solar angle and short day length. Spring, lasting from the first of March to the third week of May, is warmer than winter and also has very little rainfall. Spring is the driest of the seasons. The water table is lowest then and large areas of the surface of the Everglades, which had been submerged, are exposed. Radiation approaches the annual maximum. Summer begins in late May, or early June, with the onset of the seasonal rains. While daylength is maximum, radiation is not always maximum because of increased cloud cover. The water table rises rapidly when the rains begin and most of the Everglades basin becomes inundated. Summer, with its characteristically hot and humid conditions, prevails until about the middle of September. Daytime temperatures in fall can be as high as those in summer, but are usually lower, especially at night. Water levels in fall usually are initially high, but decline rapidly. Although days are shortening, with decreased cloud cover incident radiation can equal that measured in June. The mean temperature for January is 20°C and for August 28°C. The average rainfall is 100 to 150cm, but annual and areal variations are great. For example, the Miami area had 123cm in 1975, but during the first 10 months of 1976, it had 220cm of rainfall. Summer rainfall is extremely variable in quantity and distribution. These vagaries can exert pronounced effects on local water levels.

The climate is not the only force exerted on hydroperiod. Water levels in the Conservation Areas and water flow to Everglades National Park are controlled through impoundment and removal of water by pumping by the Flood Control District, a state agency. The canals, levees, and roads have altered the historical flow pattern of water over the surface of the Everglades basin. Instead of being inundated during the wet season and above water level during the dry season, there now are areas that are wetter for longer periods of the year (*e.g.*, the southern ends of the Conservation Areas) and those that are drier for longer periods of the year (*e.g.*, Taylor Slough and much of the eastern boundary of the Everglades) than before development.

The nutrient requirements of economically important plants have been studied and reported at great length. Those of most plants growing in

[1]Department of Biology, University of Miami, Coral Gables, Florida 33124.

the natural state, including sawgrass, have not been reported (Gigon and Rorison 1972). Steward and Ornes (1975) reported on mineral content of above ground parts of healthy sawgrass plants, the sediment, and surface water. They concluded that because sawgrass has low levels of mineral nutrients, especially phosphorus, it probably has low requirements for them and thus is able to dominate the Everglades ecosystem.

## SITE DESCRIPTION

The study site, L67, was chosen because it is in the middle of the Everglades basin, has vigorous sawgrass plants, and has shown the least change in overall appearance during the previous five years of study. It is in the north central part of the Shark River slough in an area free of tree islands. Nearby there are open glades in which either spike rush, maiden-cane, or cattail dominate. It is about 13km south of the Tamiami Trail and 200m west of Canal and Levee 67 along the northeast edge of Everglades National Park. L67 has standing surface water longer in the dry season than do areas to the east and to the west of it; it did not dry down completely during 1975. It was burned by prescription on March 16, 1972, and previously by wildfire in March 1971.

## METHODS AND MATERIALS

Samples for this study were taken during 1975 at roughly monthly intervals. The plants and muck were considered to be contiguous compartments of a community column. These compartments were as follows: green leaves, brown leaves, roots and rhizomes, inflorescences, surface water (when present), top muck (0-10cm below muck surface), midlayer muck (25-30cm below muck surface), and bottom muck (50-70cm below muck surface).

Five entire mature plants representative of each site were carefully removed from the muck by hand. The roots were rinsed in the standing water on site to remove most of the adhering muck, and the intact plants were placed in plastic bags, which were then tightly sealed. In the laboratory, the plants were divided into the compartments listed above. These compartments were weighed, dried at 105°C in a forced-draft oven to constant weight, then weighed again. Plants were processed within 4 hours of harvest or stored frozen if processing was delayed. The dried compartments were ground in a Wiley mill to pass a 40-mesh screen. The samples were stored in tightly closed glass jars until analyzed.

Muck samples were collected by hand and placed in tightly capped 12-ounce plastic cups. The muck samples included all of the water associated with the volume of muck taken. Water, when present above the surface of the muck, was collected in pyrex flasks that were closed with parafilm-wrapped rubber stoppers. Muck and water samples were placed on ice in the field immediately upon collection. If analyses were begun within 36 hours, they were stored in a refrigerator at 4°C in the laboratory, otherwise they were stored frozen. Sediment samples were prepared for analyses by throughly mixing the fresh or thawed sample with a stainless steel spatula. Undried subsamples were used in all chemical analyses. Moisture and ash content were determined on subsamples that were dried in a forced-draft oven at 105°C and then ignited in a muffle furnace at 550°C. Water samples were filtered through a washed 0.45μm Millipore filter prior to storage or analysis.

Total nitrogen and total phosphorus in plant and muck samples were determined by a Kjeldahl method, which includes nitrates and nitrites, as described by Bremner (1965). Phosphorus was converted to orthophosphate by digestion of the organic material with $Mg(NO_3)_2$ followed by ignition at 400°C, as described in AOAC (1971). Orthophosphate was then determined by the stannous chloride method after extracting it with benzene-butanol to exclude silicon (APHA 1971).

Water soluble components, i.e., ammonium, nitrate, nitrite, and phosphate, were extracted from subsamples of muck and plant material by suction filtration after shaking the material with deionized water.

Soluble nitrite-nitrogen in the water extracts of plant and muck materials was measured by the modified Griess-Ilosvay method of Barnes and Folkhard (1951). Soluble nitrate-nitrogen was reduced to nitrite by passage of an aliquot of each extract through a cadmium-copper column as described by Strickland and Parsons (1968). Each aliquot was then analyzed for nitrite. Soluble ammonium-nitrogen was determined on each extract by the phenolhypochlorite method of Sólorzano (1969). Soluble phosphate was determined as described above for orthophosphate. Water samples were analysed by the same methods used for water extracts. A Hatchi 139 spectrophotometer with 1cm and 10cm cells was used.

Known addition techniques, and positive and negative controls were routinely used to validate analytical method results.

The following sensitivities were obtained with these methods based on one gram of oven-dried material, including ash: total Kjeldahl nitrogen, 0.03mg/g; phosphorus, 0.1ppm; $NO_3$-N, 0.2ppm; $NO_2$-N, 0.16ppm; $NH_4$-N, 0.023ppm.

## RESULTS AND DISCUSSION

The results are shown in a series of bar graphs, Fig. 1, total phosphorus and soluble phosphate-phosphorus; and Fig. 2, total nitrogen, and the following water soluble components: ammonium-nitrogen, nitrate-nitrogen, and nitrite-nitrogen. The bars have varied widths to indicate that the sampling periods were not of uniform length as the four seasons are of unequal duration. Plant values are superimposed on sediment values for each component, which are given as $mg/m^2$-community unit on a uniform log scale. A community unit is defined as an area one meter square to the depth of 30cm in the sediment, and all the plants growing in that space to whatever height they may attain. The sediment depth was limited to 30cm for uniformity. At this site the sediment was generally at least 30cm deep and even where it was deeper, the living sawgrass roots were primarily found in the upper 30cm of sediment. Biomass and density are given by Hofstetter and Parsons (1975) on the basis of a square meter, thus comparisons between these data can be made. Concentrations of nutrients in the surface water, i.e., the water above the surface of the sediment, are reported as parts per million in Table 2. The water contained very low concentrations of all components.

TABLE 1. Climatic factors in the Everglades. Average values for 30 days prior to seasonal sampling date at L67, Everglades National Park.

| Season (Sample Date) | Dry Bulb Temp.,C. (range) | Wet Bulb Temp.,C. | Radiation, Langleys | Day Length, Minutes | Precip., mm (total) |
|---|---|---|---|---|---|
| Winter (1-2-75) | 21.1 (8.4-29.1) | 17.8 | 290 | 635 | 30 |
| Spring (4-21-75) | 25.5 (11.2-34.2) | 20.7 | 526 | 749 | 4 |
| Summer (6-29-75) | 27.6 (23.0-33.6) | 24.1 | 437 | 820 | 132 |
| Fall (10-11-75) | 28.2 (23.0-33.6) | 24.5 | 420 | 721 | 105 |

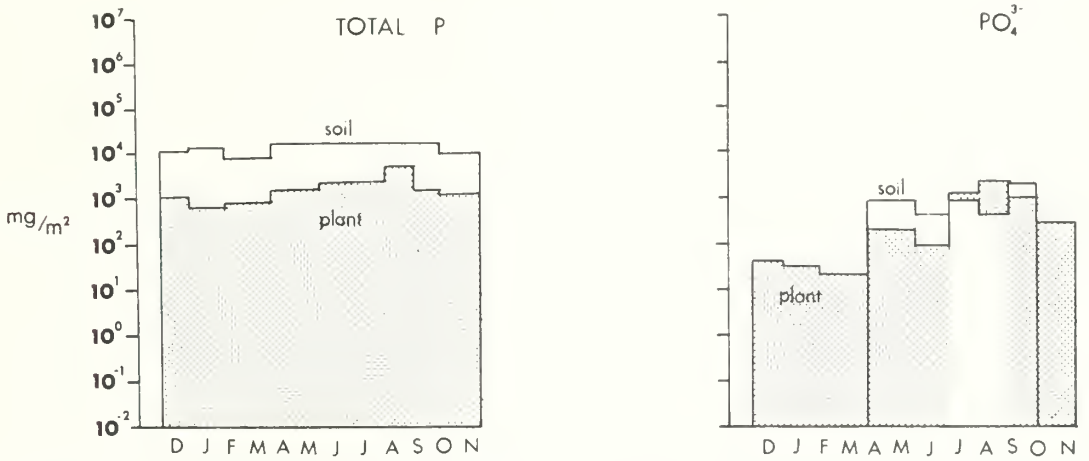



FIGURE 1. Quantity, $mg/m^2$-community unit, of total phosphorus and water-soluble phosphate contained in plants and the sediment (soil) at L67, Everglades National Park during 1975.

TABLE 2. Concentrations of soluble components found in surface water at L67, Everglades National Park.

| Sample Date | SOLUBLE COMPONENT | | | |
|---|---|---|---|---|
| | $PO_4^{3-}$-P ppm | $NO_3^-$-N ppm | $NO_2^-$-N ppm | $NH_4^+$-N ppb |
| 11-24-74 | 0 | 0 | 0 | 1.0 |
| 1-2-75 | 0 | 0.9 | 0 | 1.0 |
| 2-13-75 | 0 | 1.0 | 0.1 | 0.7 |
| 4-21-75 | 0.1 | 8.5 | 0 | 0 |
| 6-2-75 | 0.1 | 2.4 | 0 | 6.1 |
| 2-29-75 | 0.1 | 6.5 | 0 | 0.9 |
| 8-9-75 | 0 | 1.9 | 0 | 2.0 |
| 9-1-75 | 0 | 0 | 1.3 | 2.9 |
| 10-11-75 | 0 | 1.5 | 0.2 | 10.5 |
| 2-9-76 | 0 | 1.0 | 0.1 | 1.0 |

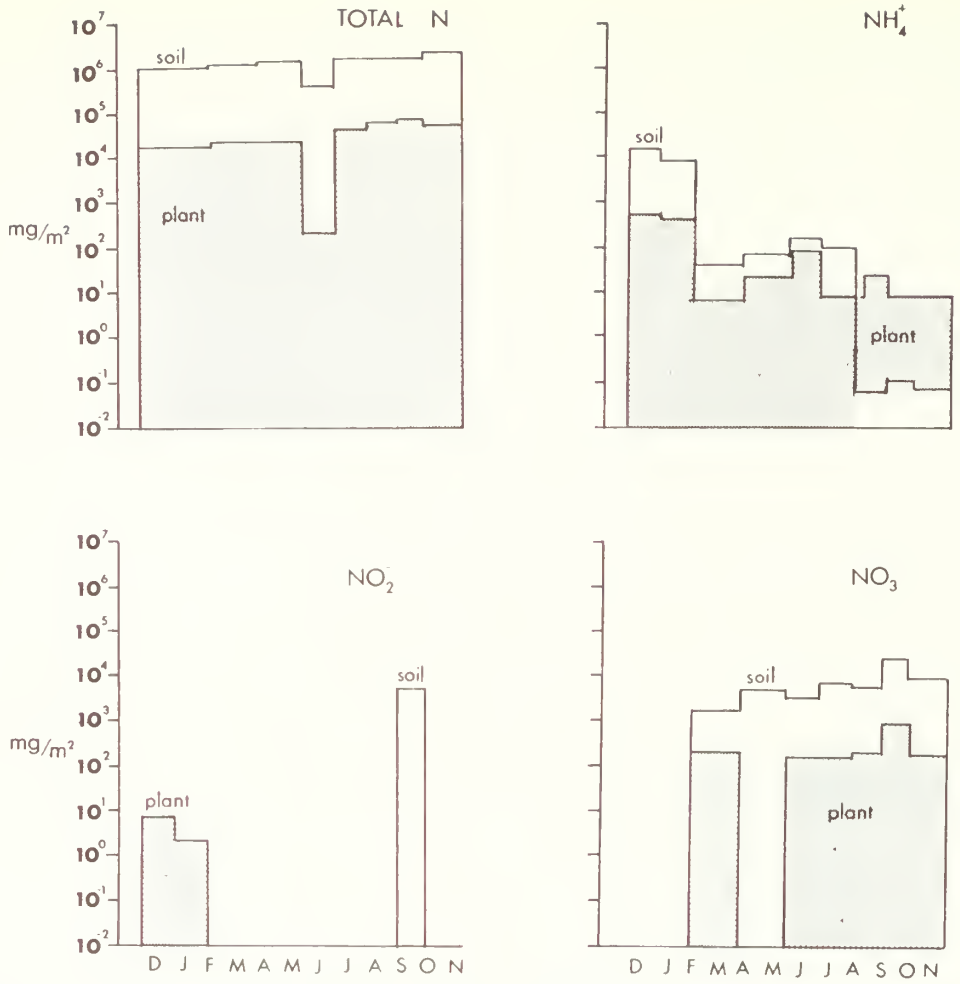



FIGURE 2. Quantity, $mg/m^2$-community unit, of total nitrogen, and water-soluble ammonium, nitrate, and nitrite contained in plants and the sediments (soil) at L67, Everglades National Park during 1975.

Total phosphorus was present in the sediment in quantities ten times greater than that found in plants. There was an appreciable increase in total phosphorus in plants in August primarily because there was an increase in biomass during summer, especially of roots, which had the greatest concentration of phosphorus. The increase in value of total phosphorus in plants from January to August was six-fold.

Soluble phosphate was present in plants throughout the year and increased in quantity at about the same time (August) as total phosphorus. Its proportional increase during summer was greater; the soluble phosphate value reached 1/2 that of the total phosphorus in plants and exceeded by a few milligrams that found in the sediment. Soluble phosphate in the sediment was found only in spring and summer.

Total nitrogen in the sediment was present in almost 100 times the quantity found in plants throughout the year. There was a decrease in the quantity of total nitrogen during June, which coincides with the beginning of the wet season. This occurred in both the sediment and plants, but the sediment quantity still exceeded the quantity found in plants by 1000 times. The decrease in soil nitrogen possibly could have been due to an increased denitrification activity. Losses of nitrogen and volatile nitrogen compounds directly from plants were studied by Pearsall and Billimoria (1937), Vickery et al. (1946), Wilson (1943), and Allison and Sterling (1948). No attempt was made to account for this loss in this study.

Ammonium was present in greatest quantities in winter in the sediment and also in the plants. This was during a period when water was fairly high, but was coolest and had the greatest amount of dissolved oxygen (e.g., at noon in January when water temperature was 26°C, saturation would be 8mg/l, the surface water had 7mg/l). Ammonium was present in greater quantities in April-May when water was shallow (7cm) than in September-October when water was at its maximum depth. The April-May value was about 100 times less than the winter value. Ammonium in plants was highest when ammonium in the sediment was highest. Ammonium increased again slightly in summer and except for one further increase in September, remained at a relatively uniform low level.

Nitrate was present in greatest quantity when ammonium was not, both in the sediment and in plants. There was a decrease in the quantity of nitrate in plants in April-May. Hageman and Flescher (1960) found that nitrate in plant tops represents a surplus of uptake over reduction in roots or leaves. This decrease in nitrate in sawgrass at this time suggests an increase in reductase activity not seen at other times.

Nitrite was found in the standing brown leaves

when nitrate was absent, ammonium was high, and nitrite was not found in the sediment. This suggests a metabolic slowdown with residual excess nitrate from the previous high-nitrate period caught in a transition state of reduction. The incidence of rather high amounts of nitrite in the sediment in fall also suggests a slow-down in the nitrifying process.

## CONCLUSIONS

The widely accepted view that submerged soils are anaerobic and contain nitrogen only as ammonium apparently does not apply to conditions at L67 in the sawgrass Everglades. Something other than the flooded condition determines the state of oxidation of nitrogen. Perhaps sawgrass aerates its substrate during its growing season sufficiently to allow aerobic nitrification during high water. In support of this conjecture, Forthman (1973) noted a growth surge in late spring, Conway (1937) demonstrated that *Cladium mariscus*, a related species, serates its roots by diffusion through the aerenchyma of mature green leaves and brown leaves. Dissolved oxygen was found at low but measurable levels in surface water even during summer at L67.

Apparently there is an adequate supply of total phosphorus in the sediment to support the plants growing in it as it is always present in the sediment in excess of that found in plants. Soluble phosphate, however, may be limiting at some times. The reason for the limited time of solubility and degree of dissolution is at present unknown. All of the soluble components were present as very small fractions of the total component.

No clear relationship between the components in the sediment or in the plants was determined. Nitrate and ammonium were mutually exclusive, but did not follow the seasonal pattern with respect to each other that one would expect. The components in sawgrass and the sediment seem to respond to some element of climatic seasonality. Hydroperiod seems to be the element of most importance, but the two major seasons coincide with differences in radiation, temperature, and increasing and decreasing day length. None of these seem to vary greatly during the year in southern Florida compared with values from more temperate latitudes, but without more information it is not possible to discount their importance.

## LITERATURE CITED


ALLISON, F. E. and L. D. STERLING. 1948. Gaseous losses of nitrogen from green plants. II. Studies with excised leaves in nutrient media. Plant Physiol. 23:601-608.

AOAC. 1970. Methods of analysis of the AOAC, 11th ed. Washington, D.C. 1015 pp.

APHA. 1971. Standard methods for the examination of water and wastewater. APHA and AWWA, Washington, D. C. 874 pp.

BARNES, H. and A. R. FOLKHARD. 1951. The determination of nitrites. Analyst 76:599-603.

BINGHAM, F. T., H. G. CHAPMAN and A. L. PUGH. 1954. Solution-culture studies of nitrite toxicity to plants. Soil Sci. Soc. Am. Proc. 18:305-308.

BONNER, J. 1946. The role of organic matter, especially manure, in the nutrition o rice. Bot. Gaz. 108:267-279.

BREMNER, J. M. 1965. Total nitrogen. *In:* Methods of soil analysis, Part 2. C. A. Black, (ed.), American So. of Agron., Madison, WI. 1572 pp.

CONWAY, V. M. 1937. Studies in the autecology of *Cladium mariscus* R. Br. III. The aeration of the subterranean parts of the plant. The New Phytol. 36:64-96.

COURT, M. N., R. C. STEPHEN and J. S. WAID. 1962. Nitrite toxicity arising from the use of urea as a fertilizer. Nature (London) 194:1263-1265.

DAVY, A. J. and K. TAYLOR. 1974. Seasonal patterns of nitrogen availability in contrasting soils in the Chiltern Hills. J. Ecol. 62:793-807.

FROTHMAN, C. A. 1973. The effects of prescribed burning on sawgrass. *Cladium jamaicense* Crantz, in South Florida. MS Thesis. Univ. of Miami, Coral Gables, FL. 83 pp.

GIGON, A. and I. H. RORISON. 1972. The response of some ecologically distinct plant species to nitrate- and to amonium-nitrogen. J. Ecol. 60:93-102.

HAGEMAN, R. H. and D. FLESCHER. 1960. Nitrate reductase activity in corn seedlings as affected by light and nitrate content of nutrient media. Plant Physiol. 35:700-708.

HELA, I. 1952. Remarks on the climate of South Florida. Bull. of Mar. Sci. of the Gulf of Mexico and Carribbean Sea. 2:438-447.

HAMMAR, H. E. 1929. The chemical composition of Florida Everglades peat soils, with special reference to their inorganic constituents. Soil Sci. 28:1-13.

HOFFSTETTER, R. H. and FRANCES PARSONS. 1975. The status of sawgrass, *Cladium Jamaicense*, in southern Florida. *In:*Hofstetter, R. H. and Frances Parsons. Effects of fire in the ecosystem. Final Report to the Dept. of the Interior. EVER-N-48. 64 pp.

HUTCHINSON, G. E. and V. T. BOWEN. 1950. Limnological studies in Connecticut. IX. A quantitative radio-chemical study of the phosphorus cycle in Linsley Pond. Ecology 31:194-203.

MILLER, C. F. 1918. Inorganic composition of a peat and of the plant from which it was formed. J. Agr. Res. 13:605-609.

NELLER, J. R. 1944. Influence of cropping, rainfall, and water table on nitrates in Everglades peat. Soil Sci. 57:275-280.

PEARSALL, W. H. and M. C. BILLIMORIA. 1937. Losses of nitrogen from green plants. Biochem. J. 31:1743-1750.

POMEROY, L. R. 1960. Residence time of dissolved phosphate in natural waters. Science 13:1731-1732.

RIGLER, F. H. 1956. A tracer study of the phosphorus cycle in lake water. Ecology 37:550-562.

SOLORZANO, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite methods. Limn. and Oceanogr. 14:799-801.

STEWARD, K. K. and W. H. ORNES. 1975. The autecology of sawgrass in the Florida Everglades. Ecology 56:162-171.

STRICKLAND, J. D. H. and T. R. PARSONS. 1968. A practical handbook of seawater analysis. Bull. 167. Fisheries Res. Bd. of Canada. Ottawa. 311 pp.

TUSNEEM, M. E. and W. H. PATRICK, JR. 1971. Nitrogen transformations in waterlogged soil. Bull. No. 657, Dept. Agr. Agr. Expt. Sta., L. S. U., Baton Rouge, LA. 75 pp.

VICKERY, H. B., A. J. WAKEMAN and C. S. LEAVENWORTH. 1946. Chemical investigations of the metabolism of plants. I. The nitrogen nutrition of *Narcissus poeticus*. Conn. Agr. Expt. Sta. Bull. 406.

VIETS, F. G., JR. 1965. The plant's need for and use of nitrogen *In:* Bartholomew, W. V. and F. E. Clark, eds., Soil nitrogen. Agronomy No. 10, Amer. Soc. of Agron., Madison, WI. 615 pp.

WILSON, J. K. 1943. Gaseous losses of nitrogen from green plants. II. Studies with excised leaves in nutrient media. Plant Physiol. 23:601-608.

# THE MAJOR PLANT COMMUNITIES OF THE FIRE ISLAND NATIONAL SEASHORE[1]

Richard Stalter[2]

## INTRODUCTION

Fire Island is a barrier island located along the south shore of Long Island extending from Southampton, L.I. to approximately the Nassau-Suffolk County line, a distance of 57 miles. It is separated from the mainland of Long Island by Great South Bay, which is from three-quarters to three miles wide. The island serves as a natural breakwater and is separated into three separate and distinct barriers by Shinnecock and Moriches Inlets.

Fire Island is of recent geological origin and developed sometime during the early Holocene. Its earliest development involved the formation of a submerged sand bar by the breaking action of waves in the shallow water some distance from shore. The steady accumulations of sand tossed up by the breakers caused the bar to emerge and migrate landward eventually developing into the chain of islands that exists today (Toumey 1959).

Other physical forces play a continuing role in the further development of the Fire Island barrier. Water movements, especially long-shore currents, are of prime importance in the maintenance of the island. These currents result when water is brought into the near-shore area by waves that approach the island at a slight angle to the shore. The result is a small, net displacement of water and drifting sand, parallel to the shore. This process is undoubtedly the most important source of sand deposition and erosion on the island today. The longshore drift runs predominantly from east to west and is responsible for the continued westward growth of the island, In the last 250 years historical records indicate a westward growth of almost six miles at Fire Island Inlet (Toumey 1959).

Beach drifting has also had its effects on the shaping of the barrier beach. The continual shifting of sand particles along the beach face by breaking waves results in the formation of a series of small ridges and valleys oriented parallel to the shore in the lower portions of the beach. These ridges and runnels have a seasonal development being partially obliterated during the winter only to be reformed during the summer. Deposition of dune sand on the landward side of the island is promoted as dry sand on the ocean side is blown landward by onshore winds.

## CLIMATE

The climate of Long Island is mild. The average killing frost occurs in late October to early November and can be expected from the middle of April to early May in the spring. The mean January temperature ranges from 30° in Medford to 32° in New York City, while the average July temperature ranges from 70° in Southampton to 77° in New York City. The average annual rainfall ranges from 43 inches to 45 inches (U.S.D.A. 1941).

## VEGETATION

There are three general plant communities on Fire Island: the sand dune community, the salt marsh community, and an evergreen forest of *Ilex opaca* (holly).

The plants of the sand dune community generally tolerate salt spray. The most common members of this community include *Ammophila breviligulata* (dune grass), *Lathyrus japonicus* (beach pea), *Artemesia stellariana* (dusty Miller), and *Solidago sempervirens* (seaside goldenrod).

The salt marsh community contains *Spartina alterniflora* (tall marsh cord grass), *Salicornia* spp. (glass wort), *Limonium carolinianum* (sea lavender), *Distichlis spicata* (spike grass), *Spartina patens* (salt meadow grass), and *Iva oraria* (high tide bush). Soil salt content and tidal flooding account for the zonation of salt marsh species.

The most unique plant community of the Sunken Forest occupies an area of approximately 64 acres behind the second dune system. *Ilex opaca* (holly) is the dominant species of the Sunken Forest which is one of the best developed evergreen maritime forests in the coastal northeastern United States.

At the present time, few workers have concerned themselves with the ecology and flora of Fire Island. Schulte (1965) prepared a floristic and ecological study of Fire Island, and commented on the parameters affecting the distribution of species in the Sunken Forest. Art et al. (1974) worked with the nutrient budget of the Sunken Forest. With the exception of individuals involved in floristic work, no investigator has attempted to study and characterize the three major communities of the Fire Island National Seashore.

The Fire Island National Seashore, consisting of 19,311 acres of land, was established as a national seashore in 1964. At the present time, the park is visited by thousands of people each year, who walk the trails to examine the vegetation of the Sunken Forest. Surprisingly, members of the Torrey Botanical Club have not organized field trips to this unique area, and many botanists are unaware of this unique ecosystem.

[1]The assistance of Professor William Nieter, who carefully reviewed and corrected the section dealing with geology is greatly appreciated.

[2]Environment Studies Program, St. John's University, Jamaica, New York 11439.

## METHODS

The present study consists of an examination of the parameters affecting the distribution of vegetation in three distinct plant communities. The vegetation of the sand dune community was examined by the quadrat method. One meter$^2$ quadrats were established at five stations, including the front of the foredune, the top of the foredune, the depression behind the foredune, the top of the second series of dunes, and a depression behind the second series of dunes (Figure 1). Soil samples were taken at the 0 to 2.5 and 15 centimeter levels and analyzed for salt content. Frequency data were prepared for the dune species and presented in Table 1. The salt content of the soil was measured following the procedure of Black et al. (1965).

The salt marsh species were surveyed using a surveyor's transit and stadia pole, and the species arranged in increasing elevation above the species (*Spartina alterniflora*) occupying the lowest elevation of salt marsh. Soil samples were taken and salinity values determined (Table 2).

Since Schulte (1965) and Art et al. (1974) have studied the Sunken Forest community, the present investigation was restricted to sampling techniques not employed by these investigators.

Ten 10 x 10 meter quadrats were established in the area of the Sunken Forest and frequency, density, basal area, and importance values calculated for the arborescent species (Table 3). In addition, size classes were established for the arborescent species of the forest (Table 4). Soil texture data was measured for the Sunken Forest community (Table 5).

Classification of the plant species follows Fernald (1950).

## DISCUSSION

### *Sand Dune Community*

The sand dune habitat is characterized by extremes of daily temperature, coarse porous soil, the affects of salt spray and drought.

Frequency data suggest that dune grass was dominant in the first three study sites (Table 1), with *Solidago sempervirens* (seaside goldenrod), *Artemesia stellariana* (dusty Miller), and *Cakile edentula* (sea rocket) important associates on the front of the ocean facing down where salt spray is heaviest (Oosting and Billings 1942 and Stalter 1974). Certain species that can tolerate lesser amounts of salt spray could be found just behind the top of the first dune. These included *Prunus maritima* (beach plum), *Parthenocissus quinquefolia* (Virginia creeper), while *Hudsonia tomentosa* (beach heather) was dominant at the depression behind the first dune. *Hudsonia*, a species that thrives in bright sunlight and shifting sand, cannot tolerate shade and high concentrations of salt spray and thus was only found in this habitat. A larger number of species was found on site 4 where the concentration of salt spray is low, and on site 5 where salt spray is minimal (Figure 1).

Studies on the east coast of the United States concerned with either the floristics or ecology of the sand dune community include Kurz (1942) and Davis (1942) for the Florida coast; Coker (1905) and Stalter (1974) for the coast of South Carolina; Kearney (1900), Oosting and Billings (1942), Boyce (1954), and Burk (1962) for the coast of North Carolina; Chrysler (1911) for Maryland; Snow (1913) for Delaware; Harshberger (1900) for New Jersey; and Boyce (1954) for Massachusetts.

Students of sand dune ecology have concurred with the findings of Oosting and Billings (1942) that salt spray and the transitory nature of the dunes (Boyce 1954, Stalter 1974) are most important in restricting sand dune vegetation.

### *Salt Marsh Community*

The salient features and causes of the establishment and development of salt marshes in the northeastern United States have been reported by Chapman (1940, 1960). Chapman reported that edaphic factors, such as chlorinity, salinity, and inter-species competition, coupled with duration and depth of flooding are important parameters that affect species distribution in salt marshes.

Results in the present study indicate that the absence of certain salt marsh species in each zone of the marsh reflects the inability of that species to tolerate salinity (Kerwin 1966); inundation (Johnson and York 1915), Chapman 1938); salinity and inundation (Chapman 1940) (Adams 1963); or a complex of several factors (Miller and Egler 1950, Stalter 1968). *Spartina alterniflora* (tall marsh cord grass) can tolerate the widest range of salinity and the longest period of flooding. The other species, *Limonium carolinianum* (sea lavender), *Salicornia virginica* (salt wort), *Suaeda linearis* (Suaeda), *Salicornia bigelovii* (salt wort), *Distichlis spicata* (spike grass), *Spartina patens* (salt meadow grass), and *Atriplex patula* (Atriplex), while tolerating varying ranges of salinity, occupy only a slight elevation gradient (usually a foot or less) in this marsh and in other marshes on Long Island (Lonergan and Stalter, unpublished data).

*Iva oraria* (high tide bush) occupies an area flooded infrequently at high tide. Soil salinities in this area are generally lower than soil salinities tolerated by other salt marsh species. *Aster tenuifolius* (salt marsh aster), while found associated with species in the upper portions of the salt marsh, is not as salt tolerant as the *Spartinas, Limonium,* or *Salicornia*. *Baccharis halimifolia* (silverling) can be found at the upper fringe of the salt marsh, but should not be classified as a strict salt marsh associate as thrives in open disturbed sites along Interstate 95 in North and South Carolina.

### *Sunken Forest*

The data from the Sunken Forest indicates that *Ilex opaca* is the dominant species. Other important associates include *Amelanchier canadensis* (shad bush), *Sassafras albidum* (sassafras); while two species of oaks, *Quercus stellata* (post oak) and *Quercus velutina* (black oak), are unimportant associates.

Many of the tree species are quite old. Cores taken from the holly on the island include one specimen with an age of 164 years while post oak, black oak, and juniper *(Juniperus virginiana* all are represented by trees over 100 years of age. Annual rings of one fallen oak were approximately 180 years. (Bullington 1976,

TABLE 1. Frequency data for species found in five study areas at the Sunken Forest, Long Island. Station 1, the front of the first dune; station 2, the top of the first dune; station 3, the depression behind the first dune; station 4, the top of the second dune; station 5, the depression behind the second dune (the Sunken Forest).

| Species | Study Areas | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| 1. *Ammophila breviligulata* | 100 | 100 | 100 | 0 | 0 |
| 2. *Cakile edentula* | 56 | 14 | 0 | 0 | 0 |
| 3. *Solidago sempervirens* | 100 | 56 | 42 | 33 | 0 |
| 4. *Artemisia stellariana* | 86 | 0 | 0 | 0 | 0 |
| 5. *Lathyrus japonicus* | 14 | 0 | 0 | 0 | 0 |
| 6. *Euphorbia polygonifolia* | 28 | 14 | 0 | 0 | 0 |
| 7. *Parthenocissus quinquefolia* | 0 | 86 | 28 | 66 | 100 |
| 8. *Prunus maritima* | 0 | 56 | 14 | 66 | 0 |
| 9. *Rhus radicans* | 0 | 14 | 0 | 100 | 50 |
| 10. *Hudsonia tomentosa* | 0 | 0 | 100 | 0 | 0 |
| 11. *Arctostaphylos uva-ursi* | 0 | 0 | 38 | 0 | 0 |
| 12. *Ilex opaca* | 0 | 0 | 0 | 84 | 100 |
| 13. *Lactuca* sp. | 0 | 0 | 0 | 33 | 0 |
| 14. *Smilax rotundifolia* | 0 | 0 | 0 | 66 | 88 |
| 15. *Achillia millifolium* | 0 | 0 | 0 | 33 | 0 |
| 16. *Rosa rugosa* | 0 | 0 | 0 | 100 | 12 |
| 17. *Prunus serotina* | 0 | 0 | 0 | 50 | 38 |
| 18. *Amelanchier stellata* | 0 | 0 | 0 | 50 | 75 |
| 19. *Smilacena stellata* | 0 | 0 | 0 | 66 | 75 |
| 20. *Rhus copallina* | 0 | 0 | 0 | 33 | 0 |
| 21. *Rubus* sp. | 0 | 0 | 0 | 16 | 12 |
| 22. *Maianthemum canadense* | 0 | 0 | 0 | 16 | 63 |
| 23. *Juniperus virginiana* | 0 | 0 | 0 | 50 | 0 |
| 24. *Myrica pennsylvanica* | 0 | 0 | 0 | 16 | 0 |
| 25. *Smilax glauca* | 0 | 0 | 0 | 16 | 0 |
| 26. *Vaccinium corymbosum* | 0 | 0 | 0 | 33 | 50 |
| 27. *Rubus hispidus* | 0 | 0 | 0 | 0 | 25 |
| 28. *Pteridium squilinum* | 0 | 0 | 0 | 0 | 25 |
| 29. *Vitis* sp. | 0 | 0 | 0 | 0 | 12 |
| 30. *Sassafras albidum* | 0 | 0 | 0 | 0 | 88 |
| 31. *ARalia nudicaulis* | 0 | 0 | 0 | 0 | 100 |
| 32. *Ribes cynosbati* | 0 | 0 | 0 | 0 | 12 |
| 33. *Lonicera japonica* | 0 | 0 | 0 | 0 | 12 |
| 34. *Viburnum dentatum* | 0 | 0 | 0 | 0 | 12 |

TABLE 2. A list of salt marsh psecies in the Fire Island National Seashore.

| Species | Salinity range |
|---|---|
| *Spartina alterniflora* | 0.5-3.5 |
| *Salicornia virginica* | 0.5-3.5 |
| *Salicornia bigelovii* | 0.5-3.5 |
| *Limonium carolinianum* | 0.5-3.0 |
| *Suaeda linearis* | 0.5-3.0 |
| *Distichlis spicata* | 0.5-2.5 |
| *Spartina patens* | 0.5-2.5 |
| *Atriplex patula* | 0.5-2.5 |
| *Iva oraria* | 0.1-1.2 |
| *Baccharis halimifolia* | 0.0-0.5 |

TABLE 3. Density (D), relative density (RD), frequency (F), relative frequency (RF), basal area (BA), relative dominance (RD), and importance value of arborescent species of the Sunken Forest, Fire Island, New York.

| Species | D | RD | F | RF | BA | RD | IV |
|---|---|---|---|---|---|---|---|
| *Ilex opaca* | 11.2 | 67 | 100 | 32 | 3445 | 57 | 156 |
| *Sassafras albidum* | 2.5 | 15 | 80 | 26 | 1031 | 17 | 58 |
| *Amelanchier canadensis* | 1.3 | 8 | 70 | 23 | 557 | 9 | 40 |
| *Nyssa sylvatica* | 1.3 | 8 | 40 | 13 | 685 | 11 | 32 |
| *Quercus stellata* | 0.2 | 1 | 10 | 3 | 247 | 4 | 8 |
| *Q. velutina* | 0.1 | 1 | 10 | 3 | 32 | 1 | 5 |

THE DOMINANT COMMUNITIES ON FIRE ISLAND
IN THE AREA OF THE SUNKEN FOREST, NEW YORK

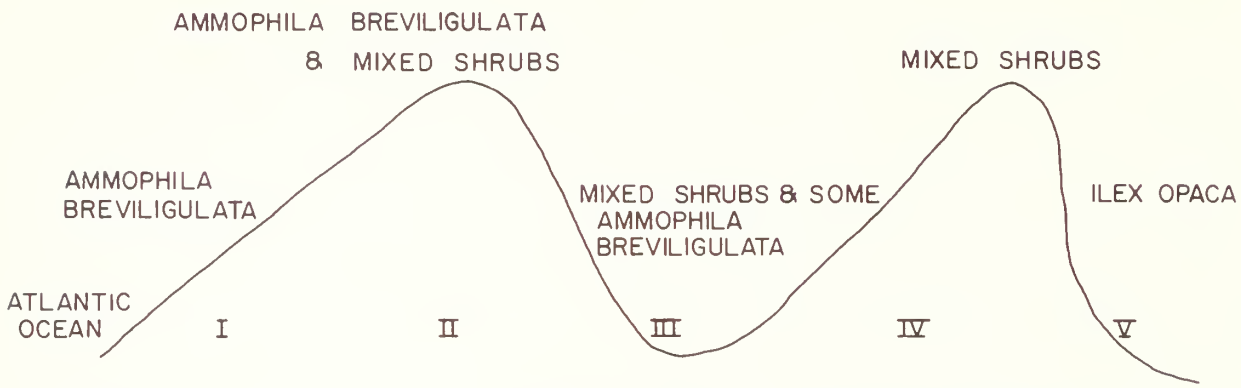



FIGURE 1. A diagram of the dune, shrub, and forest plants of Fire Island in the area of the Sunken Forest. Site I (front of first dune facing ocean), site II (top of forest dune), site III (depression behind first dune), site IV (top of second dune), Site V (depression behind second dune--the Sunken Forest).

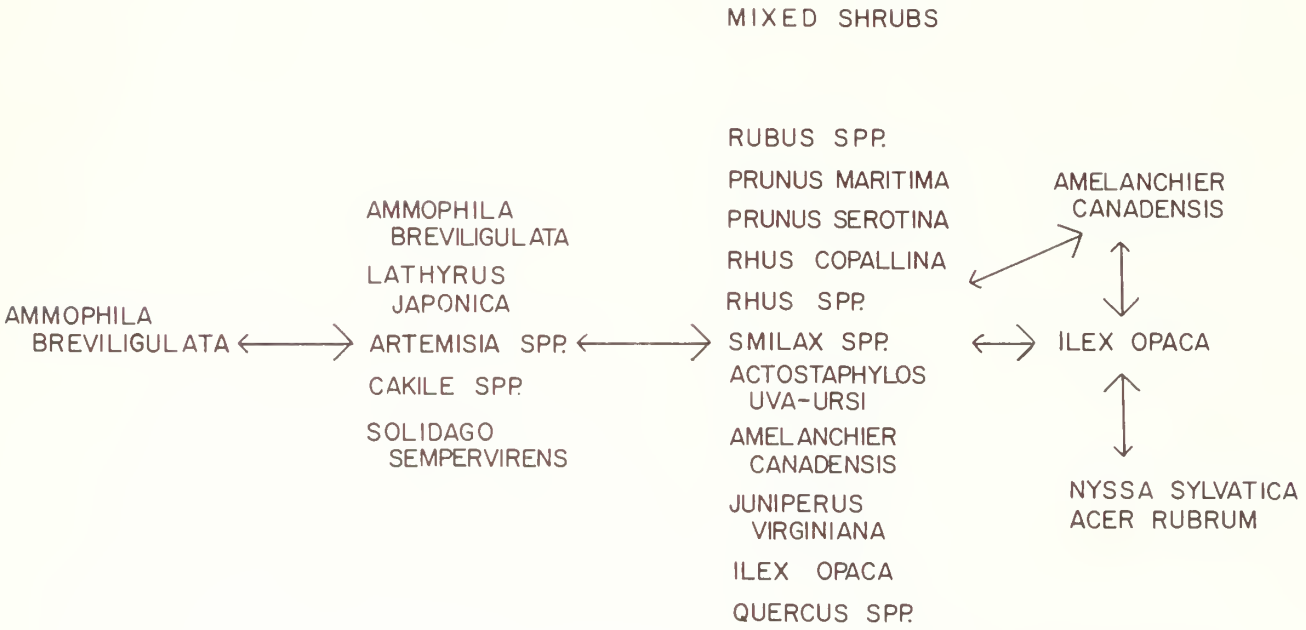



FIGURE 2. Successional trends on Fire Island in the Sunken Forest, New York.

TABLE 4. Distribution of trees in four size classes (expressed as a percent) of the Sunken Forest, Fire Island, New York.

| Species | Size class in cm | | | |
|---|---|---|---|---|
| | 0-8.9 | 9.0-15 | 15.1-22.9 | 23 |
| *Ilex opaca* | 17 | 45 | 35 | 3 |
| *Sassafras albidum* | 16 | 12 | 60 | 12 |
| *Amelanchier canadensis* | 24 | 24 | 38 | 14 |
| *Nyssa sylvatica* | -- | 11 | 67 | 22 |
| *Quercus stellata* | -- | 100 | -- | -- |
| *Q. velutina* | -- | -- | -- | 100 |

TABLE 5. Fire Island soil texture

| Sieve dimensions | Classification | % of soil fraction |
|---|---|---|
| 3.0 mm | Fine gravel | 0.3 |
| 1.5 mm | Fine gravel | 0.5 |
| 0.75 mm | Coarse sand | 16.1 |
| 0.4 mm | Medium sand | 70.0 |
| 0.25 mm | Fine sand | 12.9 |

pers. comm.).

The findings of the present study are in accord with Schulte's (1965) survey of Fire Island. The Sunken Forest, because it lies behind a secondary stable dune system, is completely protected from salt spray and wind. The October hurricane of 1938 that ravaged the eastern end of Long Island had no serious effect upon the plant species of the Sunken Forest (Bullington 1976, pers. comm.). Schulte contends that birds probably brought the original holly seeds to the island from the mainland. The copious development of plants whose fruits are favored by birds lends credence to Schulte's observations.

Schulte contends that there is a paucity of holly saplings. *Sassafras* and *Nyssa sylvatica*, that are well represented by saplings, may eventually assume greater importance in the forest canopy. An examination of size classes of the trees of the Sunken Forest (Table 4) might negate Schulte's observation, since many of the holly trees may be over 100 years of age.

Holly is well represented in all size classes. If one assumes that the smaller holly trees are younger than the larger hollies (an assumption that is not always a correct one) then it is probable that holly may maintain its dominance in the overstory.

At Island Beach State Park, a barrier island similar to Fire Island, back dune succession leads to an association of *Pinus rigida* (pitch pine), *Juniperus virginiana* (red cedar), and *Prunus serotina* (black cherry) (Martin 1959). Schulte observed several large dead specimens of *Pinus rigida* on Fire Island and maintains that *Pinus rigida* may have been more important in the Sunken Forest in the past. *Pinus rigida*, like *Ilex*, will grow in acid soil (pH 4.5 to 6) (Schulte 1965) but unlike *Ilex, Pinus* is intolerant to shade. Therefore, if *Pinus rigida* were important on Fire Island, it may have been gradually shaded out.

On Fire Island, a mixed shrub community may evolve into a community dominated by *Amelanchier canadensis* which in turn may develop into a community dominated by *Ilex*. On the wettest sites, *Nyssa sylvatica* and *Acer rubrum* (red maple) can be found. Figure 2 depicts successional trends that may occur on Fire Island in the area of the Sunken Forest. The data in this study and by other workers suggest that the location of the island, the shade tolerance of holly, the presence of a high complex dune system, and the presence of salt spray probably account for the dominance of *Ilex*.

## LITERATURE CITED


ADAMS, D. A. 1963. Factors Influencing Vascular Plant Zonation in North Carolina Salt Marshes. Eco. 44:445-456.

ART, H. W., F. H. BORMANN, G. K. BOIGHT, and G. M. WOODWELL. 1974. Barrier Island Forest Ecosystem: Role of Meteorologic Nutrient Inputs. Science 184:60-62.

BLACK, C. S., D. D. EVANS, J. J. WHITE, L. E. ENSMINGER, and F. E. CLARK. 1965. Methods of Soil Analysis. Agronomy. No. 9. Part 1 and 2, 1572 pp.

BOYCE, S. G. 1954. The Salt Spray Community. Ecol. Monogr. 24:26-67.

BURK, C. J. 1962. The North Carolina Outer Banks: A Floristic interpretation. Jour. Elisha Mitchell Sci. Soc. 78(1):21-28.

CHAPMAN, V. J. 1938. Studies in Salt Marsh Ecology; Section I to III. Jour. Ecol. 26: 144-179.

_____. 1940. Studies in Salt Marsh Ecology. Sections VI and VII. Comparisons with Marshes on the East Coast of No. America Jour. Ecol. 28:118-151.

_____. 1960. Salt Marshes and Salt Deserts of the World. The University Press, Aberdeen, 392 pp.

CHRYSLER, M. A. 1911. Ecological Plant Geography of Maryland. Md. Weather Serv. 3:148-197.

COKER, W. C. 1905. Observations on the Flora of the Isle of Palms, Charleston, S. C. Torreya 5:135-45.

DAVIS, J. H. 1942. The Ecology of the Vegetation and Topography of the sand Keys of Florida. Tortugas Lab. (Carnegie Inst. Wash.) Paps. 33:114-195.

FERNALD, M. L. 1950. Gray's Manual of Botany, 8th ed. New York: American Book Co.

HARSHBERGER, J. W. 1900. An Ecological Study of the New Jersey Strand Flora. Acad. Nat. Sci. Phila. Proc. 52:623-671.

JOHNSON, D. S. and H. H. YORK. 1915. Relation of Plants to Tide Levels. Carnegie Institution of Wash. Publication No. 206.

KEARNEY, T. H. 1900. The Plant Covering of Ocracoke Island; A Study in the Ecology of the North Carolina Strand Vegetation. U.S. Natl. Herbarium. Contr. 5:261-319.

KERWIN, J. A. 1966. Classification and Structure of the Tidal Marshes of the Poropotank River, Virginia. ASB Bulletin 13:40. Abstract.

KURZ. H. 1942. Florida Dunes and Scrub, Vegetation and Geology. Fla. Geol. Surv. Bull. 23. 154 pp.

MARTIN, W. E. 1959. The Vegetation of Island Beach State Park, New Jersey. Ecological Monographs 29:1-46.

MILLER, W. R. and F. E. EGLER. 1950. Vegetation of the Wequetequock-Pawcatuck Tidal Marshes, Connecticut. Ecol. Monogr. 20:143-172.

OOSTING, H. J. and W. D. BILLINGS. 1942. Factors Effecting Vegetation Zonation on Coastal Dunes. Ecology 23:131-42.

SCHULTE, E. 1965. A Study of the Plants in the Sunken Forest, Fire Island, New York. Unpublished Masters' Thesis. C. W. Post College, Long Island University.

SNOW, L. M. 1913. Progressive and Retrogressive Changes in the Plant Associations of the Delaware Coast. Bot. Gaz. 55:45-55.

STALTER, R. 1968. An Ecological Study of a South Carolina Salt Marsh. Unpublished Ph.D. Dissertation. 63 pp.

_____. 1974. Vegetation in Coastal Dunes of South Carolina. Castanea 39:95-103.

TOUMEY, D. 1959. Fire Island: Map 1798. Long Island Forum 22: 47-48.

U. S. DEPT. OF AGRICULTURE. 1941. Climate and Man. United States Govt. Printing Office, Wash. D. C.

# RE-ESTABLISHMENT OF PRAIRIE VEGETATION AT PEA RIDGE NATIONAL MILITARY PARK BENTON COUNTY, ARKANSAS

Edward E. Dale, Jr. and James W. Gibbons[1]

## INTRODUCTION

Pea Ridge National Military Park is located in the western part of the Oak-Hickory Association (Braun, 1950). This association, particularly in northwest Arkansas, is characterized by patches of prairie grasslands interspersed with forest (Turner, 1935).

Since such grasslands were reported by Bussey (1862) as present during the Civil War in what is now the western part of the park, a project was initiated in 1975 to re-establish prairie vegetation in this area.

Prairie restoration has been accomplished successfully in several areas of the United States including Iowa (Anderson, 1946; Christiansen, 1967), Illinois (Schramm, 1970), Wisconsin (Ode, 1970) and in Missouri (Toney, 1975), but such a project has not been previously attempted in Arkansas.

The primary objective of this project was to re-establish a prairie at Pea Ridge National Military Park that resembles original prairies of this area as closely as possible. A secondary objective was to gain experience in prairie restoration techniques so that expansion of the prairie area in the park could be facilitated later.

## METHODS

A one-acre (.405 hectares) plot was selected approximately 2.2 miles northwest of park headquarters as the site of the proposed prairie in April, 1975, and soil samples were taken for analysis by the University of Arkansas soils testing and research laboratory. The plot was plowed and disked twice, once in May and again in June to provide better soil conditions for the prairie species and to help eliminate weeds.

Results of the soil analysis indicated that soil conditions at the Pea Ridge site were essentially similar to tall grass prairie sites in northwestern Illinois (Alexander, Fehrenbacker and Ray, 1968) and to places in northwest Arkansas that supported prairie species (Phillips, 1967) except that the soil was characterized by a low phosphorus and potassium content. Accordingly, 23 pounds (20.4 kg.) of phosphorus ($P_2O_5$) and 30 pounds (13.6 kg.) of potassium ($K_2O$) fertilizer were applied.

Nitrogen was not added because the level present was considered adequate for the first year. Also, according to Owensby (1970) excess nitrogen would increase the chance of ecesis by cool season grasses which were abundant near the site.

The area was divided into sixteen square subplots fifty feet (15.24 meters) on each side and marked by stakes. Also, a 1.5 meter wide strip extending the entire length of the site on the east side was designated as a separate experimental plot.

Ecotypes of five species of prairie grasses (designated as horticultural varieties) known to be dominant or important constituents of prairies in northwest Arkansas and adjacent areas of Oklahoma and Missouri were chosen for initial re-establishment. The species and varieties used and seeding rates as shown in Table 1 were based on recommendations made by Roundtree, Bjugstad and Wheaton (1970) for Missouri, and by Stoin (1975) who has worked on pasture improvement in Arkansas.

On June 13, 1975, all seeds except *Panicum virgatum* were mixed and hand broadcast over the entire restoration area except in the experimental plot and in a few selected areas. *P. virgatum* was planted in pure stands only in the more mesic areas of the site because it is a very aggressive competitor in moist area and was observed by the senior author to increase greatly relative to other species in tall grass prairie in Oklahoma over a five-year period. Seeds of *Bouteloua curtipendula*, *Andropogon scoparius*, *Sorghastrum nutans*, and *Andropogon gerardi* respectively, were planted in pure stands on an increasing soil moisture gradient at obviously more dry or wet sites in accordance with the classification of prairie species on a moisture continuum in Wisconsin as described by Curtis (1955).

According to Schramm (1970) seeds should be raked in and then rolled or trampled after planting to increase germination. Ode (1970) states that mulch is significantly better than no mulch in establishing native grasses in Wisconsin using Nebraska seeds. Accordingly, the seeded plot was hand-raked and trampled, and fifteen bales of oat straw were evenly distributed as mulch.

Since these procedures were suggested for other areas where soil and climate conditions are different from those in Arkansas and different ecotypes were utilized, it seemed desirable to make a quantitative study of different seedbed treatments near the restoration site to test these procedures for this area.

The experimental plot area on the east side of the restoration site was divided into thirty-two 1.5 by .75 meter sub-plots, and one hundred seeds of each of the five grasses were broadcast June 20, 1975 in each sub-plot and submitted to all combinations of raking, mulching, and trampling or no treatment with four replications. After two months of growth, the number of seedlings present, by species, per treatment was counted and a two-way analysis of variance (Snedecor, 1956) was used to determine significance of results of the plot studies to the .05 level.

Percent cover of living prairie and weedy species present was determined in September, 1975, and periodically during the growing season of 1976 using a modification of the point method as described by Levy and Madden (1933).

Sods of prairie grasses and forbs were collected from an area near the park and transplanted to the prairie early in July, but further transplant-

[1]Department of Botany and Bacteriology, University of Arkansas, Fayetteville 72701.

TABLE 1. Species and varieties of prairie grasses and pounds per acre of pure live seeds (PLS) planted in prairie site at Pea Ridge National Military Park.

| Species | Variety | Seeds planted lbs PLS per acre |
|---|---|---|
| *Andropogon gerardi* Vitman | "Kaw" | 6 (2.7 kg) |
| *A. scoparius* Michx. | "Aldous" | 5 (2.3 kg) |
| *Sorghastrum nutans* (L.) Nash | "Cheyenne" | 3 (1.4 kg) |
| *Bouteloua curtipendula* (Michx.) Torr. | "El Reno" | 1.5 (.68 kg) |
| *Panicum virgatum* L. | "Blackwell | 1 (.45 kg) |

ing was terminated because of drought conditions in late July and August. Also, observations of survival of transplants and prairie grass seedlings and counts of prairie forbs that became established naturally were made throughout 1975 and in 1976.

Establishment of another acre of prairie adjacent to the restoration plot established in 1975 was initiated on June 7, 1976.

The procedures followed in establishing the new plot were similar to those used in 1975 with exceptions based on experience gained during the first year's work and on a study made by Gibbons (1976). The amount of seeds planted in 1976 was approximately twice that of 1975 for all species except *Andropogon scoparius*, in which approximately three times as much was used. This was done with the hope of obtaining better establishment in 1976. Also, raking was the only treatment given the 1976 restoration site immediately following seeding, and fertilizer was applied in July instead of June.

Photographs were taken and voucher specimens collected periodically during 1975 and 1976. All specimens are on file in the herbarium at the University of Arkansas, Fayetteville.

## RESULTS AND DISCUSSION

### 1975

Germination of grass seeds was noted approximately ten days after planting. Actual percentage of germination was obscured by heavy rains that fell approximately one week after planting when large numbers of seeds were washed from areas originally seeded. However, each tenth-square meter, except those heavily washed, contained at least one and usually several seedlings.

Seedlings had attained an average height of approximately 7.6 cm by mid-July, and by mid-August, the grasses were an average of 20 cm tall and had begun to tiller and form sods. The average height of the grasses varied from 40.9 cm in *P. virgatum* to 20.2 cm in *A. scoparius* on September 23.

First-year establishment of these grasses at Pea Ridge in 1975 resulted in plentiful flower and seed head production in August by *B. curtipendula* and isolated flowering in all others except *P. virgatum*. According to Schulenberg (1970) flowering during the first year was an indication of successful establishment in a restoration plot in Illinois.

TABLE 2. Percent cover of prairie grasses, by species, total percent cover of other species collectively and percent of bare ground or dead vegetation on different dates in plots established in 1975 and 1976. Agi, *Andropogon gerardi*; Asc, *A. scoparius*; Bcu, *Bouteloua curtipendula*; Pvi, *Panicum virgatum*; and Snu, *Sorghastrum nutans*.

| | Established June, 1975 | | | | | Established June, 1976 | |
|---|---|---|---|---|---|---|---|
| Prairie grasses | 9 7 75 | 5 20 76 | 7/8/76 | 9 7 76 | 10/7 76 | 9/7/76 | 10 13 76 |
| Agi | 7.0 | 7.8 | 4.4 | 13.0 | 5.8 | 9.0 | 6.6 |
| Asc | 4.6 | 8.4 | 15.4 | 16.0 | 7.2 | 4.5 | 2.3 |
| Bcu | .6 | 8.0 | 3.2 | 6.0 | 2.2 | 3.0 | 4.0 |
| Pvi | .6 | .1 | 1.6 | 3.5 | 1.5 | 2.5 | 2.1 |
| Snu | 4.2 | 5.8 | 9.0 | 24.0 | 27.3 | 5.5 | 4.4 |
| Total prairie grasses | 17.0 | 30.1 | 33.6 | 62.5 | 44.0 | 24.5 | 19.4 |
| Total other | 58.7 | 44.4 | 48.0 | 32.5 | 27.1 | 40.5 | 47.0 |
| Total bare or dead | 24.3 | 25.5 | 18.4 | 5.0 | 28.9 | 35.0 | 33.6 |
| Total | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |

Percentage cover of the five species of prairie grasses on September 7 ranged from 7.0% for *A. gerardi* to 0.6% each for *B. curtipendula* and *P. virgatum*. The five species covered a total of 17.0% (Table 2).

Some weeds were always present at the Pea Ridge prairie site, but they were not particularly noticeable in large numbers until mid-August. At that time *Mullugo verticillata* and *Diodia teres* covered much of the ground on bare areas. By September 7, the important weedy species were *M. verticillata, Digitaria sanguinalis, D. teres, Ambrosia artemisiifolia, Echinochloa crusgalli,* and *Bidens aristosa* (Table 3). These species alone covered a total of 42.5 percent cover. At this time the five prairie grasses covered less than a fifth of the total area.

TABLE 3. Vegetation of prairie site established in June 1975 at Pea Ridge National Military Park. September 7, 1975.

| Species | Percent cover |
|---|---|
| *Mollugo verticillata* L. | 15.8 |
| *Andropogon gerardi* Vitman* | 7.0 |
| *Digitaria sanguinalis* (L.) Scop. | 5.8 |
| *Diodia teres* Hall. | 5.6 |
| *Ambrosia artemisiifolia* (L.) Des. | 5.4 |
| *Echinochloa crusgalli* (L.) Beauv. | 5.1 |
| *Sorghastrum nutans* (L.) Nash.* | 4.8 |
| *Bidens aristosa* (Michx.) Britt. | 4.7 |
| *Andropogon scoparius* Michx.* | 4.6 |
| *Gaura biennis* L. | 3.5 |
| *Tridens flavus* (L.) Smyth | 3.5 |
| *Leptoloma cognatum* (Schult.) Chase | 2.1 |
| *Setaria glauca* (L.) Beauv. | 1.6 |
| *Euphorbia corollata* L. | 0.7 |
| *Panicum anceps* Michx. | 0.7 |
| *Solanum carolinense* L. | 0.7 |
| *Bouteloua curtipendula* (Michx.) Torr.* | 0.6 |
| *Panicum virgatum* L.* | 0.6 |
| *Rubus* sp. | 0.6 |
| *Cyperus globulosus* Aubl. | 0.6 |
| *Oenothera laciniata* Hill | 0.6 |
| *Apocynum cannabinum* L. | 0.6 |
| *Aristida oligantha* Michx. | 0.2 |
| *Desmodium* sp. | 0.2 |
| *Croton capitatus* Michx. | 0.1 |
| Bare ground or dead vegetation | 24.3 |
| | 100.0 |

*Denotes prairie grasses established by seeds.

Results from the experimental plot studies showed that significant differences at the 0.05 level were found between the number of seedlings surviving after two months.

Raking appears to be the most effective treatment for seedling establishment. None of the other treatments were significantly better for seedling survival except for *Sorghastrum nutans* which showed significantly better results when mulching was applied with raking.

Mulching only was of no benefit to seedling establishment, probably due to adequate soil moisture conditions at the site following planting. Sixty percent of the average yearly rainfall at Pea Ridge falls during the period from April to September (United States Department of Commerce, 1974), and 1975 was a particularly wet year. Hence, the moisture requirements of these species were met in 1975 and mulching to conserve soil moisture was unnecessary. However, during years with low rainfall, mulching might be required.

Trampling was also found to be of no benefit to establishment at Pea Ridge. After rains, the soil at the restoration site tended to become compacted because of its high clay content. This possibly had the same effect on seed germination as trampling would have on coarser textured soils.

Transplant experiments resulted in varying degrees of success in establishing prairie species at Pea Ridge. Sods of the five seeded species, *Elymus canadensis* L. and *Tripsacum dactyloides* L. that were transplanted into the area in July were living in September 1975.

Attempts were made to transplant ten species of prairie forbs. These transplants appeared at first to be successful, but drought conditions and excess browsing by white-tail deer eliminated all but *Asclepias tuberosa* L. and *Dalea purpurea* Vent. by fall, 1975.

It is probable that transplanting may be the best method for establishing species in a re-establishment prairie (Christensen, 1967; Bland, 1970; Schulenberg, 1970); however, the technique requires so much time and hand labor that the expense may be prohibitive. Also, sufficient amounts of transplant materials are frequently difficult to find.

An unexpected benefit to establishment of prairie forb species occurred through natural growth from roots, rhizomes, or seeds. Prairie species that became established naturally included *Vernonia missourica* Raf., *Euphorbia corollata* L., *Solidago altissima* L., *Apocynum cannabinum* L., *Schrankia Nuttallii* (DC.) Stand L., *Rudbeckia hirta* L. and *Erigeron strigosus* Muhl.

## RESULTS AND DISCUSSION

### 1976

In the discussion that follows, the prairie restoration area established in 1976 will be referred to as the one-year plot and the area established in 1975 (which has supported prairie vegetation for two growing seasons) will be designated as the two-year plot.

#### *One-Year Plot Established in 1976*

Seeds planted on June 7, 1976 did not germinate until the last week in June, primarily because of lack of moisture. However, a good stand of grass was evident over most of the area by July 8 following a heavy rain in late June.

Seedlings averaged approximately 26 cm high by mid-July and 10.4 cm by mid-August in all parts of the area except in places where fertilizer was applied in June. Average height of the grasses on the fertilized areas was 13.0 cm in mid-August, indicating that use of fertilizer on newly established prairie sites promotes better growth and faster establishment of prairie species. This is not in agreement with recommendations of Schramm (1970) who advises against fertilizer application on new prairie restoration sites. Growth in the initially unfertilized areas became more rapid after fertilizer was applied in July. Prairie grasses averaged 15.6 cm in height in both fertilized and unfertilized areas on October 7 indicating that mid-summer fertilizer applications can be beneficial.

Percent living cover of all prairie species was 24.5 on September 7, but dropped to 19.4 by October 13. However, the total cover of all other species combined (mostly weeds) increased from 40.5 to 47.0 percent (Table 2). This is not surprising since prairie species normally undergo senescence

and annual weeds frequently grow relatively faster at this time of year.

The most common weed species present was *Setaria glauca* which comprised 11 percent cover. *Paspalum laeve* was second with a percent cover of 4.5, and all others present were 2.5 percent or less (Table 4).

TABLE 4. Vegetation of prairie site established in 1976 at Pea Ridge National Military Park. September 7, 1976.

| Species | Percent cover |
|---|---|
| *Setaria glauca* (L.) Beauv. | 11.0 |
| *Andropogon gerardi* Vitman* | 9.0 |
| *Echinochloa crusgalli* (L.) Beauv. | 5.5 |
| *Sorghastrum nutans* (L.) Nash.* | 5.5 |
| *Andropogon scoparius* Michx.* | 4.5 |
| *Paspalum laeve* Michx. | 4.5 |
| *Bouteloua curtipendula* (Michx.) Torr.* | 3.0 |
| *Panicum virgatum* L.* | 2.5 |
| *Gaura biennis* L. | 2.5 |
| *Mollugo verticillata* L. | 2.5 |
| *Digitaria sanguinalis* (L.) Scop. | 2.0 |
| *Panicum anceps* Michx. | 1.5 |
| *Leptoloma cognatum* (Schult.) Chase | 1.5 |
| *Ambrosia artemisiifolia* (L.) Des. | 1.5 |
| *Diodia terres* Hall. | 1.5 |
| *Croton sapitatus* Michx. | 1.5 |
| *Bidens aristosa* (Michx.) Britt. | 1.5 |
| *Solanum carolinense* L. | 1.0 |
| *Aristida longespica* Poir. | 0.5 |
| *Panicum lanuginosum* Ell. | 0.5 |
| *Tridens flavus* (L.) Smyth | 0.5 |
| *Panicum laxiflorum* Lam. | 0.5 |
| *Trifolium reflexum* L. | 0.5 |
| Bare ground or dead vegetation | 33.0 |
| | 100.0 |

*Denotes prairie grasses established by seeds.

Naturally occurring prairie forbs present in the plot in September were *Solidago altissima* and *Gnaphalium obtusifolium* L. Others observed in the area during June and July that had completed their growth and reproductive cycles before September included *Rudbeckia hirta, Euphorbia corollata, Apocynum cannabinum* and *Shrankia Nuttallii.*

*Composition of First Year's Growth in 1975 and in 1976*

Several differences were noted in species present and growth condition during the first year's growth in the two-year plot established in 1975 and the one-year plot established in 1976.

Germination and growth began earlier in 1975 than in 1976, and average sizes of all prairie species were larger at the end of the growing season in 1975. This is attributed primarily to more favorable moisture conditions.

A heavy rain occurred the day after seeds had been planted on June 13, 1975, but it did not rain until nearly three weeks after planting on June 7, 1976. Also, rainfall was greater and more evenly distributed during the 1975 growing season.

Percent cover of prairie grasses was 17 percent on September 7, 1975 in the two-year plot and 24.5 percent in the one-year plot on September 7, 1976 (Table 2). Apparently the greater seeding rate must have favored the higher survival percentage and compensated somewhat for the poorer growth conditions.

It is noteworthy that weed populations were different near the end of the growing season of both years. Principal species present in 1975 were *Mollugo verticillata, Digitaria sanguinalis, Diodia teres, Ambrosia artemisiifolia, Echinochloa crusgalli* and *Bidens aristosa.* In 1976, the principal species were *Setaria glauca, Echinochloa crusgalli,* and *Paspalum laeve.* Also, there was less bare ground in 1975 than in 1976 (Tables 3 and 4).

*Two-year Plot Established in 1975*

Increased growth and spreading of prairie species during the second year was noted on May 20 1976, when cover of prairie species had increased to 30.2 percent. Cover percentage was 33.6 on July 8 and 62.5 on September 7, but it declined to 44.0 percent on October 7 near the end of the growing season (Table 2).

The general trends of increasing cover percentages from May to September and decline in October occurred in all prairie species except *Sorghastrum nutans* which had the highest percent cover in October, and in *Bouteloua curtipendula* which had a cover percentage of 8 percent on May 20.

Total percent cover of all other species collectively declined from May until October, probably because of competition with the increasing prairie grasses. The percentage of bare areas or dead vegetation declined from 25.5 percent on May 20 to 5 percent on September 7. It increased to 28.9 percent on October 7 primarily because of natural senescence.

Populations of weed species changed considerably during the growing season with *Aristida longispica, Trifolium reflexum,* and *Bidens aristosa* occurring as principal species in September (Table 5).

TABLE 5. Vegetation of prairie site established 1975 at Pea Ridge Natioanl Military Park. September 7, 1976.

| Species | Perce cove |
|---|---|
| *Sorghastrum nutans* (L.) Nash.* | 24.0 |
| *Andropogon scoparius* Michx. | 16.0 |
| *Andropogon gerardi* Vitman* | 13.0 |
| *Bouteloua curtipendula* (Michx.) Torr. | 6.0 |
| *Aristida longespica* Poir. | 5.0 |
| *Trifolium reflexum* L. | 5.0 |
| *Bidens aristosa* (Michx.) Britt. | 4.5 |
| *Panicum virgatum* L.* | 3.5 |
| *Gerardia fasciculata* Ell. | 3.0 |
| *Cassia fasciculata* Michx. | 3.0 |
| *Solanum carolinense* L. | 2.5 |
| *Panicum lanuginosum* Ell. | 1.5 |
| *Tridens flavus* (L.) Smyth | 1.5 |
| *Apocynum cannabinum* L. | 1.0 |
| *Ambrosia artemisiifolia* (L.) Des. | 1.0 |
| *SEtaria glauca* (L.) Beauv. | 1.0 |
| *Paspalum laeve* Michx. | 1.0 |
| *Rubus* sp. | 0.5 |
| *Euphorbia corollata* L. | 0.5 |
| *Diodia teres* Hall | 0.5 |
| *Eupatorium serotinum* Michx. | 0.5 |
| *Solidago altissima* L. | 0. |
| Bare ground or dead vegetation | 5. |
| | 100. |

*Denotes prairie grasses established by seeds

It was noted that many weeds present in both 1975 and 1976 were generally much smaller and less numerous during the second year. This was particularly true of *Ambrosia artemisiifolia* and *Bidens aristosa* which were very conspicuous in 1975.

Prairie forbs transplanted into the plot in 1975 that appeared to be established in August, 1976 were *Asclepias tuberosa, Dalea purpurea* and *Echinacea pallida* Nutt.

All species of naturally occurring prairie forbs present in 1975 were present in 1976 also. New species noted in 1976 included *Gerardia fasciculata* and *Gnaphalium obtusifolium*.

## CONCLUSIONS

It is concluded that satisfactory progress is being made toward the establishment of a prairie in both the one- and two-year plots using the techniques presently employed. This is based on the great increase in prairie species relative to weeds at the end of two years and the relatively higher percentage of prairie species present in the one-year plot established in 1976 as compared to first year's growth in 1975. Also, it is encouraging to note that a comparison of vegetation of the two-year plot with a native mixed lowland prairie near Harrison, Arkansas, shows that percent cover and species composition of grasses in these two areas are similar. The forb population on the two-year plot lacks many species present in the native prairie and the weed population is still too high. In addition, there are several bare places that will require reseeding of prairie grasses and more intensive work on establishment of forbs is needed. However, indications are that with proper management most of the difficulties described can be greatly reduced or eliminated.

## LITERATURE CITED


ALEXANDER, J. D., J. B. FEHRENBACHER, and B. W. RAY. 1970. Characteristics of dark colored soils developed under prairie in a toposequence in northwestern Illinois. *In:* Schramm, Peter (ed.). Proceedings of a symposium on prairie and prairie restoration. Knox College Biol. Field Stat. Special Publ. No. 3.

ANDERSON, W. A. 1946. Development of prairie at Iowa Lakeside Laboratory. Amer. Mid. Nat. 36:431-455.

BLAND, MARILYN K. 1970. Prairie establishment at the Michigan Botanical Gardens. *In:* chramm, Peter (ed.). Proceedings of a symposium on prairie and prairie restoration. Knox College Biol. Field Stat. Special Publ. No. 3.

BRAUN, E. LUCY. 1950. Deciduous forests of eastern North America. Blakiston Co., Philadelphia. 596 pp.

BUSSEY, COL. CYRUS. 1862. Description of vegetation during the Battle of Pea Ridge. O. R., Ser. 1, Vol. VIII:233.

CHRISTIANSEN, PAUL A. 1967. Establishment of prairie species in Iowa by seeding and transplanting. Ph.D. Thesis. Iowa State Univ., Ames, Iowa.

CURTIS, J. T. 1955. A prairie continuum in Wisconsin. Ecology 36:558-566.

GIBBONS, JAMES W. 1976. Reestablishment of prairie vegetation at Pea Ridge National Military Park, Benton County, Arkansas. Master's Thesis. University of Arkansas, Fayetville.

LEVY, E. B., and E. A. MADDEN. 1933. The point frame method of pasture analysis. New Zealand Jour. Agri. 46:1933.

ODE, ARTHUR H. 1970. Some aspects of establishing prairie species by direct seeding. *In:* Schramm, Peter (ed.) 1970. Proceedings of a symposium on prairie and prairie restoration. Knox College Biological Field Station Publication No. 3. Galesburg, Illinois.

OWENSBY, CLENTON E., R. M. HYDE, AND K. L. ANDERSON. 1970. Effects of clipping and supplemental nitrogen and water on loamy upland bluestem range. J. Range Manage. 23(5):341-346.

PHILLIPS, WILLIAM WALLACE. 1967. Prairie soils: properties and classification in northwest Arkansas. Master's Thesis. University of Arkansas. Fayetville.

ROUNDTREE, B. H., A. J. BJUGSTAD and H. N. WHEATON. 1970. Big bluestem, switchgrass and Indian grass. Science and Technology Guide. University of Missouri. Columbia Extension Division. Columbia.

SCHRAMM, PETER. 1970. Practical restoration method for tall grass prairie. *In:* Schramm, Peter (ed.) 1970. Proceedings of a symposium on prairie and prairie restoration. Knox College Biological Field Station Publication No. 3. Galesburg, Illinois.

SCHULENBERG, RAY. 1970. Summary of Morton Arboretum prairie restoration work, 1963 to 1968. *In:* Schramm, Peter (ed.). Proceedings of a symposium on prairie and prairie restoration. Knox College Biol. Field Stat. Special Publ. No. 3.

SNEDECOR, GEORGE W. 1956. Statistical methods applied to experiemtns in agriculture and biology. Iowa State College Press, Ames, Iowa. 534 pp.

STATEN, H. W. 1943. Seeding native grasses. Okla. Agr. Exp. Stat. Cir. 108.

STOIN, HARLAN. 1975. Personal communication.

TONEY, TOM. 1975. Personal Communication.

TURNER, LEWIS M. 1935. Notes on forest types of northwest Arkansas.

UNITED STATES DEPARTMENT OF COMMERCE. 1974. Climates of the States, Vol. II. National Oceanic and At mospheric Administration Water Information Center, Inc., Port Washington, N.Y. 527-537.

# AIR POLLUTION - VEGETATION EFFECTS STUDIES IN TWO NATIONAL PARKS[1]

S. V. Krupa, R. J. Kohut and J. A. Laurence[2]

Air pollution is a source-transport-effect phenomenon. Knowledge concerning the importance of air pollutants and their effects on the human environment is continuously increasing across the U.S. In the last few years several investigations have shown that air pollutants and their potential effects are not restricted to the urban areas only. A significant amount of data has been gathered to demonstrate long distance transport of air pollutants and/or their precursors to the rural environment. The decline of ponderosa pine in the San Bernardino mountains due to the urban plume generated in the Los Angeles Basin is an excellent example of such a phenomenon (Miller and Taylor, 1976).

Air pollutants influence our environment through their effects on: 1) terrestrial vegetation, 2) aquatic systems, 3) soils and 4) materials. Air pollutants occur as gases, aerosols, large particulates, and wet fallout (rain and snow). The major sources of national air pollution are summarized in Table 1.

In general, ozone and sulfur dioxide are considered to be the most important phytopathogenic air pollutants. Plants respond rapidly to these and other air pollutants. Based upon their comparative response, plant species are classified as sensitive, intermediate and resistant to a given air pollutant. A list of some plants known to be sensitive to ozone, sulfur dioxide and gaseous fluoride is presented in Table 2. Variation occurs in plant response to air pollutants at the community, generic, species and varietal levels. Further, plant age and stage of growth, aerial and edaphic environmental factors influence the plant response. The research has emphasized the effects of air pollutants on economically important crop, ornamental and tree species; very little is known about the response of herbaceous native vegetation to air pollution.

Air pollutant effects on vegetation may be acute, chronic or subtle. Acute effects generally result from the exposure of plant species to high concentrations of air pollutants over few to several hours, while chronic effects result from exposure to lower air pollutant concentrations over days or weeks. While the effects of acute and chronic injury are evident in many cases through specific symptoms, subtle effects are evaluated only as reductions in growth, productivity, reproduction and community decline.

Wester, of the National Park Service, (personal communication) made extensive observations of the effects of air pollutants on plants in the Capital National Parks. However, no detailed studies have been conducted on air pollution-vegetation effects with reference to park management. The long-term goal of our investigation is to conduct a comparative investigation of the air quality and vegetational effects in a remote and an urban park system. The specific objectives are as follows:

1. to monitor continuously over several vegetational growth seasons, ambient concentrations of ozone, oxides of nitrogen and sulfur dioxide,

2. to establish permanent vegetational study plots and evaluate for symptoms of air pollutant-induced injury,

3. to evaluate selected plant species in these study plots for the foliar accumulation of total sulfur, fluoride and metals, over several growth seasons,

4. to monitor the changes in soil chemistry within the study plots with reference to the aforementioned elements,

5. to evaluate the air pollution response of indicator plant species introduced into the study area, over several growth seasons, and

6. to evaluate the possible relationships between air quality and effects on terrestrial vegetation.

## AIR QUALITY AND VEGETATIONAL EFFECTS IN A REMOTE NATIONAL PARK

The Voyageurs National Park is relatively new and unused and is located in northern Minnesota approximately 15 miles east of International Falls, Minnesota. This area is detached from urban influence and is covered by a hardwood-coniferous forest. The understory is composed of over 100 different plant species. Before one can assess the contribution of man's activities to the atmospheric loading of air pollutants in such a remote park, it is essential to characterize the baseline levels of various air pollutants. In this context, ozone and oxides of nitrogen are considered to be most important because of the: 1) remoteness of the Park, 2) generation of ozone through natural processes, and 3) possible increase in the automobile traffic (a source for the ozone precursors - oxides of nitrogen and hydrocarbons).

During the summer of 1974, ambient ozone concentrations were monitored in the park over a period of 676 hours, oxides of nitrogen for 491 hours and sulfur dioxide for 824 hours (Laurence *et al.*, 1975). Throughout the period of observation, sulfur dioxide was not detected. Ozone concentrations ranged from 0.0075 ppm to 0.08 ppm. The latter concentration occurred once during the summer for 20 minutes. Mean hourly concentrations were lowest from 4 a.m. to 7 a.m. (0.025 ppm) and reached a maximum between 2 p.m. and 8 p.m. (0.035 ppm) (Figure 1). There were no correlations between ozone concentrations and frontal systems, storm systems or wind direction. During this period, the average hourly concentration of total

---

[1]Paper No. 9792, Scientific Journal Series, Minnesota Agricultural Experiemtn Station, St. Paul, Minnesota 55108.

[2]Department of Plant Pathology, University of Minnesota, St. Paul 55108.

nitrogen oxides ranged from 0.32 ppm to 0.397 ppm (Figure 1) and the nitrogen dioxide levels varied daily from 0.0 ppm to 0.1 ppm.

It is considered that the ozone concentrations measured in the Voyageurs National Park are not the result of man-related activities or long-distance transport. The daily ozone pattern is indicative of typical photochemical oxidation. It is suggested that the precursors for ozone generation, both oxides of nitrogen and hydrocarbons, are produced by the potentially high biological activity in the ecosystem. The measured hourly ozone concentrations are considered to represent what is generally accepted as background levels.

During the summers of 1974 and 1975 no symptoms of air pollutant-induced vegetational injury were observed in the Voyageurs National Park.

## AIR QUALITY AND VEGETATIONAL EFFECTS IN AN URBAN NATIONAL PARK

The urban National Park, the Indiana Dunes National Lakeshore, is located along Lake Michigan in northern Indiana. This area presents a wide variety of habitats ranging from young unstable dunes and interdunal ponds, to mixed hardwood forests on fully stable ancient dunes. During the late 1800's Henry Cowles conducted his classical ecological studies here, which showed that plant communities changed over time in predictable patterns. This observation led to his concept of dynamic succession. This geographic area continues to serve an important function in research for midwest ecologists, botanists and zoologists. The Lakeshore also serves as a premier recreation center for the population of the Chicago-Gary-Michigan City urban complex.

It is extremely important to understand the effects of the air pollutants in the urban plume on the plant communities of the National Lakeshore. Air pollutant stress can alter the plant community composition by eliminating the sensitive species. In addition, air pollutants can also modify the rate of plant community succession.

There are several, diverse air pollutant sources in the vicinity of Indiana Dunes National Lakeshore. To the west of the Lakeshore, metropolitan Chicago serves as a major source for the urban plume. The most important phytopathogenic air pollutants from this area are considered to be ozone and the oxides of nitrogen. The Gary-Hammond area west of the Lakeshore is intensively industrialized. The myriad industries in this area probably contribute a vast variety of emissions to the atmosphere. Sulfur dioxide, gaseous fluorides and various forms of heavy metals are considered to be the major air pollutants from this are. In addition, several major point sources are located in the immediate vicinity of the National Lakeshore. These consist of two coal-fired power plants and a steel mill.

During the spring of 1976, a continuous ambient air pollution monitoring station was established within the National Lakeshore. Ozone, oxides of nitrogen and sulfur dioxide were monitored over the vegetational growth season (April through August).

To determine the effects of these pollutants on vegetation, 24 field evaluation sites were established in the Dunes area. Vegetation in these study plots was evaluated every month during the study period for air pollution-induced injury. Selected plant species in these plots were also sampled for foliar chemical analysis of total sulfur, fluoride and metals. Soil was also sampled for similar chemical analysis. These chemical analyses are currently in progress.

Since the plant communities in the Indiana Dunes National Lakeshore have been subjected to air pollution stress for a substantial period of time, it seems possible that the most sensitive members of the plant communities may have been eliminated. If this process has occurred, many of the existing individuals of a plant species will be those with greater resistance and their response to air pollutants will not be representative of the original plant community. To aid in the evaluation of air pollutant-vegetation effects and their future trends, a limited number of air pollutant sensitive plant species such as white ash and hybrid poplar were introduced into the study area. These plants will be monitored over several growing seasons for their response to air pollution.

To determine whether the air pollution stress has altered the pollution sensitivity of the plant in a population of a given species, plants grown from seeds collected at the Indiana Dunes National Lakeshore are being exposed to ozone and sulfur dioxide in controlled laboratory experiments. The average levels of injury produced on these plants will be compared with the response of plants growr from seed collected from areas not subjected to the air pollution stress. Air pollutant-response studies are also being conducted on a number of herbaceous native plant species obtained from outside the Indiana Dunes area.

During the summer of 1976, ozone injury was observed on vegetation in 12 of the 24 study plots in the Indiana Dunes National Lakeshore area. These 12 plots were distributed at random, three within the National Lakeshore, one within the adjacent state park and the remaining eight outside the park system. Plant species exhibiting ozone injury (Figure 2) included witch hazel, grape, strawberry, poison ivy, elm, milkweed, blueberry, ash, tulip-poplar, hickory, spicebush, aspen and soybean. Sulfur dioxide injury (Figure 2) was observed on four field sites located outside the park system. This injury was observed on blackberry, American hazel, elm and nightshade.

Since the sulfur dioxide injury appeared to be rather common at one of the field sites, a series of supplementary evaluation sites was established nearby to determine the spatial extent of the injury. Species injured included blackberry, ash, sweet cicely, boxelder, violet, cherry and basswood. The sulfur dioxide injury occurred in a ba approximately 3.5 miles to 5.0 miles south of an industrial complex consisting of a steel mill an a coal-fired power plant. Sufficient air qualit and meteorological data are not available at thi time to determine the actual source(s) of this pollution.

In general, during the study period elevated concentrations of sulfur dioxide were not detect in the atmosphere at the air quality monitoring station within the National Park. Atmospheric concentrations of sulfur dioxide were usually le than the expected phytotoxic concentrations. Average hourly sulfur dioxide concentrations exceeded 0.1 ppm over less than 10 hours during th vegetational growth season. It seems likely tha the location of the air quality monitoring stat was not appropriate to receive the elevated sulfur dioxide concentrations which must have occurred to produce the vegetational injury at th

TABLE 1. Major sources of national air pollution.[1]

| Source | Percent |
|---|---|
| Transportation | 60 |
| Industry | 18 |
| Generation of electricity | 14 |
| Space heating | 5 |
| Refuse disposal | 3 |

[1]From Middleton (1967).

TABLE 2. Some plant species known to be sensitive to ozone, sulfur dioxide or fluoride air pollutants.[1]

| Ozone | Sulfur dioxide | Fluoride |
|---|---|---|
| Alder | Alfalfa | Blueberry |
| Alfalfa | American elm | Blue spruce |
| Bent grass | Big-leafed aster | Boxelder |
| Brome grass | Birch | Dock |
| Boxelder | Clover | Douglas fir |
| Eastern white pine | Curly dock | Eastern white pine |
| Grape | Eastern white pine | Grape |
| Ponderosa pine | Hybrid poplar | Lodgepole pine |
| Quaking aspen | Larch | Ponderosa pine |
| Silver maple | Plaintain | Smartweed |
| White ash | Ponderosa pine | St. John's-wort |
| Wild buckwheat | Ragweed | Western larch |

[1]From Jacobson and Hill (1970).

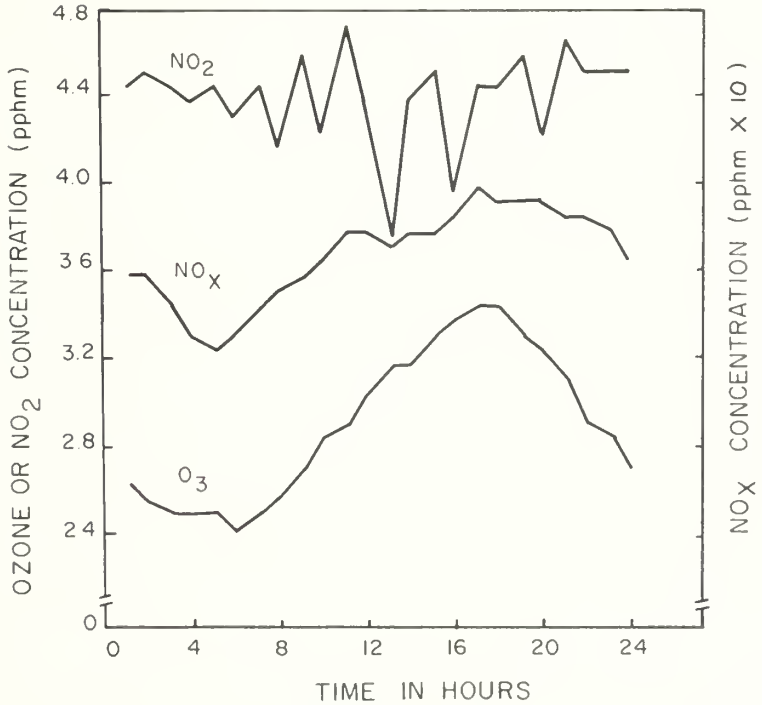



FIGURE 1. Ambient $O_3$-$NO_X$-$NO_2$ concentration at Voyageur's National Park.

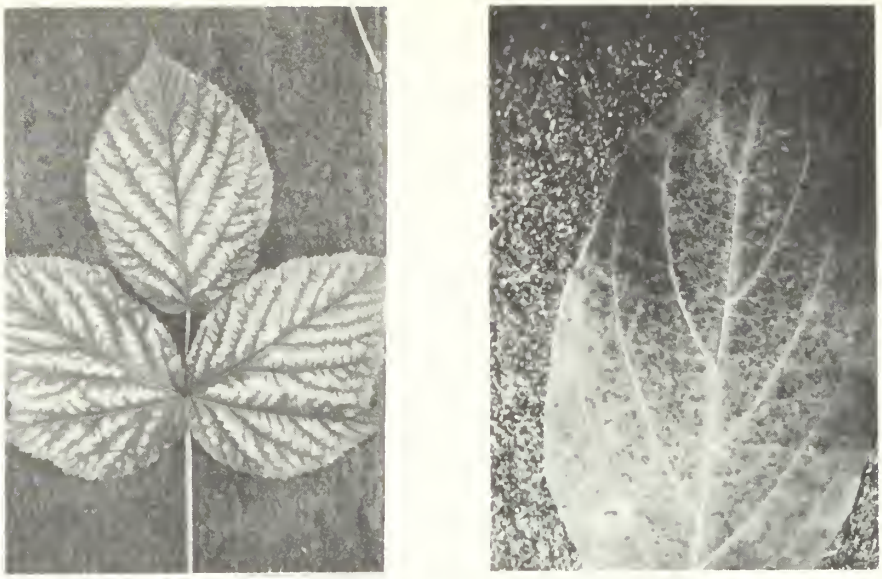


FIGURE 2. Air pollutant effects on vegetation in the Indiana National Lakeshore area. (left) Blackberry showing symptoms of $SO_2$ injury. Note the typical interveinal necrosis. (right) Dogwood showing upper surface stipple, a symptom of $O_3$ injury.

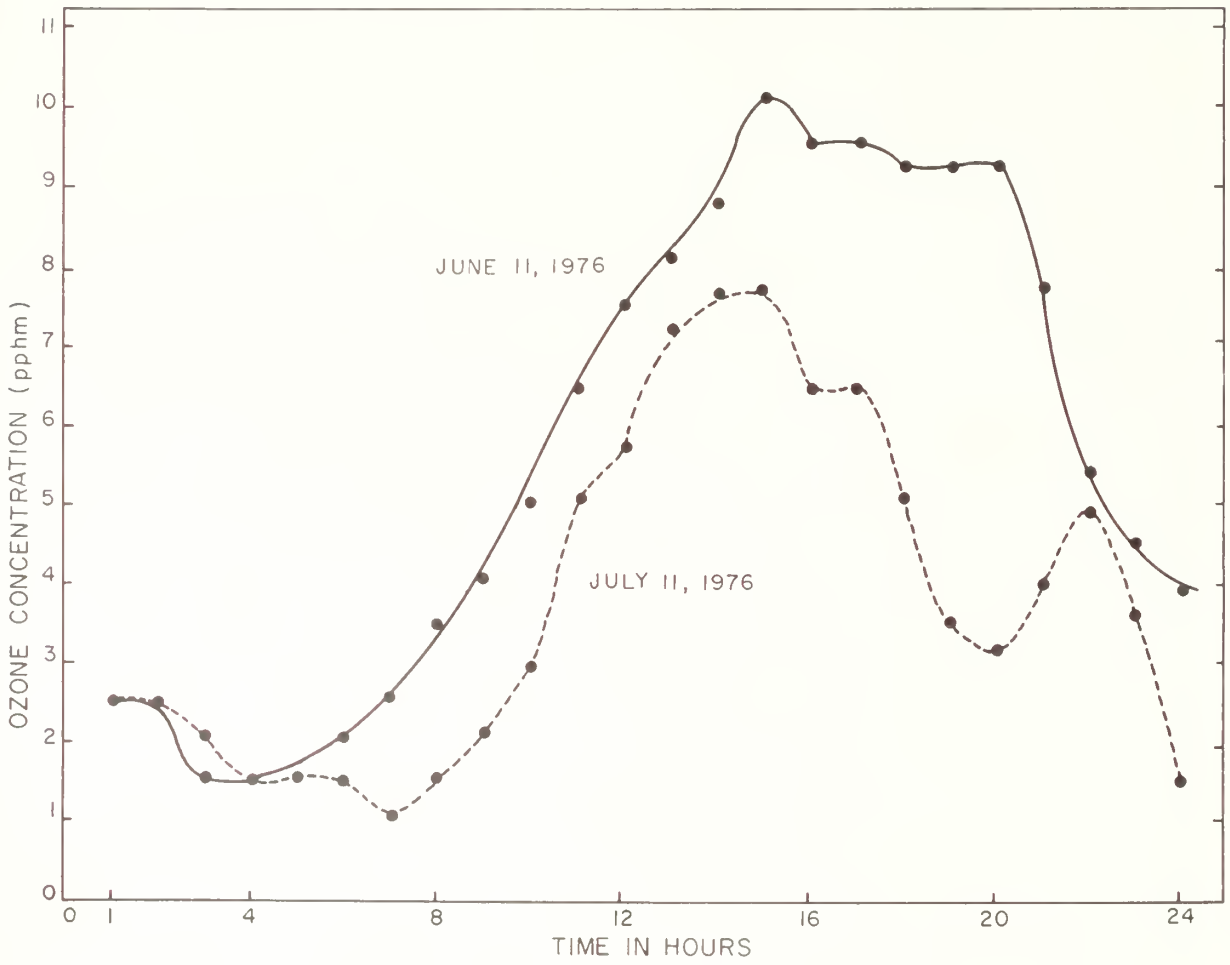



FIGURE 3. Ambient $O_3$ concentration in Indiana Dunes National Lakeshore.

TABLE 3. The percentage of plants injured following exposure to a given dosage of ozone.[1]

| Plant species | | Ozone Dosage | | | | | |
|---|---|---|---|---|---|---|---|
| | | 8pphm/ 2 hr | 8pphm/ 3 hr | 8pphm/ 4 hr | 15pphm/ 2 hr | 15pphm/ 3 hr | 15pphm/ 4 hr |
| Buckwheat | *Polygonus convolvulus* | 4 | 8 | 0 | 50 | 60 | 80 |
| Chicory | *Cicorium intybus* | 4 | 12 | 16 | 4 | 10 | 60 |
| Daisy | *Chrysanthemum leucanthemum* | 0 | 0 | 0 | 30 | 50 | 10 |
| Dwarf columbine | *Aquilegia* | 0 | 0 | 0 | 8 | 10 | 12 |
| Giant columbine | *Aquilegia* | 0 | 0 | 0 | 0 | 0 | 0 |
| Lambsquarters | *Chenopodium album* | 12 | 20 | 20 | 8 | 4 | 16 |
| Lupine | *Lupinus angustifolius* | 0 | 0 | 0 | 0 | 0 | 0 |
| Monkeyflower | *Mimulus* | 0 | 0 | 0 | 16 | 8 | 0 |
| Mustard | *Brassica kaber* | 0 | 25 | 5 | 30 | 50 | 50 |
| Ragweed | *Ambrosia artemisifolia* | 0 | 0 | 0 | 0 | 0 | 0 |
| Ribes | *Ribes* | 8 | 8 | 0 | 15 | 65 | 50 |

[1]Kohut and Krupa (unpublished).

field sites. It can be concluded that the average atmospheric levels of sulfur dioxide must have reached at least 0.3 ppm for several hours to cause injury on blackberry (a sensitive species) at the field sites.

Average hourly ozone concentrations at the air quality monitoring station were always less than 0.15 ppm. Exposure of vegetation to concentrations of 0.15 ppm ozone for one hour will not generally result in injury. The hourly ozone concentrations at Indiana Dunes frequently showed the diurnal cycling associated with urban ozone generation (Figure 3). On certain days, however, the hourly concentrations showed little fluctuation and the pattern did not correspond to the urban ozone generation. Concentrations of the oxides of nitrogen were below those levels considered to be phytotoxic.

## VEGETATIONAL RESPONSE TO OZONE UNDER CONTROLLED ENVIRONMENT

Some of the herbaceous native plant species exposed to ozone under controlled conditions include wild buckwheat, chicory, daisy, dwarf columbine, giant columbine, lambsquarters, lupine, monkeyflower, mustard, ragweed and ribes. The average vegetational injury level did not exceed 10% in any of these exposures. Wild buckwheat, chicory, daisy, mustard and ribes were the species with the greatest percentage of sensitive plants in the population exposed. The symptoms produced on the above plants and lambsquarters and monkeyflower consisted of a yellow to light tan bifacial necrosis. Dwarf columbine exhibited a purple stipple. Giant columbine, lupine and ragweed were resistant in all of the exposures. Average ozone concentrations during the exposure was 0.08 ppm or 0.15 ppm for 2, 3, or 4 hours (Table 3).

## CONCLUSION

Two national parks comprising diverse ecosystems have been examined in the present study on air pollution-vegetation effects. The Voyageurs National Park is located in northern Minnesota in a remote area relatively unaffected by man's activities. Ambient pollutant concentrations in that Park were representative of the generally accepted background levels. No visible impact of air pollutants on the Voyageurs Park vegetation was observed. At this time the aforementioned studies at the Voyageurs National Park have been discontinued. However, as this Park system develops further, it would be beneficial to reestablish the study to evaluate the increased anthropogenic activity in the region in terms of park management. Since the vegetation in the Voyageurs National Park has not been previously subjected to air pollution stress, it can be anticipated that the initial effects of increased air pollution on the native plant communities could be quite noticeable. Although few pollutant sources exist in the general area at this time, future mining and smelting operations nearby could have a significant impact.

In contrast, the Indiana Dunes National Lakeshore represents an urban ecosystem which has been subjected to an air pollution stress for a substantial period of time. Our study provided the first documented evidence of air pollution injury to vegetation in the Indiana Dunes area. Although this geographic region has been under air pollution stress for some time, observation of the vegetation in the study area indicates that ambient pollutant concentrations are sufficiently high to injure the vegetation and that the selection process by air pollution may be still in progress. Additional air quality and meteorological data would be beneficial in determining the relationship between ambient air pollutant concentrations and vegetational effects. This information is vital for the park management and the implementation of emission standards through the state regulatory agency. To accurately assess the air pollutant effects on the vegetation in the Indiana Dunes National Lakeshore, a long term study is critical.

## LITERATURE CITED

JACOBSON, J. S. and HILL, A. C. 1970. Recognition of air pollution injury to vegetation: A pictorial atlas. Air Poll. Control Assoc. Pittsburgh, Pa.

LAURENCE, J. A., SCHREIBER, M. C. and KRUPA, S. V. 1975. Ambient concentrations of phytopathogenic air pollutants in Voyageurs National Park, Minnesota. Proc. Amer. Phytopah. Sco. 2:29.

MIDDLETON, J. 1967. The case for clean air. Special Rep. Mill and Factory. Conover-Mast. 16 p.

MILLER, P. R. and TAYLOR, O. C. 1976. Response of predominant species in a coniferous forest ecosystem to chronic oxidant exposure. Preprint Air Poll. Control Assoc. 76-25. 6:1-12.

# VEGETATION IN RELATION TO ENVIRONMENTS OF CANYONLANDS NATIONAL PARK[1]

Walter L. Loope and Neil E. West[2]

## INTRODUCTION

Canyonlands National Park is centered near the confluence of the Green and Colorado Rivers in southeastern Utah. The Park was established in 1964 and enlarged to its present 1303 $km^2$ (337,000 acres) in 1971. The Park's major scenic resources are its dramatic erosional landforms and brightly colored rock strata. The geologic section includes mostly horizontal Mesozoic sandstones and shales.

The Park is located near the center of the Colorado Plateau, a tectonically stable area that has been gradually uplifted since Pliocene time (Thornbury, 1965). The Canyonlands landscape is one dominated by rock. Rainfall is low, and its distribution erratic. Soil development is weak or absent. Seen from a distance (for example, a LANDSAT-1 photo), vegetation is hardly noticeable. From a closer vantage, vast tracts of woodlands, grassland, and brushland are evident.

Livestock use of the more accessible portions of the area were intense in the 60 to 80 years before a park was designated and domestic grazing was phased out. The area has been a center for uranium-vanadium exploration and development. Fairly extensive exploration for petroleum has also occurred. As development of the master plan for the Park began a need for understanding vegetation and its dynamics became apparent. The following report highlights some of our findings during studies of the flora and vegetation in relation to environments of Canyonlands National Park. Further details can be found in Loope (1977).

## PHILOSOPHY, SCOPE, AND METHODS OF THIS STUDY

Reports on vegetation of southeastern Utah are few, therefore, our studies had to be done on a first approximation level.

Initially, our questions about the vegetation were as follows:

1. What is the species composition, structure, and pattern of the various vegetation types?
2. What is the location of and total area in each vegetation type?
3. What major environmental factors control patterns of vegetation?
4. How have human activities affected the vegetation?

In this landscape dominated by rock, aspects of physical environment define several major differences in plant habitat. It appeared reasonable to use different combinations in these physical factors to divide the Park into major environmental subdivisions for sampling purposes. Substrate type, regolith depth, elevation, slope, exposure, and position in relation to the water table were combined as criteria for identifying landscape segments. The resulting subdivisions were:

1. Low elevation benches underlain by tight clay substrata
2. Deep eolean sand deposits
3. Benches underlain by uniformly shallow regolith
4. Skeletal soils
5. Benches of alluvial deposits

Because of the nature of the geologic section, some of these occur at one general elevation, some at several elevations.

After environmental subdivisions were established, an effort was made to characterize the vegetation of each subdivision through sampling. We felt it desirable to include the entire park in the analysis. Limited time and budgets, large area considered, dissected topography, and difficult access forced some sacrifices in objectifying the placement of sampling sites. Sites within each environmental subdivision were selected as "typical." Sampled sites were scattered throughout the Park.

After selection of each sampling point, a 100 meter steel tape was extended from the point in the direction of the most visually homogeneous vegetation. An estimate of vegetal cover was taken as the percent intercepted cover of plant canopies along the 100 meter tape. Twelve small plots were positioned at random intervals along the steel tape. Frequency was recorded as the percent of the small plots where a given species was present. Frequency plots of 1 $m^2$ size were used for herbaceous vegetation; 4 $m^2$ plots were used for non-herbaceous plants. Density was estimated by a count of individuals in a 5 m x 50 m rectangular macroplot positioned along the tape with one corner at the sampling point. In a subsample of the sites within each environmental subdivision, measurements of soil texture, pH and total electrical conductivity were taken. Slope, exposure, geologic formation, regolith depth, elevation and position in relation to the water table were noted for each site. Constancy values for all species were calculated as the percent of transects within each environmental subdivision in which the species occurs. One hundred fifty-seven transects were read.

## RESULTS AND DISCUSSION

Results of sampling are shown in condensed form in Table 1. "Importance index" (constancy x frequency) (Curtis, 1959) was calculated for all species. Species with an importance index greater than 1000 are included in the table. It is clear from Table 1 that distinct groups of species

[1]The encouragement of David May and partial support from the Canyonlands Natural History Association is gratefully acknowledged.

[2]Department of Range Science and the Ecology Center, Utah State University, Logan 84322.

typify each environmental subdivision.

The environmental subdivision defined by outcroppings of shale with high clay content (tight soil benches) supports a sparse shrubland dominated by several species of *Atriplex*. The community composition varies from dominance by *A. garrettii* on most sampled areas to *A. cuneata* and *A. confertifolia* at other sites within this environmental subdivision.

On deep eolean sand deposits, grasslands occur almost exclusively. *Hilaria jamesii, Stipa comata* and *Oryzopsis hymenoides* are grasses found to have highest importance values. The shrubs, *Ephedra viridis* and *Ceratoides lanata* are common associates in some areas. Deep eolean deposits that incurred historically heavy livestock grazing use were found to support a modified grassland vegetation. On these sites, the grazing-resistant grasses, *Hilaria jamesii, Sporobolus cryptandrus* and *Aristida fendleriana* are more important. *Gutierrezia* spp. are also more common in these areas than those grasslands that were lightly grazed by livestock or escaped livestock use altogether.

*Coleogyne ramosissima*-dominated brushland occupies most sites where regolith is uniformly shallow. The shrubs, *Ephedra torreyana* and *Atriplex confertifolia,* and the grass, *Hilaria jamesii,* are the most important subordinates in this community.

Jointed, exposed bedrock areas with skeletal soils support pinyon-juniper woodlands with various upland shrubs in the understory. Vegetation is generally confined to cracks in bedrock. *Coleogyne ramosissima* and *Artemisia bigelovii* occur frequently with *Pinus edulis* and *Juniperus osteosperma*.

Deep alluvial deposits with access to capillary water are characterized by brushlands dominated by *Artemisia tridentata* and *Atriplex canescens*.

Two distinctive vegetation types were not sampled like the others because of their very limited area. Species lists and collections of vouchers were made during visits to these habitats, however. These minor vegetation types are the dense riparian thickets along the Green and Colorado Rivers and the "hanging gardens" that occupy topographically favored alcoves and overhangs supplied with moisture from seeps. The dense thickets of vegetation along the rivers depend on free water at their roots and are composed chiefly of *Tamarix pentandra, Pluchea sericea, Baccharis emoryi* and several species of *Salix*. "Hanging gardens" are characterized by diverse groupings of mesic species such as *Aquilegia micrantha, Primula specuicola, Mimulus eastwoodiae* and *Smilacina stellata. Betula occidentalis, Prunus virginiana* and *Ostrya knowltoni* are mesic trees that often occur in these situations.

Dark-colored cryptogamic soil crusts, composed of lichens, mosses, fungi, and algae are widespread throughout Canyonlands National Park. Their distribution is partially a function of livestock use history. Heavily used areas generally have low cover values of cryptogamic soil crust. In some areas substrate appears to be important in controlling their distribution. Sandy soils have more of these crusts than clayish or silty soil surfaces.

After major vegetation units were defined, type signatures were identified on aerial photos and a vegetation map of the Park was made. A 15 minute topographic map was used as the base. This map and a full floristic list for the Park may be found in Loope (1977).

The distinctness of vegetation units suggests sharp environmental gradients. In areas were evapotranspiration greatly exceeds precipitation, soil moisture will generally be a very important environmental factor. Effective soil moisture appears to be a critical controlling factor for vegetation patterns in Canyonlands.

In many areas of the western United States soil moisture is chiefly a function of elevation, slope and exposure. The most mesic sites occur at high elevation on north-facing slopes with a gradient of increasing dryness toward lower elevation, south-facing slopes. These gradients have a much smaller influence in Canyonlands National Park. Effective soil moisture in Canyonlands appears to be primarily controlled by regolith depth and position in relation to the water table.

Effective soil moisture can be related to regolith,relationships in the following ways (Figure 1). When disintegrated bedrock is uniformly shallow (ca. 25 cm), soil moisture is concentrated on top of impermeable bedrock at a shallow depth. This perching effect allows time for gradual uptake of moisture by plant roots. Blackbrush dominates the vegetation in this situation. Hunt (1966) similarly observed impermeable layers causing moisture concentration and concomitant distinctions in the desert vegetation patterns of Death Valley, California. When regolith is deeper than 50 cm, this perching effect is lost and blackbrush gives way to grassland vegetation. Grass root systems are apparently better adapted to take up rapidly percolating soil moisture, particularly during growing season rainy periods. In areas where regolith is restricted to bedrock fissures, pinyon-juniper/shrub vegetation occurs. These sites get a "moisture subsidy" of runoff from areas between cracks and thus support the relatively mesic pinyon-juniper vegetation. Tight clay substrate restricts movement of moisture to plant roots and thus limits rooting to a shallow soil profile. Outcroppings of this type of substrate controls the occurrence of *Atriplex*-dominated vegetation.

Access versus non-access to free or capillary water controls the occurrence of species in riparian and hanging garden habitats.

The pattern of regolith-controlled soil moisture and associated vegetation types remains distinctive and repeats itself at various elevations within the Park. Figure 2 illustrates this recurring pattern. In Canyonlands, the influence of elevation on effective soil moisture is apparently overshadowed by the influence of regolith depth.

Fire does not appear to play a role in the maintenance of the brushlands or eolean grasslands of Canyonlands. Topographic breaks highly dissect the landscape. Isolated pockets of vegetation are often separated by rock walls or steep canyons. Blackbrush, a species that is intolerant of fires (Bowns and West, 1975), dominates the largest percentage of the Park. Neither is fire important to the pinyon-juniper woodlands since there is rarely enough fuel to carry fire across the landscape.

Soils in Canyonlands display very weak development (Wilson et al., 1975). Annual rainfall is very low (averaging approximately 210 mm). Most substrate is fine quartz sand or rocks that weather to fine quartz sand. The distinctive topography of the Park has been formed by rapid stripping of the rock mantle. Material is eroded and

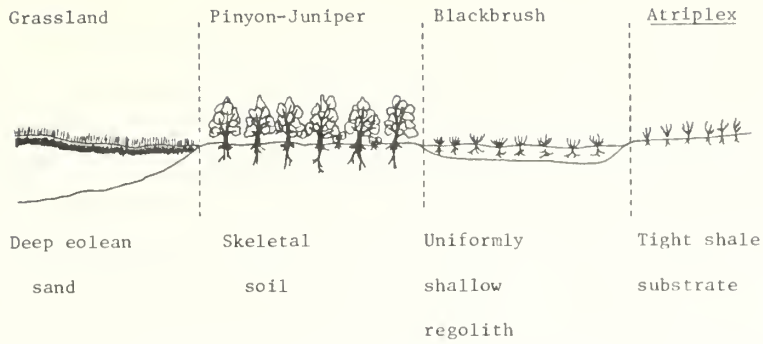



FIGURE 1. Regolithic control of soil moisture and vegetation types.

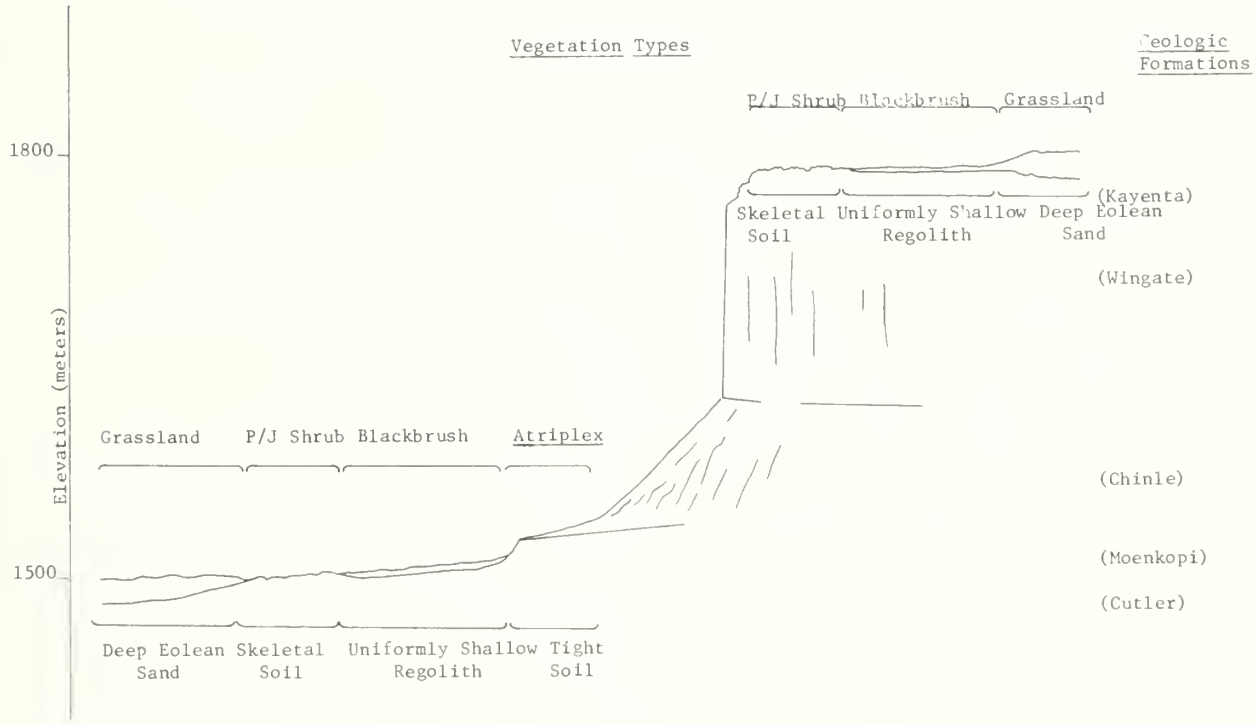



FIGURE 2. Vegetation types controlled by regolith depth recurring at various elevations.

TABLE 1. Percent frequency (F), density (d, common plants/$m^2$), and percent cover (C) values for species with constancy X frequency index greater than 1000. Environmental subdivisions are arranged to show an effective soil moisture gradient from xeric (left) to mesic (right). The symbol, t, indicates less than 1% cover (trace).

| | Environment Subdivision | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Low elevation benches/ tight soil | | | Eolean sand deposits (heavy use) | | | Eolean sand deposits (light use) | | |
| Palant name* | F | D | C | F | D | C | F | D | C |
| *Artemisia tridentata*--big sagebrush | | | | | | | | | |
| *Atriplex canescens*--four wing saltbush | | | | | | | | | |
| *Opuntia* spp.--prickly pear | | | | | | | | | |
| *Chrysothamnus nauseosus*--rubber rabbitbrush | | | | | | | | | |
| *Sarcobatus vermiculatus*--black greasewood | | | | | | | | | |
| *Lepidium fremontii*--desert pepperweed | 14 | 1 | t | | | | | | |
| *Bromus tectorum*--cheatgrass brome | 66 | | 8 | | | | | | |
| *Sporobolus contractus*--spike dropseed | | | | | | | | | |
| *Descurainia sophia*--flixweed tansymustard | | | | | | | | | |
| *Aster bigelovii*--Bigelow aster | | | | | | | | | |
| *Lappula redowskii*--bluebur stickseed | | | | | | | | | |
| *Juniperus osteosperma*--Utah juniper | | | | | | | | | |
| *Pinus edulis*--pinyon pine | | | | | | | | | |
| *Artemisia bigelovii*--Bigelow sagebrush | | | | | | | | | |
| *Hymenoxys acaulis*--stemless actinea | | | | | | | | | |
| *Machaeranthera grindeloides*--goldenweed | | | | | | | | | |
| *Coleogyne ramosissima*--blackbrush | | | | | | | | | |
| *Ephedra torreyana*--Torrey mormon tea | | | | | | | | | |
| *Atriplex confertifolia*--shadescale saltbush | | | | | | | | | |
| *Hilaria jamesii*--galleta | 25 | | t | 81 | | 7 | 64 | | 5 |
| *Ephedra viridis*--green mormon tea | | | | | | | 55 | 5 | 3 |
| *Ceratoides lanata*(Pursh) J.T.Howell--winterfat | | | | | | | 21 | 10 | 3 |
| *Stipa comata*--needle and thread | | | | | | | 61 | | 5 |
| *Oryzopsis hymenoides*--Indian ricegrass | | | | | | | 39 | | 2 |
| *Bouteloua gracilis*--blue gramma | | | | | | | 71 | | 9 |
| *Plantago patagonica*--wooly plantain | | | | | | | 57 | | 3 |
| *Eriogonum cernuum*--nodding wild buckwheat | | | | | | | 59 | | 1 |
| *Gilia inconspicua*--shy gilia | | | | | | | 38 | | 3 |
| *Gutierrezia* spp.--snakeweed | | | | 34 | 15 | 3 | | | |
| *Cryptantha confertiflora*--cryptantha | | | | 41 | 16 | 1 | | | |
| *Shaeralcea coccinea*--scarlet globemallow | | | | 43 | 16 | 1 | 33 | 18 | 1 |
| *Hymenopappus filifolium*--fineleaf hymenopappus | | | | 51 | 21 | t | | | |
| *Sporobolus cryptandrus*--sand dropseed | | | | 60 | | 2 | | | |
| *Aristida fendleriana*--Fendler threeawn | | | | 29 | | 1 | | | |
| *Vulpia octoflora* (Walt.) Rydberg--sixweeks fescue | | | | 47 | | 1 | 29 | | 1 |
| *Malacothrix sonchoides*--desert dandelion | | | | 46 | | 1 | 44 | | 1 |
| *Oenothera caespitosa*--tufted evening primrose | | | | 26 | | t | | | |
| *Cymopterus fendleri*--Fendler rpring parsley | | | | 31 | | t | | | |
| *Atriplex garrettii*--Garrett saltbush | 54 | 51 | 5 | | | | | | |
| *Eriogonum inflatum*--desert trumpet | 24 | 2 | 1 | | | | | | |
| *Gaillardia pinnatafida*--blanketflower | 50 | 3 | 1 | | | | | | |
| *Salsola kali*--Russian thistle | 18 | | t | | | | | | |
| *Phacelia crenulata*--scorpionweed | 31 | | 1 | | | | | | |

*Nomenclature in the table and text follows Holmgren and Reveal (1966) except where authorities are given. Common names follow Beetle (1970).

transported out of the area faster than it can be modified (Hunt, 1974). It is probably true that surface soil texture is more a function of substrate than of soil development. Horizonation was undetected in the profiles observed by authors. Neither were differences obvious in pH, total conductivity or surface texture measurements, except that textural analysis of samples from tight soil benches showed a higher percentage silt and clay than other samples. Petrocalcic horizons (caliche), common in the Great Basin Desert, were not found in soil profiles of Canyonlands.

Grasslands have undergone more change due to human activities than other vegetation types within the Park. Evidence of grassland disturbance by domestic livestock use is greatest in the southeastern section (Needles District) of Canyonlands National Park. Other areas display much less modification. High percentages of the total vegetal cover in some areas with historically heavy livestock use are made up of cheatgrass *(Bromus tectorum)*, sixweeks grass *Vulpia octoflora)*, Russian thistle *(Salsola kali)* and snakeweed *Gutierrezia* spp.) Grassland modifications are probably the result of differences in accessibility to early cattlemen. Grasslands of the southeastern portion of Canyonlands National Park were, by far, the most accessible. Elsewhere, grasslands are isolated by steep cliffs or broken topography.

Disturbance due to uranium-vanadium and petroleum exploration has occurred in all vegetation types. Total area of this damage is relatively small, but it is spread throughout the Park. Secondary plant succession on these sites has been extremely slow. Most old access roads through blackbrush vegetation on shallow regolith remain essentially bare 20 years after abandonment. Some areas where blackbrush was destroyed have been invaded by exotics such as *Halogeton glomeratus*

| Shallow regolith benches | | | Skeletal soil | | | Alluvial benches | | |
|---|---|---|---|---|---|---|---|---|
| F | D | C | F | D | C | F | D | C |
| | | | | | | 66 | 34 | 17 |
| | | | | | | 52 | 14 | 10 |
| | | | | | | 35 | 11 | 1 |
| | | | | | | 22 | 9 | 6 |
| | | | | | | 28 | 9 | 6 |
| | | | 19 | 2 | t | 27 | 9 | 1 |
| | | | | | | 50 | | 10 |
| | | | | | | 63 | | 2 |
| | | | | | | 30 | | 1 |
| | | | | | | 35 | | 1 |
| | | | | | | 19 | | 1 |
| | | | 22 | 5 | 3 | | | |
| | | | 21 | 5 | 3 | | | |
| | | | 22 | 1 | 1 | | | |
| | | | 26 | 5 | t | | | |
| | | | 37 | 3 | t | | | |
| 76 | 76 | 11 | 31 | 2 | 2 | | | |
| 25 | 10 | 2 | | | | | | |
| 23 | 11 | 2 | | | | | | |
| 88 | | 3 | 20 | | 1 | | | |
| | | | | | | | | |
| | | | | | | | | |
| 26 | | 3 | 15 | | 1 | | | |
| | | | | | | | | |
| | | | | | | | | |
| | | | 30 | 3 | 1 | | | |
| | | | | | | | | |
| | | | | | | 42 | | 3 |

and *Salsola kali* or aggressive native species such as *Gutierrezia* spp. and *Opuntia* spp. Secondary succession appears to be more related to the physical recovery of the site than with any modification by vegetation. Road cuts through deep eolean material appear to recover faster than cuts through skeletal soil or shallow regolith. Revegetation efforts, where attempted, have met with very limited success.

## SUMMARY AND CONCLUSIONS

The purpose of this study was to provide a description of the flora and vegetation of Canyonlands National Park and to relate vegetation types to major environmental variables within the Park. One hundred fifty-seven transects were located throughout the Park to represent major environmental situations. Areas that underwent historically heavy grazing were included. Measurements of species frequency, density and cover were taken at each site, and soil and geologic parameters were noted. Abandoned roads and drill sites were examined for evidence of secondary succession. Two hundred thirty vascular plant species were collected in the Park. A vegetation map of the Park was constructed using aerial photographs.

The results of this study support the following conclusions:

1. There are five major vegetation types within the Park. Each type appears dependent on specific environmental conditions.
2. Soil moisture is the key factor influencing vegetation distribution in Canyonlands.
3. Major control over soil moisture is exerted by regolith depth and water table relationships.
4. Secondary control over soil moisture (and thus vegetation patterns) is exerted by geologic substrate, elevation, slope and exposure.
5. Secondary plant succession is very slow in all vegetation types. In shallow regolith situations, secondary succession, in the sense of site preparation by seral plants, may not occur at all.
6. Livestock use has caused measurable alterations of grasslands on eolean deposits in Needles District.
7. Fire has not been a pervasive or important factor in the maintenance of any vegetation type in Canyonlands.
8. The physical environment is dominant in determining vegetation structure and distribution in Canyonlands National Park.

## LITERATURE CITED


BEETLE, A. A. 1970. Recommended plant names. Wyo. Agr. Expt. Sta. Res. J. 31. 124 p.

BOWNS, J. E., and N. E. WEST. 1976. Blackbrush *(Coleogyne ramosissima)* on southwestern Utah rangelands. Utah Agr. Exp. Sta. Res. Rpt. 27. 30 p.

CURTIS, J. T. 1959. The vegetation of Wisconsin. Univ. Wisc. Press, Madison. 657 p.

HOLMGREN, A. H., and J. L. REVEAL. 1966. Checklist of the vascular plants of the intermountain region. U.S.D.A. For. Serv. Res. Pap. INT-32. 160 p.

HUNT, C. B. 1966. Plant ecology of Death Valley, California. U.S. Geological Survey Prof. Paper 509. 68 p.

HUNT, C. B. 1974. Natural Regions of the U.S. and Canada. W. H. Greeman and Co., San Francisco. 725 p.

LOOPE, W. L. 1977. Vegetation-environmental relationships in Canyonlands National Park, Utah. Ph.D. diss., Utah State Univ., Logan. 138 p.

THORNBURG, W. D. 1965. Regional geomorphology of the United States. John Wiley and Sons, New York. 505 p.

WILSON, L., M. E. OLSEN, T. B. HUTCHINGS, A. R. SOUTHARD, and A. J. ERICKSON. 1975. Soils of Utah. Utah Agr. Exp. Sta. Bull. 492. 94 p.

DISTRIBUTION AND ECOLOGICAL RELATIONSHIPS OF TWO MOUNTAIN HEATHS (*Phyllodoce*) IN OLYMPIC NATIONAL PARK

Ingrid Olmsted
College of Forest Resources
University of Washington
Seattle 98195

Reprints of this paper are available from Dr. Olmsted.

OBSERVATIONS ON SNOW ALGAE IN CALIFORNIA

William H. Thomas
Institute of Marine Resources
Scripps Institution of Oceanography
University of California, San Diego
La Jolla 92037

This paper is published in Journal of Phycology
8(1):1-9, 1972

# FOREST ECOSYSTEMS OF MOUNT RAINIER NATIONAL PARK

W.H. Moir, F.D. Hobson, M. Hemstrom, and J.F. Franklin[1]

## INTRODUCTION

We began studies of forest ecosystems at Mount Rainier National Park (MRNP) in the summer of 1975. Our objectives were to idenitfy and describe the different forest types, characterize their environmental features and patterns of occurrence. within the Park, and determine causes and rates of succession. The initial forest classification presented here is based on data from 242 plots distributed over all the major drainage systems. During our second summer (1976) we sampled an additional 158 plots, mostly younger forests. This paper reports the major forest types resolved from these data, some generalized patterns of occurrence of these types in selected landscapes at MRNP, the major soil types, and important factors initiating succession. We also give forest age spectra for three drainages and compositional chronosequences in three of the forest types.

## METHODS

Most data were obtained by the reconnaissance method for forest classification (Franklin et al. 1970). The usual procedure for the field crew would be to travel a slope, trail, road segment, or whatever path through a forested landscape and establish a string of sampled plots that revealed both the typical and changing forest patterns along that path. In 1975 we sought stands from late seral to climax condition, i.e., old-growth relatively free of recent disturbances; in 1976 we focused mostly upon forests of early to middle seral condition.

Circular plots mostly 500 or 1,000 $m^2$ (depending on mature tree density) were our sample units. Understory vascular plant cover was recorded as described by Franklin et al. (1970) and Dyrness et al. (1974). All tree stems exceeding 1.4 m in height were tallied by species and diameter. Tree regeneration (< 1.4 m in height) was subsampled in a 50 $m^2$ circular plot either at the center of the larger plot (1975) or at four 12.5 $m^2$ circular plots, one in each quadrant of the larger plot. We also made field description of soils, and recorded elevation, exposure, slope, degree of canopy closure, landform, position in the landscape (lower, middle, upper slope, ridge, draw, bench) and location on topographic map. Supplemental notes included disturbance evidence (fire, biotic, wind-throw, etc.) and inclusions or mosaics of other forest types.

The classification was obtained by subjectively sorting releve´ or stand table data from late seral to climax plots into subsets based upon general similarities in dominance within each of the tree shrub, and herb strata. The technique is described by Dyrness et al. (1974) and Shimwell (1971, p. 188 ff).

Stand ages were measured from increment cores of dominant specimens of *Pseudotsuga menziesii*, *Abies procera*, or other trees judged to have been among the first wave of regeneration after disturbance. We sought the oldest speciments of a seral cohort to set a time limit on whatever disturbance event gave ooportunity to establish that cohort. Cored trees were aged by counting rings in the field and adding to that age corrections for center and age to core height. For large specimens these corrections were sometimes a source of considerable sample error.

## MAJOR FOREST TYPES

We can recognize four broad elevational zones of forests at MRNP. At highest elevations (generally over 1,620 m) are subalpine parklands where mosaics of three copses and meadow communities occur. These communities and environments have been previously described (Franklin and Mirchell 1967, Franklin et al. 1971) and are not the subject of this study. Below about 1,620 m elevation are mostly closed canopy forests. The *Tsuga mertensiana* zone occurs at the hightest elevations with *Abies lasiocarpa, Tsuga mertensiana, Chamaecyparis nootkatensis*, and *Abies amabilis* as characteristic trees. At mid-elevations *Abies procera, Pseudotsuga menziesii, Tsuga heterophylla*, and *Thuja plicata* are important canopy dominants. These forests are within the *Abies amabilia* zone generally between 730 and 1,475 m elevation at MRNP. We have provisionally recognized 3 high-elevation and 9 mid-elevation forest types at MRNP (Table 1). Below about 730 m elevation are four forest types of the *Tsuga heterophylla* zone (Franklin and Dyrness 1973). Such forests are more extensive outside the Park, but reach their upper elevational limits in valleys and south-facing slopes near Park boundaries. *Pseudotsuga mensiesii, Tsuga heterophylla, Thuja plicata, Abies grandis*, and *Picea sitchensis* are trees of these lowest elevations.

The forests of MRNP can also be divided into mature and immature types. The classification of Table 1 is based upon mature forests that are generally about 250 years or older and well stocked. Immature stands are either well below stocking potential or less than about 250 years old. Seral forest types (or community types) include *Abies lasiocarpa* forests at high elevations, *Pseudotsuga menziesii/Pteridium aquilnum* community types at intermediate elevations, and red alder (*Alnus rubra*) communities of lower slopes and valley bottoms.

## VEGETATION-LANDSCAPE PROFILES

Moisture and temperature gradients are major environmental complexes affecting forest patterns. For each drainage system at MRNP these complexes can be delimited by elevation, relief, and position in the landscape. Thus each forest type embraces a relatively narrow environmental span illustrated by the profiles of Figures 1-3.

*White River.* Our profile (Fig. 1) extends from Clover Lake to Sunrise road in the White River Valley, an elevational range of 740 m (2,430 ft). The road to Sunrise Visitor Center crosses the entirety of this sequence of forest types. Subalpine parkland is common along

[1]United States Forest Service, Forest Sciences Laboratory, Corvallis, Oregon.

TABLE 1. Major forest types at Mount Rainier.

| Forest Type | Dominant Trees[1/] Overstory | Regeneration | Important Understory Species |
|---|---|---|---|
| I. LOW ELEVATION (< 730 m) | | | |
| Western hemlock/Salal | PSME, TSHE | TSHE | Gaultheria shallon, Vaccinium parvifolium, Berberis nervosa |
| Western hemlock/Vanillaleaf | PSME, TSHE, THPL | TSHE | Acer circinatum, Achlys triphylla, Viola sempervirens |
| Western hemlock/Swordfern | PSME, TSHE, THPL | TSHE | Acer circinatum, Polystichum munitum, Berberis nervosa |
| Western hemlock/Devil's club | PSME, TSHE, THPL | TSHE | Oplopanax horridum, Athyrium filix-femina, Gymnocarpium dryopteris |
| II. INTERMEDIATE ELEVATION | | | |
| W. hemlock-Silver Fir/Oregongrape | PSME, TSHE | TSHE, ABAM | Acer circinatum, Berberis nervosa, Achlys triphylla, Vaccinium parvifolium |
| W. hemlock-Silver Fir/Swordfern-Deerfern | PSME, TSHE, THPL | TSHE, ABAM | Polystichum munitum, Blechnum spicant, Berberis nervosa |
| Silver Fir/Salal | PSME, TSHE, THPL | TSHE, ABAM | Gaultheria shallon, Xerophyllum tenax, Berberis nervosa |
| Silver Fir/Alaska huckleberry | TSHE, ABAM | ABAM | Vaccinium alaskaense, Linnaea borealis, Rubus lasiococcus |
| Silver Fir/Alaska huckleberry-Trailing raspberry | TSHE, ABAM | ABAM | Vaccinium alaskaense, Vaccinium ovalifolium, Rubus pedatus |
| Silver Fir/Foam flower | PSME, ABPR, TSHE | ABAM | Tiarella unifoliata, Achlys triphylla Streptopus roseus, Clintonia uniflora |
| Silver Fir/Devil's club | TSHE, ABAM, CHNO | ABAM | Oplopanax horridum, Gymnocarpium dryopteris, Tiarella unifoliata |
| Silver Fir/Devil's club/Trefoil foamflower | TSHE, ABAM, CHNO | ABAM | Oplopanax horridum, Vaccinium spp., Gymnocarpium, Rubus pedatus, Tiarella trifoliata |
| Silver Fir/Huckleberry/Beargrass | TSHE, PSME, ABAM | ABAM, TSHE | Vaccinium membranaceum, Xerophyllum tenax |
| Silver Fir-Yellow cedar/Oval-leaf huckleberry | TSHE, CHNO | ABAM | Vaccinium ovalifolium, Tiarella unifoliata, Gymnocarpium dryopteris |
| III. HIGH ELEVATION (> 1300 m) | | | |
| Silver Fir/Huckleberry/Herb | TSHE, ABAM, CHNO, TSME | ABAM | Vaccinium membranaceum, Erythronium montanum, Rubus pedatus |
| Silver Fir/Rusty leaf | TSHE, ABAM, CHNO, TSME | ABAM | Rhododendron albiflorum, Menziesia ferruginea, Vaccinium ovalifolium |

1/ PSME = Pseudotsuga menziesii, TSHE = Tsuga heterophylla, TSME = T. mertensiana, ABAM = Abies amabilis, ABPR = A. procera, CHNO = Chamaecyparis nootkatensis, THPL = Thuja plicata

Sunrise Ridge and in the upper Sunrise Creek basin along the trail to Clover Lake (elevations generally over 1,620 m). A small finger of Silver fir/Rusty leaf forest type occurs along Sunrise Creek below Clover Lake. Elsewhere on steep slopes between 1,500 to 1,620 m are closed subalpine fir forests, as, for example, along Sunrise Road. The Silver fir/Foam flower forest type centered around 1,500 m elevation. The boundary is visually apparent because subalpine fir (dark greenish canopies) suddenly yield dominance to noble fir (bluish canopy). At 1,280 m is a narrow, wet bench on which occurs the Silver fir-Alaska yellow cedar/Oval-leaf huckleberry type. Below this the Western hemlock-Silver fir/Oregongrape forest extends along middle and lower slopes. The lower slopes and valley bottoms along the White River have forests of Silver fir/Alaska huckleberry type, with Silver fir/Devil's club type in seep and smaller drainage areas. Occasional Engelmann spruce and Alaska yellow cedar along the White River may indicate cold airflow and other environmental features of this major valley drainage.

*Ohanapecosh River.* The southeastern sector of Mount Rainier is the driest of the Park's drainages -- the rain shadow of Pacific westerlies swirling around the volcanic cone. Our profile (Fig. 2) extends from Cowlitz Divide, across the steep, narrow Ohanapecosh Valley to the southeast boundary of the Park on the ridge of the Ohanapecosh rock formation. The Steven's Canyon road crosses the east-facing slope of this profile and offers a bird's eye view of forests across the valley. The ridge forming the Park's east boundary has forests of the Silver fir/Foam flower and Silver fir/Rusty leaf types. Below 1,300 m and extending all the way to the valley floor are forests dominated almost entirely by Douglas fir and western hemlock along west-facing slopes. At higher elevations are forests of Western hemlock-Silver fir/Oregongrape type; lower slopes are Western hemlock/Salal type. The Ohanapecosh River valley contains forest mosaics of Western hemlock/Salal, Western hemlock/Vanilla-leaf, and Western Hemlock/Devil's club. The very steep canyon sideslopes leading up to Cowlitz Divide generally mirror the zonation pattern of the opposite slope. Cliffs and rocky talus, however, frequently interrupt the forests. Shallow, cobbly soil between the cliffs and ledges may exhibit xeric variations of Western hemlock/Salal and Western hemlock-Silver fir/Oregongrape forests. But Silver fir/Foam flower forest type can be found on more stable slopes with deep tephra soils (Fig. 2 just below the road). The ridges and upper slopes of Cowlitz Divide have forests of Silver fir/Huckleberry/Beargrass and Western hemlock-Silver fir/Oregongrape with the former on more exposed sites.

*Mowich River.* This westerly trending drainage system is (together with the Carbon River drainage) the wettest of the Park's watersheds. Figure 3, Paul Peak to the Golden Lakes upland, shows great variation of forest pattern from south-facing to north-facing slopes. Forest sequences along slopes of Paul Peak are not unlike the west-facing slopes of the Ohanapecosh River (Fig. 2). The lower slopes along Mowich River, however contain stands of the Western hemlock/Swordfern

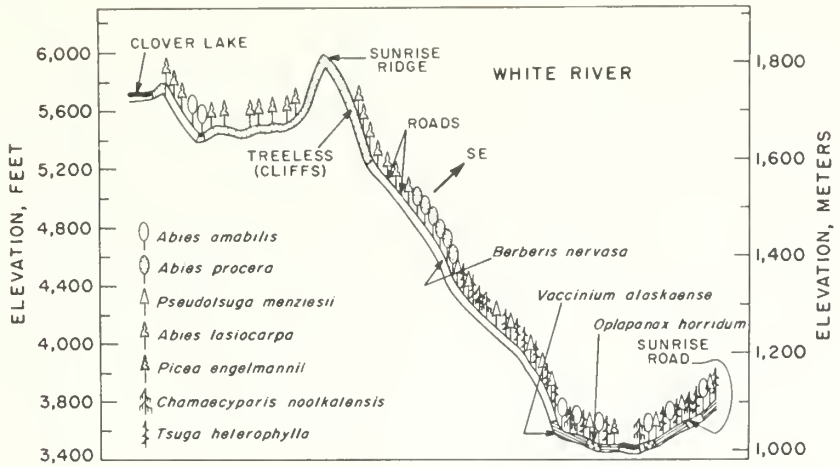



FIGURE 1. Generalized vegetation cross-section across Sunrise Ridge from Clover Lake to the White River Valley.

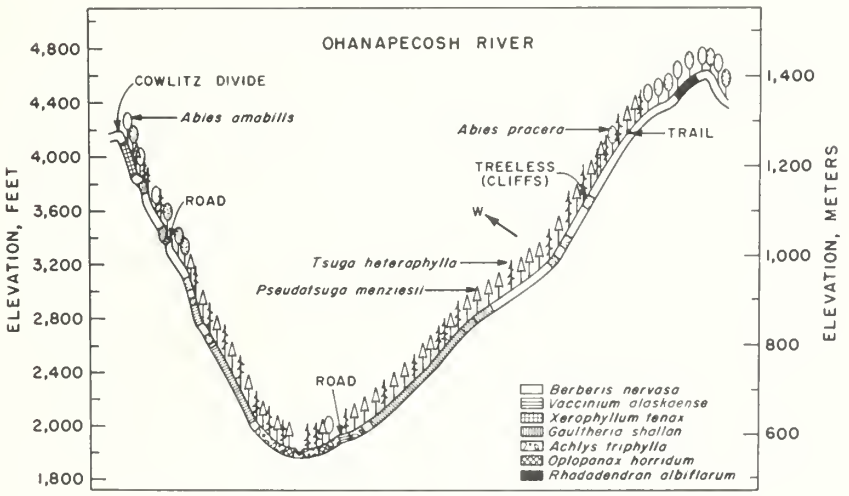



FIGURE 2. Generalized vegetation cross-section of the Ohanapecosh Valley near the ranger station and campground.

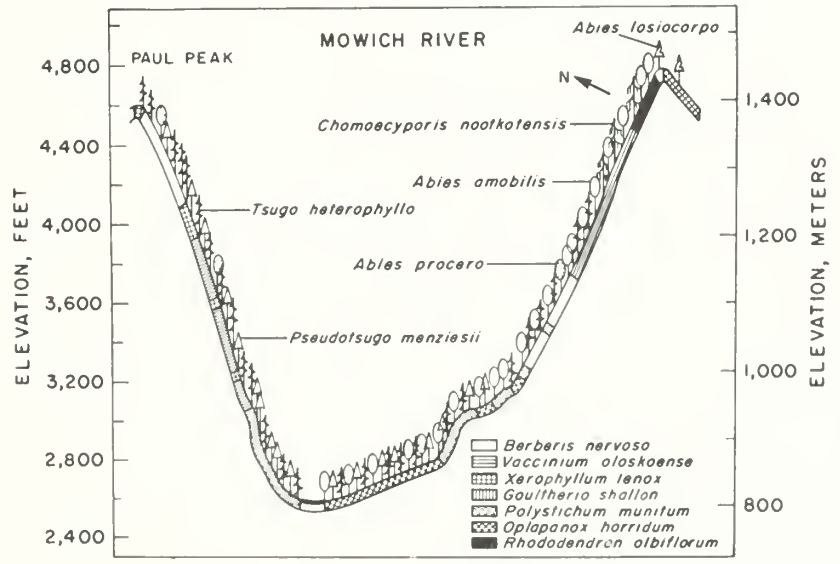



FIGURE 3. Generalized vegetation cross-section of the Mowich River Valley.

type. The Mowich River bottomlands are mantled primarily by forests of Silver fir/Devil's club/Trefoil foamflower. Colluvial lower slopes and draws with northerly aspect feature the Silver fir/Swordfern-Deerfern forest type. Around 1,100 m elevation the trail to Golden Lakes passes through stands dominated by western hemlock and silver fir, but with a very depauperate, sterile appearing understory. Infrequent deerfern or huckleberry give only faint suggestion of the Silver fir/Swordfern-Deerfern or Silver fir/Alaska huckleberry forest types. The latter is better defined as understory flora becomes more diverse and abundant upslope (ca 1,200 m elevation). The uppermost north-facing slopes are forested with the Silver fir/Rusty leaf type. The ridgetop and upperslopes of the Golden Lakes basin area contain open, fire-derived forests of the Silver fir/Huckleberry/Beargrass type with occasional subalpine fir among early successional trees.

## SOILS

The forest soils at MRNP are extremely variable and grade from one kind of soil to another. Major soil-forming activities are accumulation of forest floor organic matter and development of iron pans. Podzolization may sometimes be indicated by very weak to moderately-developed spodic horizons. Four basic parent materials (Hobson 1976) are pyroclastic deposits (tephra), mudflow, colluvium, and alluvium. Tephras, alluvial, laharic, and glacial materials have periodically been deposited during the history of forest vegetation at MRNP (Mullineaux 1974, Crandell 1971, 1967), and most parent materials of the rooting zone are of Holocene age. Differences in soil mineralogy and depths of various parent materials within the profile generally seem to have little influence upon the composition of forest vegetation. But soils considered in the broader context of landform, internal drainage, and position in the landscape (Table 2) can affect vegetation. For example, the colluvial soils of steep midslopes may be physiologically drier than deeper, fine-textured tephra soils of midslope benches.

## DISTURBANCES

Fire is the most extensive forest disturbance and its evidence is found in the majority of our sample plots. Fires appear to have influenced the composition of wetter valley forests as well

TABLE 2. Modal soil profiles of forests at Mount Rainier National Park (after Hobson 1976).

| | | |
|---|---|---|
| 1. Tephra-Slope-No Iron Pan | | |
| 01 | 6-4 cm | Litter |
| 02 | 6-0 cm | Duff; abundant medium and fine roots; smooth, abrupt boundary to |
| A21 | 0-3 cm | Dark gray (moist) fine sand (post-W tephra); loose; fine and medium roots abundant; smooth, abrupt boundary to |
| IIA22 | 3-9 cm | Mixed brown and gray (dry) coarse sand (tephra W); loose grained; fine and medium roots common; occasional subangular cobbles; wavy, clear boundary to |
| IIIBir | 9-25 cm | Brown (moist) loamy sand (tephra C) with fine distinct areas of dark gray fine sand; massive breaking to loose weak, moderate subangular blocks, very friable; few roots; 5 percent lapilli, occasional subangular cobble; smooth clear boundary to |
| IVC1 | 25-32 cm | Dark gray sand (moist) with common fine distince brown mottles; massive breaking to loose and very weak subangular block, very friable; few roots; 10 percent lapilli; smooth abrupt boundary to |
| IVC2 | 32-68 cm | Mixed brown, dark gray, and yellowish brown very coarse sand (tephra Y); loose; very few roots to none; occasional cobble |
| 2. Tephra-Bench-Strong Iron Pan | | |
| 01 | 6-4 cm | Litter |
| 02 | 4-0 cm | Duff; saturated; abundant roots |
| A2 | 0-7 cm | Gray (wet) very coarse sand (tephra Y); loose; roots abundant, more so at 02/A2 boundary; smooth clear boundary to |
| B1 | 7-18 cm | Mixed light brownish gray and dark yellow brown (wet) very coarse sand; loose grain; roots common; smooth gradual boundary to |
| B2ir | 18-36 cm | Dark brown (wet) very coarse sand; massive breaks to structureless, friable becoming firm with depth; very few to no roots. |
| 3. Colluvial | | |
| 01 | 9-7 cm | Litter |
| 02 | 7-0 cm | Duff; roots common |
| A21 | 0-2 cm | Dark gray (moist) fine sand (post-W tephra); loose; roots common; smooth abrupt boundary to |
| IIA22 | 2-5 cm | Mixed gray and yellowish brown (moist) coarse sand (tephra W); single grain; roots common; irregular abrupt boundary to |
| IIIB | 5-60 cm | Yellowish brown (moist) gravelly sand; 25 percent lapilli and angular gravels increasing with depth; loose; roots abundant to 40 cm grade to few. |
| 4. Alluvial | | |
| 01 | 3-2 cm | Litter |
| 02 | 2-0 cm | Duff; fine roots abundant |
| A1 | 0-3 cm | Very dark grayish brown (moist) fine sand; massive breaks to moderate medium crumb, friable; fine roots common; smooth clear boundary to |
| B | 3-14 cm | Dark yellowish brown (moist) fine sand; massive breaks to moderate coarse subangular block, very friable; fine roots common; smooth clear boundary to |
| IIC | 14-63 cm | Dark gray (moist) sand; massive breaks to single grain; few fine and medium roots. |

as those of drier ridges and upper slopes. Plummer (1899, p. 133) observed that "ancient burns, of which traces still remain in the standing timber, cover probably 40 to 50 percent of the [Mount Rainier Forest] reserve, but being restocked with trees of large size cannot be called burns." We are not yet prepared to relate fire frequency or burning characteristics to the various forest types. Evidence for multiple fires can be found in most drainages at MRNP. In the Ohanapecosh Valley, for instance, fires evidently took place about 260, 450, and 670 years ago, as suggested by three widely occurring age classes of *Pseudotsuga menziesii*. Charred bark on survivors of 450 age class can be attributed to the fire about 200 years later. Evidence of repeated fires can also be found in places where charcoal occurs *in situ* both above and below the tephra W, a pyroclastic deposit about 450 years ago (Mullineaux 1974). Many younger stands were initiated by white man's fires. The Sheepherder Burn of the White River (oldest trees dating about 118 years) is a good example. The Cowlitz Valley appears to be the most extensively burned within the last 150 to 200 years. Plummer (1899) reported "great burns" of the Cowlitz (possibly outside the Park boundaries) in 1841 and 1856 and reburns at intervals around 1889-1899.

Avalanches are another common disturbance, affecting forests at mostly high and intermediate elevations (Table 1). Their extent is particularly apparent on air photographs. The start zone, trimline, and runout zone can be contrasted to more irregular patterns produced by fire. The aerial extent of successional vegetation of avalanche paths is not proportionately reflected in our sample of 400 plots. Vegetation composition of avalanche areas has been studied in the North Cascades by Cushman (1976). She found species of *Alnus, Acer circinatum,* and *Pteridium aquilinum* to be important dominants on south-facing tracks.

Lahars (Crandell 1971) are another widespread agent of disturbance. The 1947 Kautz lahar is a conspicuous example of almost primary succession on newly deposited surface. Root burial produced total mortality of the tree overstory. Dominant seral shrubs and herbs include *Alnus rubra, A. sitchensis* (at higher elevation), *Salix, Pteridium aquilinum, Epilobium angustifolium,* and *Anaphalis margaritacea*. Another lahar surface adjoining the 1947 lahar but older than 450 years has forest of the Silver fir/Alaska huckleberry type that we aged at about 590 years. As we were unable to find any charcoal residues that might have indicated a fire history, the forest might be first generation primary succession. The surface might correlate to the Electron lahar about 600 years of age (Crandell 1971). This forest differs little from stands of Silver fir/Alaska huckleberry in the Ohanapecosh Valley of about the same age but evidently fire-originated. Lahar deposits as soil material differ little from recent alluvium, pyroclastic deposits, or colluvium in affecting old-growth vegetation composition.

Alluvial and glacial processes also cause forest succession. A common tree invader of new river bars is *Populus trichocarpa*. Glacial outwash torrents and meltwater deposits destroy old banks and cause primary succession on new surfaces. Our plot 356 (Table 3) thus originated. Glacial advances create forest disturbance, and recessions initiate succession on primary surfaces (Sigafoos and Hendricks 1972). Strong trimlines can be seen along the Nisqually River near the highway bridge. Plot 375 (Table 3) below that trimline occurs on morainal drift exposed around 1840 (Crandell 1969).

Windthrow was extensive enough in several of our plots to qualify as a major disturbance. But we could not ascertain whether the blowdown itself was the immediate agent of succession or followed upon another event such as root rot, tree kill by insects, or fire.

Biotic influences on forest succession at MRNP are important and varied. Effects can be local or widespread. Examples include beetle kill of *Pinus monticola* during the 1960s, beaver impoundments creating red alder communities, pockets of root rot (*Phellinus weirii*), tree girdling by foraging bears, and feeding behavior of large herds of elk. Elk activities are apparent in many of our plots in the Ohanapecosh, Cowlitz, and Mowich River sectors. The migrating herds have seasonal impacts in several of the forest types. Recurrent usage of the same areas by elk could result in significant shifts of vegetation dominance. For example the greater abundance of devil's club (*Oplopanax horridum*) in the Carbon River (no elk) than at Ohanapecosh Valley (numerous elk) may reflect both climatic and elk-use factors, since this is a favorite browse plant.

## FOREST AGE PATTERNS

Figure 4 shows the distribution of tree ages in samples from Cowlitz, White, and Ohanapecosh River drainage systems. Our selection of trees for age determination was intended to provide an estimate of time since disturbance, so that the histograms are a sample of only the older, seral trees. Douglas fir was usually present in most disturbed forests at low and intermediate elevations. Other seral species included noble fir and western white pine. At higher elevations we sometimes had to resort to mountain hemlock, Alaska yellow cedar or silver fir, recognizing that these could be early- to mid-seral as well as late seral or climax.

These age patterns reflect a variety of disturbances discussed above, but principally fire. The histogram for the Ohanapecosh drainage shows three modes. Peaks occur at 225, 675, and 975 years. As seedling establishment can lag many years after the disturbance event, it is not unreasonable to speculate major disturbance periods at about 275-300, 750-800, and 1000 or more years ago. Of course other times of forest disturbance are likely too (e.g., specimens of Douglas fir aged at 450 years or noble fir at 310 years), and possibly our sample has not adequately revealed these periods.

The Cowlitz drainage has been heavily burned in the past two centuries. Our histogram shows major modes at 75 and 175 and minor peaks at 675 and 1000 years. The 75-year peak may reflect Plummer's (1899) burns of 1896 and earlier. Yet another sequence is apparent in the White River drainage. Ages of seral trees there show maxima at 75, 475, and 775 years. The youngest peak probably again reveals fires contemporaneous with white man's activity, especially the so-called "Sheepherder Burn" on Crystal Mountain. The older peaks may show periods of "ancient burns" mentioned by Plummer (1899).

Regard Figure 4 as only a first approximation to disturbance periodicity in forests at MRNP. The samples are not necessarily proportionate to the actual aerial extent of the various disturbance types and periods within forest populations. As stands mature and mortality reduces the old tree record, the probability of sampling the oldest trees of the earliest seral cohort diminishes. Multiple disturbances long ago may also be impos-

sible to resolve from sparse records of the old-growth survivors.

## CHRONOSEQUENCES

Figures 5 and 6 were made by arranging by age plots of the Silver fir/Foamflower and Western hemlock-Silver fir/Oregongrape forest types. One problem making chronosequences is recognition of early members when continuously intergrading samples up to old-growth climax do not exist. Our samples had a gap in the record about 400-500 years ago. But the plots before and after this gap were floristically similar enough to reasonably assign to the appropriate chronosequence.

We detect some rather uncertain understory trends in the Silver fir/Foam flower forest type (Fig. 5). Foam flower (*Tiarella unifoliata*) itself is rather variable, but has higher cover percentages in plots over 500 years than those younger than 400 years. Bracken fern does not persist after about 200 years. Similarly both twinflower *(Linnaea borealis)* and bunchberry *(Cornus canadensis)* seem more associated with younger plots of the noble fir successional stage. In the Western hemlock-Silver fir/Oregongrape forest only bracken fern revealed any trend: it occurred (from 1 to 10 percent cover) in only four plots under 125 years of age.

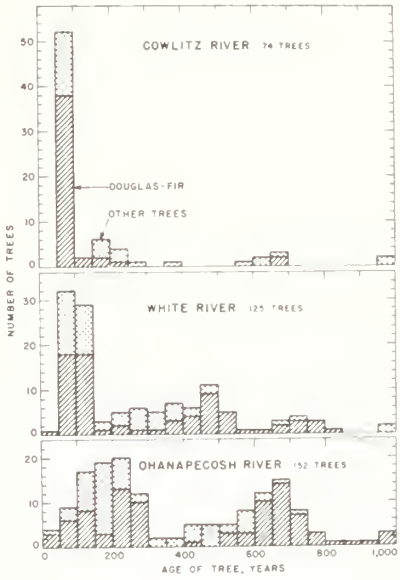



FIGURE 4. Sampled age distribution of oldest trees from various forest stands in three river drainages.

Rapid understory recovery after disturbance in two of the wetter forest types is also suggested in Table 3. Plots within each type were compared by calculating percentage similarity from 14 dominant understory species. Comparisons included young plots (secondary succession after fire and primary succession on new geological substrates) with old-growth. We regard vegetation between plots to be similar if calculated similarities exceed about 25 percent. Similarities of each plot with others of the same forest type often exceeded 25 percent regardless of forest age or disturbance type. We discerned no striking or consistent difference in dominant understory vegetation whether 100 or 500 years after the disturbance.

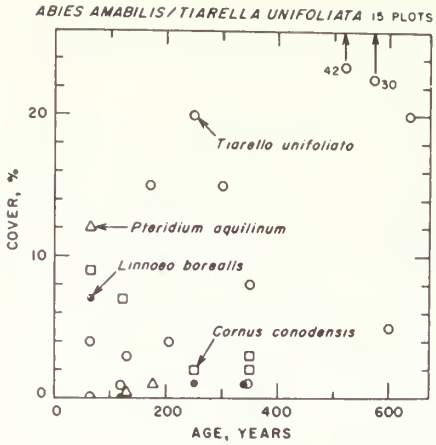



FIGURE 5. Cover of selected herbs in relation to plot age, Silver fir/Foamflower forest type.

Tree composition (Fig. 6) is the most indicative state of the sere. Noble fir usually dominates the Silver fir/Foam flower habitat during the first several centuries after fire. (All plots of figure 6 were apparently fire initiated.) Alaska yellow cedar, western hemlock, Douglas fir, and silver fir may also be seral, however. But after 500 years silver fir is usually the leading and sometimes the exclusive dominant. By contrast western hemlock or Douglas fir are several dominants after fire in the Western hemlock-Silver fir/Oregongrape type. The proportion of Douglas fir gradually declines, with replacement by the hemlock. Silver fir achieves very small share of the canopy dominance only in the oldest plot. Tree regeneration patterns differ in the two forest types. Western hemlock has continuous regeneration pressure throughout the time span of the Western hemlock-Silver fir/Oregongrape chronosequence, but decays to minor status in old growth of the Silver fir/Foamflower type. In both chronosequences silver fir is the eventual (after about 200 years) regeneration dominant.

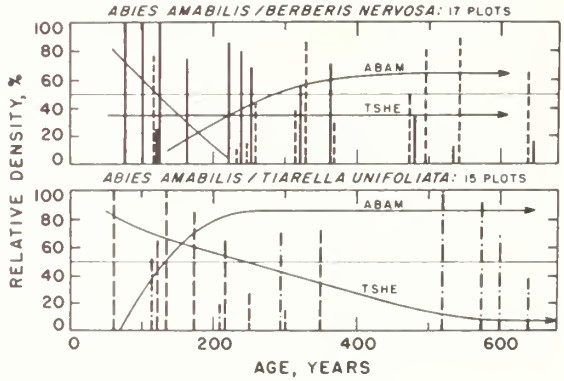



FIGURE 6. Tree chronosequences in two forest types. Canopy dominants are Douglas fir (solid bars), wester Hemlock (short dashes), noble fir (long dashes), and silver fir (dash-dot bars). Regeneration is silver fir (ABAM), western hemlock (TSHE), and Douglas fir (unlabeled curve).

TABLE 3. Comparison of dominant understory composition (computed as percentage similarities) between young and old-growth forests in two forest types.

| Forest Type | Plot | Age (Years BP) | Geology[1/] | Disturbance | Similarity[2/] (%) |
|---|---|---|---|---|---|
| TSHE/OPHO | 356 | 135 | QA | New substrate | 34, 18, 21 |
| | 45 | 146 | QA | Fire | 34, 44, 45 |
| | 127 | >500 | QA | | 18, 44, 42 |
| | 131 | >500 | QA | | 21, 45, 42 |
| ABAM/OPHO | 273 | 119 | QO | Fire | 21, 30, 39 |
| | 375 | 120 | QG | New substrate | 21, 57, 27 |
| | 263 | 660 | TBR | | 30, 57, 30 |
| | 389 | 900 | TBR | | 39, 27, 30 |

1/ QA = Quaternary alluvium, QO = Osceola mudflow, QG = Garda drift TBR = Tertiary volcanic rock.

2/ Each plot compared to others of the same forest type sequenced from top to bottom of column 2.

We feel that the first few decades after disturbance is the period of greatest vegetation contrast between young and old stands. After about 100 years in mesic forest types of valleys, draws, or lower slopes the sere has assumed most of the attributes of climax. Successional trends seem slower, however, on drier or more exposed sites such as Backbone Ridge or upper elevations at Sunset Park where forest closure and stabilized understory composition may require centuries.

## CURRENT STUDIES

We have summarized much of our present state-of-knowledge concerning forest ecosystems at MRNP. Our efforts are now directed to better resolving the mature forest types with computer help and mapping these and their seral derivatives from air photo information. More analysis of succession is needed in some of our hot, dry as well as high elevation forest types. We need better resolution of the frequency, extent, and nature of natural and man-caused forest disturbances at MRNP. These studies should help provide park managers some insights into ecological processes that have brought about in past centuries the complex forest mosaics existing at Mount Rainier today. Land use practices both within MRNP and outside the Park may or may not disrupt or modify certain of those processes. The ability to predict forest responses on both short and long term should give management necessary perspectives for the job of both utilizing and preserving the forest ecosystems.

## LITERATURE CITED


CRANDELL, D. R. 1970. Postglacial lahars from Mount Rainier Volcano, Washington. Geol. Surv. Prof. Paper 677, iv, 75 p., map.

_____. 1969. Surficial geology of Mount Rainier National Park, Washington. Geol. Surv. Bul. 1288, vi, 41 p., map.

CUSHMAN, MARTHA J. 1976. Vegetation composition as a predictor of major avalanche cycles, North Cascades, Washington. M.S. thesis, Univ. Washington, Seattle, vii, 99 p.

DYRNESS, C. T., J. F. FRANKLIN, and W. H. MOIR. 1974. A preliminary classification of forest communities in the central portion of the western Cascades in Oregon. US/IBP Coniferous For. Biome, Bul. 4, viii, 123 p., Univ. Washington-AR-10, Seattle.

FRANKLIN, J. F. and C. T DYRNESS. 1973. Natural vegatation of Oregon and Washington. USDA Forest Serv. Gen. Tech. Rep. PNW-8, viii, 417 p.

_____. W. H. MOIR, G. W. DOUGLASS, and C. WIBERG. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Arctic & Alpine Res. 3:215-224.

_____, C. T. DYRNESS, and W. H. MOIR. 1970. A reconnaissance method for forest site classification. Shinrin Richi XII:1-12.

_____ and R. G. MITCHELL. 1967. Successional status of subalpine fir in the Cascade Range. USDA Forest Serv. Res. Paper PNW-46, 16 p.

HOBSON, F. D. 1976. Classification system for the soils of Mount Ranier National Park. M.S. thesis, Wash. State Univ., Pullman, 79 p.

MULLINEAUX, D. R. 1974. Pumice and other pyroclastic deposits in Mount Rainier National Park, Washington. Geol. Surv. Bul. 1326, viii, 83 p.

PLUMMER, F. G. 1899. Mount Rainier Forest Reserve, Washington. Geol. Surv. 21st Rep. 1900[1901], Pt. 5:81-143.

SHIMWELL, D. W. 1971. The description and classification of vegetation. Univ. Wash. Press, Seattle, xiv, 322 p.

SIGAFOOS, R. S. and E. L. HENDRICKS. 1972. Recent activity of glaciers of Mount Rainier, Washington. Geol. Surv. Prof. Paper 387-B, vi, 24 p., 6 maps.

# ECOLOGY OF ALPINE TIMBERLINE IN OLYMPIC NATIONAL PARK

R. W. Fonda[1]

## INTRODUCTION

Timberline is a fascinating ecotonal area, where there is a pronounced shift in physiognomy from trees to meadow forbs, grasses, and dwarf shrubs. This area is created by a complex interplay of factors that shift as elevation and exposure increase on a mountain.

Many researchers have tried to explain the causes of timberline (Table 1). Many scientists and lay persons have favored low temperature as the limiting factor. Others have settled on wind, both in winter and during the growing season, as a limiting factor, and snow has often been cited. One general theme that is evident among the investigators listed in Table 1 is that Americans have described the forest communities at timberline and have generally speculated on the climatic controls, while Europeans have selected individual dominant species and have looked intensively at physiological responses to certain factors, in the laboratory. In every case, the studies have been characterized by a common theme: all have searched for the single limiting factor causing timberline.

I hypothesize that the vegetative pattern at timberline is the result of the interaction of topography, exposure to wind, snow accumulation, timing of snowmelt, soil moisture, air temperature, and soil temperature. A principal result of this interplay is that a site with neither too much nor too little snow, nor too little water, supports trees at the limits of their distribution in the Olympic Mountains.

## EAGLE POINT TIMBERLINE

Since 1971 my students and I have studied the hypothesis shown in Fig. 1, and we are continuing to test all the elements of this hypothesis. Our work in the Olympics has centered on Eagle Point (1829 m), a prominence along the Hurricane Ridge complex in the northeastern portion of the park. Here, timberline forests of subalpine fir *(Abies lasiocarpa)* contact alpine and subalpine meadows. Furthermore, these trees encounter the entire range of environmental conditions described in Fig. 1. Sites with low wind, heavy snowpack, and late snowmelt are available, as are sites with high wind, light snowpack, and early snowmelt. The snowmelt pattern was established by Canaday and Fonda (1974). In brief, there are four meadow communities plus the treeline. True alpine vegetation is snowfree during winter; a mesic grass community occupies the outer portions of the meadow, and it is released from snow in early June; next is a tall sedge community that is released from snow in July; the center of the snowfield supports a dwarf sedge community, released from snow in August. The trees at Eagle Point are free of snow by mid-July, about the same time as the tall sedge community. The band of trees that our intensive work is conducted upon is bordered by a mesic grass community to the windward side, and a tall sedge community to the leeward side.

Eagle Point appears to be almost a constant environment. Although the site is basically a convexity, it behaves as a concavity because of the line of trees forming timberline. There is a limit to the maximum snow accumulation, because any snow that accumulates above the influence of the trees will be blown off the ridge. Consequently, year after year about 4-5 m of snow piles into the center of this meadow. This tapers to about 1 m over the tall sedge community, and to less than 1 m over the mesic grass community. Rate of snowmelt is constant, if the summer is not overly cloudy and rainy.

The summer of 1972 characterizes the typical climatic relationships during the growing season at Eagle Point. Summers are generaly sunny, warm, and dry. Daily mean VPD is seldom greater than 5 mm Hg, with a mid-day maximum of 9-11 mm Hg. Lowest hourly values occur between 0200-0700 hrs. Most days have over 500 langleys of radiation, and mean daily air temperature consistently exceeds 10 C, except during storms. Mean daily soil temperatures do not reach 10 C. The treeline station at Eagle Point has a Temperature Growth Index (TGI) of 27. Waring et al. (1972) found that mountain hemlock stands near timberline in the Siskiyou Mountains have a TGI=30, so that our data appear to reflect the typical temperature regime for such stands in the Pacific Northwest. (See Cleary and Waring 1969, Waring 1969, and Waring et al. 1972, for a definition and use of TGI).

Figure 2 shows soil moisture values for four stations at Eagle Point in 1972. Note that soil moisture regime at the treeline station is most like the mesic grass/tall sedge ecotone, and that beginning in August the mesic grass community is significantly drier than the trees. The dwarf sedge community is significantly wetter than the treeline station. This is certainly enough moisture to support trees, but the August snow release mitigates against the tree growth form.

Most, but not all, summers have these kinds of environmental relations. The pathways depicted in Fig. 1 need not obtain every year for trees to be limited in their distribution. The summer of 1976, for example, was atypical, because it was wetter and cooler, with many cloudy days. Most days in 1976 had less than 500 langleys, and mean daily air temperature frequently stayed below 10 C. Almost the same total precipitation was recorded during the summers of 1972 and 1976: 94 mm and 90 mm. But, in 1972 precipitation was almost equally distributed among the summer months, whereas in 1976 about 60% fell during August. The principal difference between the summers of 1972 and 1976 was the almost constant cloud cover of 1976, which delayed snowmelt and kept sites from drought. Subalpine fir was subjected to water stress in 1972, but not in 1976.

## ENVIRONMENTAL CONTROLS AT TIMBERLINE

Basins and leeward concavities, which accumulate much snow during winter, mark the limits of timberline along one end of the environmental gradient at Eagle Point. The problems of too much

[1]Biology Department, Western Washington State College, Bellingham, Washington 98225.

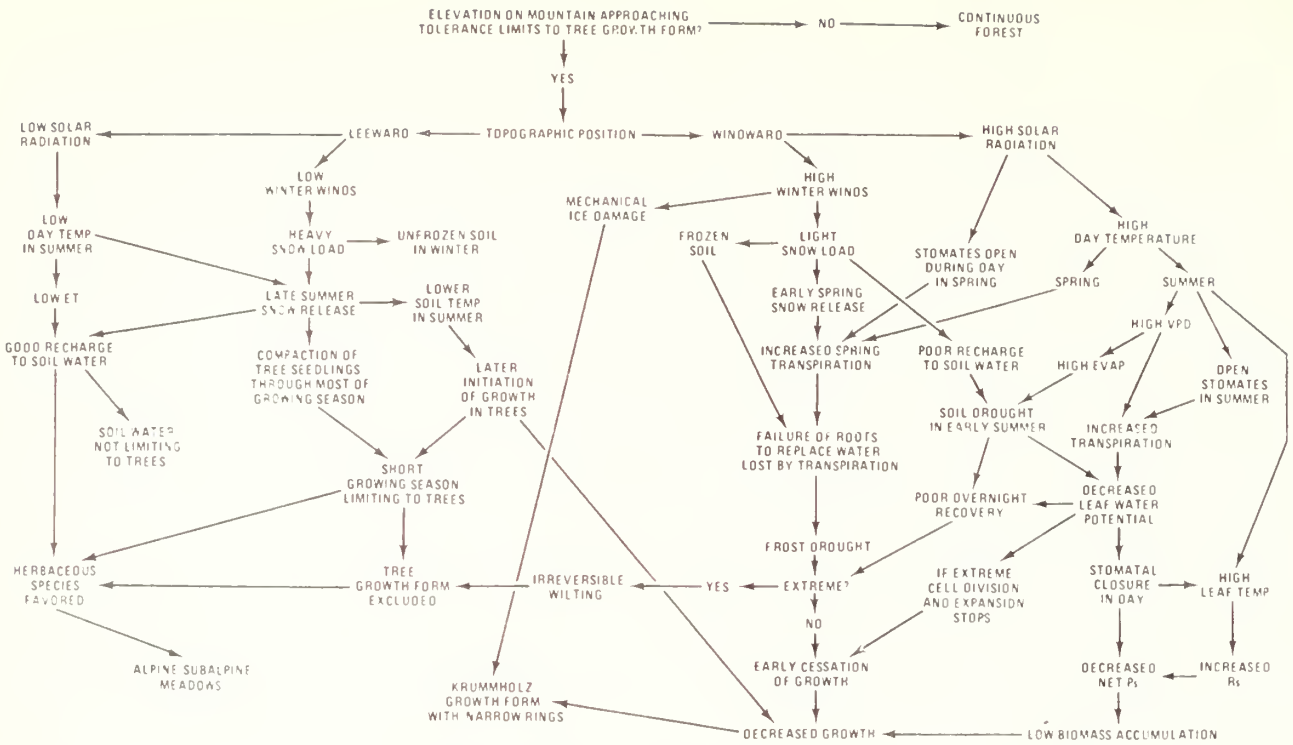



FIGURE 1. The interaction of environmental factors and plant physiological responses that produce timberline and meadow vegetation in the Olympic Mountains, Washington.

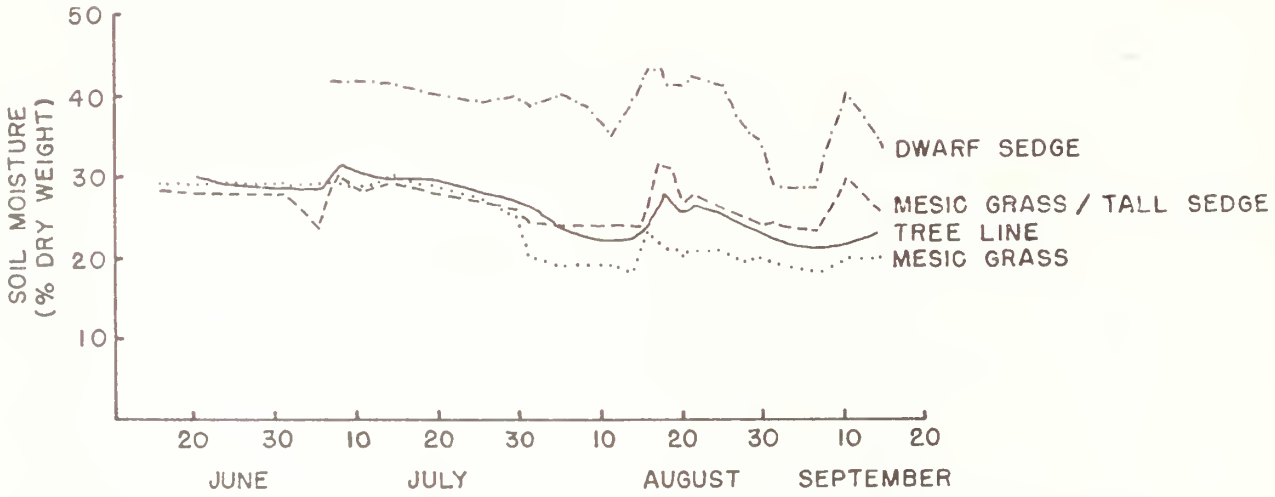



FIGURE 2. Soil moisture trends at Eagel Point during summer 1972. Each soil moisture record was begun when the soil thermistor block leads were exposed by snowmelt.

TABLE 1. Important environmental controls at timberline and associated effects.

| Factor | Effect | Investigators |
|---|---|---|
| Low temperature | Duration of non-photosynthetic period | Tranquillini |
| | Photosynthesis and production | Tranquillini; Mooney; Daubenmire |
| | Freeze-thaw cycles in cells | Tranquillini |
| Winter wind | Remove snow cover | Klikoff |
| | Cause snow accumulation | Kronfuss; Tranquillini; Canaday & Fonda |
| | Frost drought | Tranquillini |
| | Frost hardiness | Wardle |
| Summer wind | Increase transpiration | Caldwell; Griggs; Daubenmire; Seaman |
| | Lower leaf water potential | |
| Snow | Protection from freeze-thaw | Wardle; Klikoff |
| | Compaction of trees | Billings; Arno; Franklin et al; Fonda & Bliss |
| | Block winter transpiration | Tranquillini |
| Summer drought | Excessive transpiration | Tranquillini |
| | Internal water stress | Klikoff |
| | Decrease photosynthesis-respiration | Kuramoto & Bliss |
| Fire | Succession | Morris; Billings; Griggs; Fonda & Bliss |
| Microtopography | Differential snow accumulation | Several of the above |

TABLE 2. Mean plant water potential (bars) at Eagle Point, 1972; morning measurements.

| | SUBALPINE FIR TREELINE 7-14 July snowmelt | | TALL SEDGE MEADOW 16 June snowmelt | | MESIC GRASS MEADOW 20 May snowmelt |
|---|---|---|---|---|---|
| Date | West krummholz | East krummholz | Subalpine fir | Lupine | Juniper |
| 8 Aug | -10.1 | -11.3 | -12.3 | -6.6 | -15.6 |
| 14 Aug | -12.2 | -13.3 | -11.9 | ... | -18.0 |
| 25 Aug | -12.8 | -12.6 | -10.4 | -6.3 | -8.4 |
| 5 Sep | -10.3 | -10.3 | -10.9 | ... | -14.3 |

snow have been amply documented (Franklin et al 1971, Fonda and Bliss 1969, Canaday and Fonda 1974). Heavy snow damages the trees, so that if they are able to survive at all they are twisted and stunted into krummholz forms. More importantly, however, the August release of a site that accumulates several meters of snow results in a growing season that is too short for the tree to produce the necessary wood, harden off tissues for the dormant season, and perhaps complete a reproductive cycle (Fig. 1). Wood and perennial tissues above ground are a luxury for which few timberline plants have a strategy. Instead, meadow species are favored, and they are well adapted to the sequential release of snow at Eagle Point (Canaday and Fonda 1974).

Snow does not accumulate on windward sides of ridges in winter, and frost drought can be a problem in spring (Fig. 1). On windward sites high winds, high daytime temperatures, and low soil moisture combine to act against trees during the growing season. Because precipitation is so light at Eagle Point, the principal recharging agent for soil moisture is snowmelt. Light snow results in a poor soil moisture recharge, and a possibility of drought during the growing season (Fig. 1). The growing season at timberline is short. Based on phenological observations and dendrometer measurements, subalpine fir at timberline begins to show bud swell and an increase in trunk diameter around 1 July. These trees cease growth between 12-22 August, although cones continue to mature after that date. About 300 m lower on the slope, subalpine firs in the closed forest begin to break dormancy shortly before those at timberline, but they continue to grow for about four weeks after those at timberline have stopped.

One factor that contributes to cessation of growth at timberline is low water potential in August (Table 2). Data on water potential were gathered with a pressure bomb, from dawn to early morning during August and early September 1972. On sites that either support subalpine fir or that behave similarly (ie, tall sedge), the water potential values were slightly less than -10 bars (Table 2). On the windward side of the treeline at Eagle Point is a mesic grass community. There are no subalpine firs growing there, so that dwarf juniper, a common component of the community, was used for water potential measurements (Table 2). The values for juniper in the mesic grass community are lower than values obtained for subalpine fir at the same time, which indicates that low soil moisture may be a barrier to subalpine fir invasion.

A water potential of -10 bars is an important division point, because subalpine fir can easily tolerate internal water potentials as low as -10 bars. Once the values drop below -10, however, photosynthesis, respiration, and transpiration decrease sharply for subalpine fir (Puritich 1973). Early morning values less than -10 bars indicate that the timberline trees are below that critical point throughout the day during August, and that growth should cease. Consistent with our observations, Waring et al. (1972) found that forest stands near timberline did not show water potentials less than -10 bars.

## SUMMARY

Figure 1 summarizes the main environmental problems facing subalpine fir at timberline in the Olympic Mountain. These trees must adapt to many possible limiting factors, all of which have extreme expression in a space of a few meters. At Eagle Point these factors combine to limit the effective growing season for subalpine fir. Consequently, timberline represents a point where trees show an early cessation of growth and low biomass accumulation, in addition to other physiological stresses. My students and I have gathered data on some of these relationships. Our present work focuses on summer water balance, especially stomate behavior, phenology, and growth response. Once we fully understand the water status of subalpine fir during summer drought, we hope to move to the next set of related responses: photosynthesis/respiration rates and productivity at timberline.

## LITERATURE CITED


CANADAY, B. B. and R. W. FONDA. 1974. The influence of subalpine snowbanks on vegetation pattern, production, and phenology. Bull. Torrey Bot. Club 101:340-350.

CLEARY, B. D. and R. H. WARING. 1969. Temperature: collection of data and its analysis for the interpretation of plant growth and distribution. Can. J. Bot. 47:167-173.

FONDA, R. W. and L. C. BLISS. 1969. Forest vegetation of the montane and subalpine zones, Olympic Mountains, Washington. Ecol. Monogr. 39:271-301.

FRANKLIN, J. F., W. H. MOIR, G. W. DOUGLAS, and C. A. WIBURG. 1971. Invation of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Arc. Alp. Res. 3:215-224.

PURITICH, G. S. 1973. Effects of water stress photosynthesis, respiration, and transpiration of four *Abies* species. Can. J. For. Res. 3: 293-298.

WARING, R. H. 1969. Forest plants of the eastern Siskiyous: their environmental and vegetation distribution. Northw. Sci. 43:1-17.

WARING, R. H., K. L. REED, and W. H. EMMINGHAM. 1972. An environmental grid for classifying coniferous forest ecosystems, p. 79-91. *In:* J. F. Franklin, L. J. Dempster, and R. H. Waring (eds.). Research on coniferous forest ecosystems - a symposium. USDA For. Serv., Portland, OR.

# PRIMARY VERSUS SECONDARY SUCCESSION AT GLACIER BAY NATIONAL MONUMENT, SOUTHEASTERN ALASKA

Donald B. Lawrence[1]

## INTRODUCTION

An alternative title could have been: "Some results of sixty years of research by the University of Minnesota Department of Botany at Glacier Bay National Monument." The work was begun in 1916 by Professor William S. Cooper, who is now 92 years old. This paper is dedicated to him on the 60th anniversary of the first expedition. That was long before there was a National Monument. It was through Cooper's efforts that the Monument was established in 1924 (Cooper 1956). I shall emphasize the wonderful opportunities there for studying patterns and processes of physiographic ecology. Primary succession has occurred following catastrophic glacial recession in the main bay (Figs 1-3) from maximum ice positions of the Little Ice Age, or Neoglacial as it is otherwise known, about 225 years ago, or roughly 1750 A.D. Secondary succession can be studied at Lituya Bay on the west coast of the Monument (Figs. 4-5) where giant waves generated by huge rockslides, most recently in 1958, swept away the forest but not all the soil from the lower slopes of that bay. Secondary succession at Lituya Bay has attained about the same development in 15 years as primary succession has in 50-100 years on the shores of Glacier Bay, both starting mainly from seeds and spores. This is a maritime region of relatively mild moist climate and there is no permanently frozen ground.

Generous assistance of National Park Service staff has been received in recent years, especially by former Park Superintendent Robert Howe, and by Naturalists Gregory P. Streveler, and Bruce Paige, and by Captain James Sanders of the Motor Vessel *Nunatak*, and mate Eugene Chaffin. My wife, Elizabeth, has cooperated in the work. Several other colleagues have helped, especially Lloyd Hulbert, Robert Crocker, Roderick Sprague, Roland Schoenike, William Reiners, Ian Worley, Gordon Nichols, and James Taylor; the last two were members of the staff of the National Park Service of New Zealand at the time. William O. Field invited me to participate in his 1941 trip, my first to Glacier Bay; he has been of continuing help and inspiration, as has Cooper over the years.

Cooper selected Glacier Bay for study because he wanted to gain a better understanding of how vegetation became established in Minnesota following recession of the continental ice sheets of the Pleistocene. His dream of this study as a model for understanding the development of the Minnesota landscape has been so successful that it was possible to predict that fossil evidence of alpine avens *(Dryas)* would eventually be found in Minnesota sediments (Schoenike 1958). This suggestion was published several years before fossil Dryas leaves were actually discovered in 1961 in northern Minnesota (Watts 1967) where this genus of plants no longer lives today.

[1]Department of Botany, University of Minnesota, St. Paul, Minnesota 55108.

I am glad that the early observations of this study were made before there was much visitation by tourists because the validity of the results has depended on absence of human influences. People are recognized dispersers of plants into natural areas (Ridley 1930). Their activities in altering the biota and pattern and rate of succession have been dramatic in some national parks, as for example in Hawaii, and in New Zealand. In conducting this research I have always been careful to begin the observations at the youngest sites, wearing carefully cleansed clothing, and to proceed to older and older sites so that I would not myself be altering the progress of the succession (Cooke and Lawrence 1959: 531-532). Much more care is needed in this respect by visitors who go ashore especially in the upper bay today.

## PRIMARY SUCCESSION ON GLACIAL TILL AT GLACIER BAY

We may define primary succession as the process of development of ecosystems on raw parent material that has no soil profile and contains no viable remains of organisms; community establishment must commence anew by immigration from other areas. This region is perhaps the most interesting portion of the earth's surface for the study of history of glaciers and the development of vegetation following recession of ice. This is true because of the extraordinary rate of recession since the position of maximum advance about the middle of the 18th century. Since then there has been recession of 105 km (65 mi) to the faces of Grand Pacific Glacier and Johns Hopkins Glacier at the heads of the west arm of the bay, and of 80 km (48 mi) to the Muir ice front at the head of Muir Inlet (see Fig. 1 based on USDI NPS map). This process has exposed new fiord systems, U-shaped valleys, and numerous habitats including bare rock, till, outwash, ponds, and many erect stumps ranging in radiocarbon age from 7000 yrs near the head of Muir Inlet to about 300 yrs near the mouth of the bay (Lawrence 1958).

The map of Glacier Bay (Fig. 1) shows known positions of the ice fronts (solid lines), and estimated positions (broken lines) based on a variety of sources. We are indebted to John Muir for a sketch (Fig. 3 top) of the position of "The Pacific Glacier" at the head of the main bay in 1879, when it extended northeast from the southern part of Russell Island to the mainland (Muir 1895; 243, and Bohn 1967: 48). Early positions of the front of Muir Glacier are based on a description by John Muir in 1880, on photographs by G. F. Wright in 1886, and surveys by H. F. Reid in 1890 and 1892 (Gilbert 1904: 21, Fig. 10). More recent positions are known mainly from surveys by Field (1947), and Goldthwait *et al.* (1966). The known history of these glaciers and other mountain glaciers of the whole northern hemisphere has been assembled in detail by Field (1975). Time of recession from the mouth of the bay about 1750 is estimated from growth layer counts from basal cores of oldest Sitka spruce trees by Cooper on the terminal moraine near the east shore, and our own there and on the west shore where seedling establishment occurred a few years earlier.

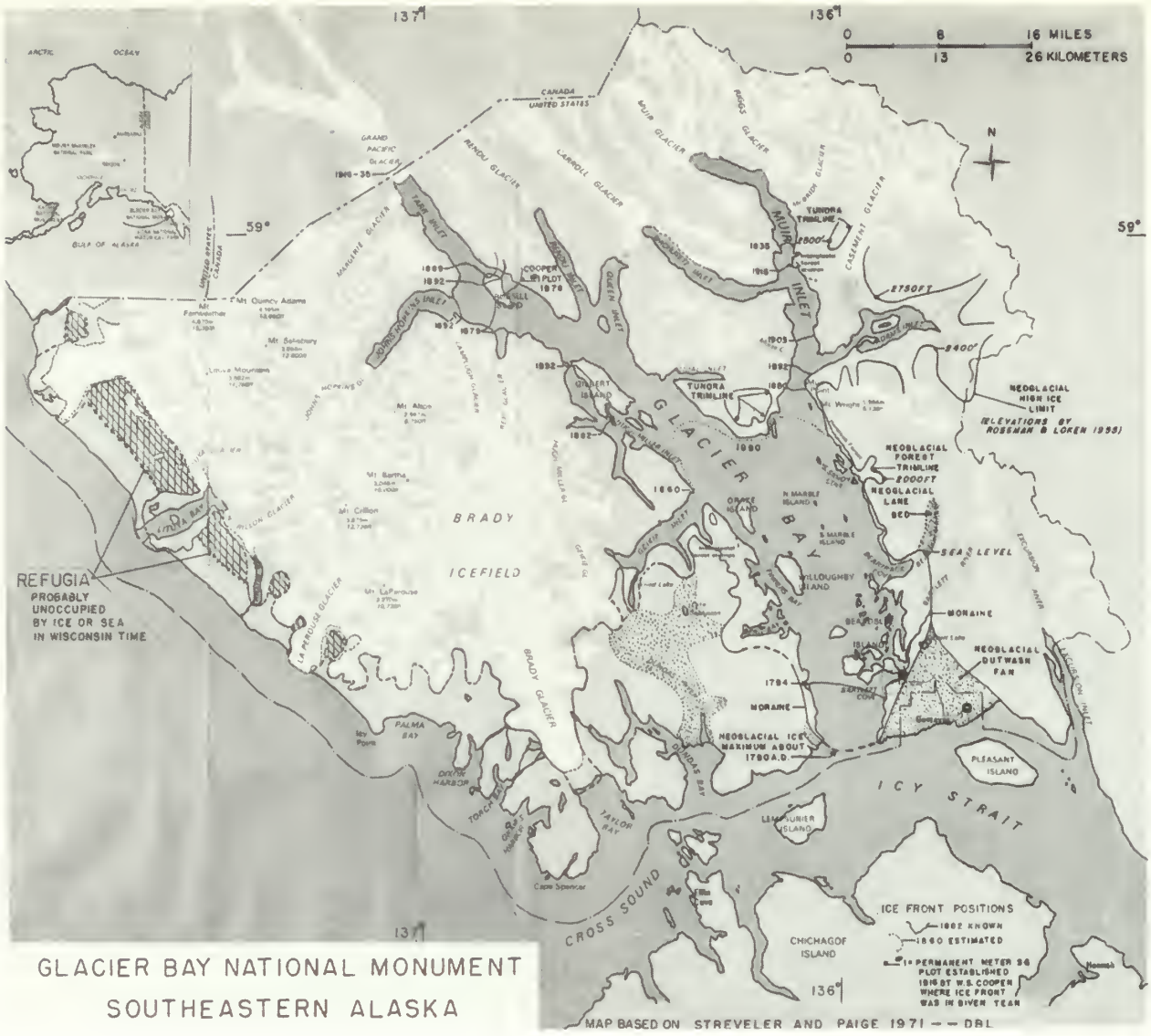



FIGURE 1. Map of Glacier Bay National Monument showing history of glacial recession, 105 km (65 mi) in the main bay, and 80 km (48 mi) in Muir Inlet in the last 225 years since the Neoglacial (Little Ice Age) maximum when the glacier reached Icy Strait. Note location of Cooper Plot #1 near the head of the main bay where ice front stood in 1879. Lituya Bay is at the left between the two main areas of pre-Wisconsin refugia.

The general progress of vegetation development on till can be demonstrated most readily on the shores of Muir Inlet (Fig. 2) because there have been large portions of glaciers, cut off from sources of supply, gradually melting away on relatively level surfaces (Fig. 2A). Their margins have been observed almost annually so that one can know quite precisely where the ice edge was in a particular year and be sure that no vascular plants were growing on debris overlying buried ice. Thus the time relations of development of vegetation and soil (Crocker and Major 1955, Ugolini 1966) can be documented beginning with soil parent material of age zero years.

*Whence came the plants to occupy the new surfaces?* -- We have discovered by observation that reproductive parts of plants, at least of green plants, cannot survive beneath glaciers through even a "Little Ice Age" of only a few hundred years. The process of vegetational development must begin with immigration of mobile seeds and spores from adjacent areas of living vegetation blown in by wind or carried on the pelts and in the digestive tracts of wild animals, or on the clothing of human visitors. There are two main sources of spores and seeds at Glacier Bay. One is the floristically rich undisturbed lowland forest and muskeg beyond the Neoglacial (Little Ice Age) ice limit near the mouth of the bay; the other is above the Neoglacial high ice limit, mainly alpine tundra with scattered mountain hemlocks on the mountain slopes that flank the bay. The locations of these may be seen on the map of Figure 1; they are based on the map of Streveler and Paige (1971, Fig. V). It will be noted that the vegetational trimline which was carved by the glacier as it advanced down the bay, lies at sea level in the first 26 km (16 mi) northward from the mouth of the bay to Beartrack Cove, rises northward rather steeply along forested slopes in the next 13 km (8 mi) to 610 m (2000 ft) east of Sandy Cove, then rises much more gently mainly above tree line for the next 35 km (22 mi) to 760 m (2500 ft) on the slopes of Red Mountain east of Muir Inlet. These elevations were measured by Rossman and Loken (1955 personal communication) from a small plane with altimeter and pocket level.

Northwestward from the isolated tundra area on the promontory that separates Glacier Bay from Muir Inlet, and northwestward from the ridge just south of the mouth of Geikie Inlet no relict areas of high vegetation have been found above the Neoglacial high ice line from which seeds and spores could be carried to the deglaciated areas about the head of the main bay. However, the mountains above the high ice line are almost unexplored, and isolated refuge areas may yet be discovered. Cooper (1942) described an isolated colony including 15 species of seed plants at elevations of 1250 m (4100 ft) to 1830 m (6000 ft) on an eastward ridge of glacier-clad Mt Bertha, a peak of 3100 m (10,800 ft) which juts up from the northern part of the Brady Icefield (Fig. 1). He considered this to be a pre-Wisconsin relict community. From these facts it becomes obvious that the distance that had to be traveled by seeds and spores was very short when the ice was receding from the mouth of the bay about 1750 A.D., but only a few of the species present in the mature forest would have pioneering capabilities. At the head of the main bay, and especially in the very isolated area along the shores of Johns Hopkins Inlet, the sources of plant reproductive parts are far away. But as the glacier has receded gradually up the bay and up Muir Inlet, plants with greatest dispersal mobility and capability for developing promptly to the reproductive stage on raw substrata following ice recession have become established in vacated areas, leaving a bare zone of varying width near the melting ice. Because the ice sheet has receded vertically as well as horizontally, the upper slopes have naturally become vacated before the adjacent lower ones so that with passage of time there was less distance to be traveled by the disseminules of pioneering plants that had reached reproductive maturity in order to colonize the new bare areas near sea level. Thus it may be seen that the progress of succession moved across the landscape in a wave-like motion from the older to the younger surfaces gradually filling in the barren U-shaped belt left along the tip and edge of the receding ice.

*What kinds of plants pioneer?*--Several kinds of habitats are left as the ice recedes, in addition to marine surfaces which we cannot consider here. The soil parent material in a number of places is a mixture of gravel, sand, and silt, but generally very little clay, a mixture of size classes we call loam. After the glacier has melted there is no permafrost. Before any plant cover develops, freezing and thawing near the surface in the first few years bring the uppermost gravel to the top and result in a pebble pavement. It is in the cracks between pebbles and on the pebble surfaces that plants begin to establish. In other places where gravel is absent a silty or sandy surface occurs, on which a "black crust", actually very dark green, develops within a very few years. Worley (1973) has made a careful study of this and has been able to distinguish three types: 1) *Lophozia Mat,* a minute leafy liverwort, in some places mixed with various algae and mosses; 2) *Cyanophyta Mat,* consisting of a tough layer of bluegreen algae, the cells of which are imbedded in a gelatinous sheath forming a rubbery layer; in some places *Lophozia* and mosses are also present; 3) *Lichen Mat,* consisting of colonies of small bristle-like lichen *Lempholemma radiatum* 2-4 mm tall, and another unidentified lichen. These crusts are constructive in that they have a stabilizing role; they greatly restrict the movement of soil particles under the effect of rain drops, solifluction, freezing and thawing. In places, movement of the whole mat occurs on the steeper slopes "not unlike a carpeting sliding upon a flooring", according to Worley, making the directions of motion obvious by the patterns of convex flowlines that develop. Worley considered that these mats are not an essential precursor for any later successional community, but we shall reconsider this because, as he points out, they may absorb heat due to their dark color, as well as consolidate the upper 1-2 cm of the substratum. Furthermore, he found that the variegated scouring rush *(Equisetum variegatum)* "is common in or adjacent to the crust habitats, its rhizomes often underlying the mat." We shall see that this member of the fern allies forms an important and long-surviving component of the developing community, and it probably becomes established in the black crust. Bierhorst (1971a) has pointed out that although the minute *Equisetum* gametophytes derived from spore germination often die young, they may continue to grow for some years with individuals forming discs 3 cm in diameter, but that they are rarely seen in nature, and if seen are often not recognized because of their similarity to filamentous algal growths or to masses of moss protonemata. It would seem likely therefore that these early stages of *Equisetum* occur in the black crust, and further search for them would be in order.




FIGURE 2. Stages of progress of primary succession following recession of Muir Glacier emphasizing importance of two N-fixing shrubs: B-F alpine avens (*Dryas*), and F-G Sitka alder (*Alnus*) showing 11 yrs of change. H-I Muir Point a few years after ice recession and 50 years later.

Other plants are successful pioneers on the pebble pavements mentioned earlier. The moss *Rhacomitrium canescens* and the lichen *Stereocaulon* sp. start on many pebbles. Seedlings of willows of several species and black cottonwoods may become established within the first few years as well as Dryas, a mat-forming shrub, and various herbaceous plants such as willow herbs of the genus *Epilobium* (Cooper 1923, Decker 1966). It is only at this very early stage before other plants have formed a dense cover that these species can become established, partly because they cannot endure shade and partly because they need a mineral surface or some special physical, chemical or microbial characteristics that are present only at this early stage. This fact has not been adequately emphasized heretofore. These species have the most mobile disseminules, being small, or, in some, being equipped with delicate plumes or parachutes of hairs which carry them with the gentlest breeze.

Somewhat later, other species with larger seeds, such as Sitka alder and Sitka spruce arrive, both bearing wings which increase their mobility with wind, especially on snow crusted over with ice. These species are sometimes accompanied within the first decade by an occasional western hemlock, also with winged seeds, by two herbaceous members of the pea family, *Astragalus alpinus* and *Hedysarum alpinum,* and the soapberry shrub, *Shepherdia canadensis;* these last three have large wingless seeds transported mainly by birds, and the soapberry often by bears, and perhaps all by voles which are very numerous in some years. Plant communities that develop close above the strand line are salt-tolerant and have a very different composition. I shall not consider them here.

*From what sources come the combined forms of nitrogen so necessary to the health and rapid growth of ordinary green plants?*--All of the pioneer plants above the strand line except Dryas, alder, soapberry, the members of the pea family, and those of the black crust, are of a sickly yellowish color with very slow growth rate and prostrate stature, even the willows, black cottonwood, Sitka spruce and hemlock which are capable of rapid erect growth later in life. These are symptoms of deficiency of soil nitrogen as has been demonstrated (Lawrence 1958) by the spectacular improvements induced through experimental applications of ammonium nitrate to the soil around test cottonwood saplings near the head of Muir Inlet. Small amounts of available nitrogen, enough for minimal growth of pioneer plants with lowest nitrogen requirements, may be present in the rain water. Another small supply may come from the ammonium chloride in many igneous rocks (Ingols and Navarre 1952) such as some of those here in the raw till. But the major source here must come via the process of biological fixation of atmospheric nitrogen. The soil is too cold for effective fixation of nitrogen by free-living bacteria, even by the photosynthetic ones known to have that capability. But some blue-green algae long known to be able to fix nitrogen (Singh 1961) thrive here in quantity within the black crust, both independently in the Cyanophyta Mat and in symbiosis within the bodies of *Lempholemma* in the Lichen Mat (and also in *Stereocaulon* lichen). Furthermore, Griggs (1933) in his study of the colonization of the Katmai volcanic ash farther to the north found that liverworts grew on the ash in pure stands, and in experimental studies (Griggs and Ready 1934) demonstrated that these same liverworts would thrive on a medium too low in combined nitrogen to support growth of ordinary plants. Thus, it seems possible that the Lophozia Mat liverwort may possibly fix nitrogen either independently or by some obscure symbiotic relationship.

All vascular plants mentioned above as having healthy green color and early rapid growth rate have root nodules inhabited by star molds (actinomycetes) or bacteria, both of which are capable of fixing atmospheric nitrogen (Stewart 1966, Becking 1970).

Two of the woody plants mentioned above, the Dryas or alpine avens, a member of the rose family, and the Sitka alder *(Alnus crispa* subsp. *sinuata),* belonging to the birch family, have extraordinarily rapid growth rates; both are endowed with coralloid root nodules in which atmospheric nitrogen is fixed symbiotically (Lawrence *et al.* 1967, Lawrence 1958). The Dryas, capable only of horizontal growth, forms rapidly enlarging disc-shaped clones (Fig. 2B, E) that soon coalesce to form a continuous blanket (Fig. 2C) over the landscape in many places. While that is going on the alder becomes established in open areas where there is yet no Dryas mat (Fig. 2F), and in the following decade forms a nearly continuous thicket (Fig. 2G); subsequently the Dryas dies from shading. The alder can become established over a longer period even beneath a continuous willow canopy, but it seems unable to establish new seedlings beneath its own canopy or on the forest floor beneath a cottonwood or conifer canopy; again, this fact has not been adequately emphasized in the literature. Both Dryas and alder have enormous influence on the appearance of the landscape as may be seen in Figure 2, and on the lives of their associated organisms (Fig. 3), as has been described by Lawrence (1958). Each one either kills off the plants beneath it, or else stimulates them to very rapid growth. The stimulation can result from digestion of the protein-rich leaves of the nitrogen fixers by fungi to liberate nitrogen in available forms. In addition, Bierhorst (1971b: 646) has observed that micorrhizal fungi from one plant incapable of fixing nitrogen can penetrate root nodules of an adjacent symbiotic nitrogen fixer to obtain nitrogen compounds more directly.

By the time 50 years have passed since melting of the ice, a dense alder thicket up to 10 m (33 ft) tall had developed at Muir Point (Fig. 2H,I) from which have emerged the same cottonwood trees that became established soon after ice recession, but which could not grow erect, at some places for over 40 years, until the alders provided them with adequate amounts of nitrogen for rapid erect growth. Thus the "law of succession" in which each stage is supposed "to prepare the way for the next stage, and thereby bring about its own elimination", is turned topsy-turvy, for in this case the pioneer cottonwoods rise above the succeeding alders and kill them by shading. At Muir Point by surface age 96 years, as Noble and Sandgren (1976) have recently shown, a dense vegetation has developed with varied flora consisting of 126 recognizably distinct taxa of vascular plants and lichens. Sprague (1960) had already found in 1952 at surface age 72 years, an abundance of parasitic and saprophytic fungi at this site including a number of mushrooms, one forming a fairy ring.

The later stages of development of vegetation and soil on Neoglacial till farther down the bay will not be dealt with here; they have been described by Cooper (1939), Crocker and Major (1955), Lawrence (1958), Decker and Ugolini (1966), and

Reiners *et al.* (1971). Let us, instead, follow in detail changes at a given site over a period of 88 years following ice recession.

## THE PERMANENT QUADRAT STUDIES

When Cooper first visited Glacier Bay in 1916 he established nine permanent plots, each one meter square, three on each of three surfaces of known age: 17, 24, and 37 years (Cooper 1923) since glacial recession where John Muir (1895) had sketched the positions of ice fronts in 1879, and Reid (1896) had mapped them in 1892, and Gilbert (1906) in 1899. One of these plots has been lost (destroyed by wave erosion before 1921); the other eight have been remapped and rephotographed eight times between 1916 and 1972, four times by Cooper in 1916, 1921, 1929, and 1935, and the rest by myself, beginning in 1941. These permanent plots now have the longest history of observation in Alaska, and may be the oldest permanent plots in the world, on terrain of known age following glacial recession.

*Rationale for establishing the permanent plots.*--In Cooper's words (1923: 355-365) "We are fortunate, here at Glacier Bay in having a most unusual opportunity to apply the method of the permanent quadrat, in the use of which we obtain accurate, unimpeachable data as to the movements and activities of the plant population of small areas typical to the whole." He emphasized "the unique advantage of this region for exact successional study; the rapidity of vegetational development, and especially the known history of glacial behavior extending back a century and a quarter." Cooper was referring to Vancouver's visit and his map of the mouth of the bay in 1794 (see Fig. 1), when the terminal face of the ice had receded 10 km (6 mi) from its maximum extent at the mouth of the bay, and subsequent maps by geologists and others showing the location of the ice margins in different years. He continued: "It is thus possible, through a study of localities of known subaerial age, to determine the net results of vegetational activity in a given period of years, and to make comparisons between areas of different lengths of history. Moreover, because of the rapidity of vegetational change, it is possible to watch the course of succession from year to year--actually to observe the development of the climax forest from pioneers to spruce and hemlock, almost complete within the bounds of a single lifetime."

*Enlargement of scope envisioned.*--Cooper considered the size of his plots adequate when he established them because of the small size of the plants. But he soon realized that they were too small. He wrote in 1923: "My study of permanent quadrats has been carried on, up to the present [1916 & 1921] upon a rather small scale, and yet results solidly grounded and of distinct value have already been obtained from it. It is my hope in the continuation of the investigation greatly to enlarge its scope." In his second trip in 1921 he actually enlarged one of the plots (#2) because the single Dryas plant had extended to fill the original square meter and far beyond, expanding its cover "over 1000%" in five years. But in the two subsequent research trips of 1929 and 1935 he became more interested in the glacial history, and the contribution which could be made by a study of the distribution and identification of the fossil stumps that occur in so many places along the shore north from the mouth of the bay to the head of Muir Inlet (Cooper 1937). Furthermore, he found that as the plant cover of these small plots increased in density of numbers, diversity of species, and complexity of stature, from a sparse, nearly two-dimensional film of mosses, or of scattered seedling willow herbs *(Epilobium latifolium)*, or alpine avens *(Dryas drummondii)* mats, or tufts of young scouring rush *(Equisetum variegatum)*, or creeping willow shrubs *(Salix* spp.), the time required to rechart and rephotograph the eight surviving plots (Plot #9 had been washed away by waves), was all the time he could afford. In those days, boats had to be chartered out of Juneau or beyond at increasingly higher daily rates. In subsequent trips beginning in 1941 I have continued the study of these plots and have conducted a number of other studies, but I have added only one plot, also a single square meter, in the isolation of Johns Hopkins Inlet near Tyeen Glacier 22 km (13 mi) southwest of Cooper Plot #1.

*Description of the study sites.*--Cooper described the location of his permanent plots in great detail, because, as he pointed out: "Since my own activities in Glacier Bay sooner or later must cease, and since a study of such permanent areas grows continually more valuable with increasing time, it is advisable to put on record the exact position and means of location of each quadrat, with the hope that some future visitor may carry on the work." I shall quote an example of his description for the area I discuss here in detail.

"*Station 26* (quadrats 1-2-3) is on the northeast shore of Reid Inlet [now considered the upper part of Glacier Bay proper], opposite the center of Russell Island, and just southeast of a rather extensive alluvial fan. A short gravel spit, visible only at half-tide or lower, forms a small cove [a circular ice-block pit now called "Teacup Harbor"] protected from ice, with good anchorage, opening southwestward. ... Go ashore on north side of cove; go north a few paces to a conspicuous dark glacially smoothed boulder 8 by 12 feet and 5 feet high, marked on opposite sides and top with white crosses." The paint was nearly invisible by 1941 so I repainted and added a white marble capstone on my first visit that year (Fig. 3A)

"Quadrat 1. From this boulder go north 37° east, magnetic bearing, 43 yards, to cairn 3 feet high, at northeast corner of quadrat. This is marked by stones at corners with white stripes bordered with black to show direction of bounding strips which run N. S. E. W. Station for oblique photograph is 6 feet from center of quadrat and marked by white cross on black ground." On a later visit he installed steel rods as corner markers. These instructions have led me without difficulty to Plot #1 in 1941 and subsequent years, but relocating most of the other plots would have become impossible if I had not at each visit photographed from special vantage points toward each plot and away from each plot. In 1972 a metal detector was needed to relocate the iron corner rods at one plot where they were completely submerged by Dryas mat. In that year, with the help of Park Service Naturalist Bruce Paige, I installed a pair of durable new markers near each of the plots with the plot midway between them to help insure the terms of Cooper's wish for their long continued relocation and study.

*History of Cooper Plot #1.*--I shall trace here briefly the changes that we have observed since 1916 in only this one plot, partly for lack of space and time, but mainly because it is the most accessible, the most easily relocated, one of the three on the oldest surface (now nearly a century) and it lies on a nearly level surface (slope angle 12°). Inspection of Figure 3 (top) shows the front of the Grand Pacific Glacier extending northwest

from Russell Island as it looked to John Muir in the autumn of 1879 when he first saw it. It was at the ice edge of that year that Cooper established his Plot #1 in 1916. By then the glacial front had receded 23 km (14 mi) up to Tarr Inlet to the Canadian border (Fig. 1). However, the developmental history of this plot's vegetation is atypical in that we know of only a few seedling Dryas plants that have been seen on it, and these did not survive long. Cooper's 1929 chart (1931:74, Fig. 3) shows an area reputedly occupied by Dryas, but in a later article (1939: 147) he indicated that it was actually a new mat-forming moss, wrongly recorded on the published 1929 chart as "Dryas". In 1916, when first studied (Cooper 1931: 74), it had about 30% cover of *Rhacomitrium* moss mats, 5 well-established prostrate shrub willows (4 *Salix barclayi*, 1 *S. arctica*, 2 Carex sedges, nearly a hundred scouring rush tufts *(Equisetum variegatum)*, about 34 willow seedlings (mostly *S. barclayi*), and a tiny tuft of *Stereocaulon* lichen. Changes over the next 19 years included increase in established willows to 14 with gradual increase in height of stems, but still less than 0.3 m (1 ft) tall. Carex sedges increased in numbers and the scouring rush held its own, but over half of the plot area was still bare in 1935 (Cooper 1939: 142, Fig. 7). Progress from 1941 to 1967 can be seen at a glance in Figure 3 both for the area (Cooper's Station 26) as a whole (A, C, E) and within his Plot #1 (B, D, F). Much bare gravel was still evident in 1941, 62 years after glacial recession. No alder shrubs (*Alnus crispa* subsp. *sinuata*) were yet established either in 1941 or 1949, and the nearest fruiting alder that year was 37 m (120 ft) away and 2.4 m (8 ft) tall. The nearest tree species noted were a Sitka spruce *(Picea sitchensis)* 13.7 m (45 ft) away and 0.6 m (2 ft) tall, and a black cottonwood *(Populus balsamifera* subsp. *trichocarpa)* 12.2 m (40 ft) away and 1.8 m (6 ft) tall. But by 1955 there was one alder established within the plot near the closer edge; it was in its third or fourth year of growth since germination, 0.53 m (21 in) tall, and its corrugated leaves are seen near the center of the photo (Fig. 3D); it had grown 0.43 m (17 in) taller in that season, 81% of its whole height. There were numerous alder seedlings but these all died later from shading by the rapid growth of this first established alder. A soapberry shrub *(Shepherdia canadensis)* rooted outside the far side of the plot spread its branches over half the plot but its maximum attainable height is only about a meter here. Both these shrubs have nodulated roots, and their star mold symbionts fix atmospheric nitrogen, accounting for their rapid increase in size. Furthermore, the nitrogen in the amino acids and proteins in their fallen leaves incorporated in the soil and perhaps direct transport of nitrogen compounds via mycorrhizal fungus threads have stimulated the formerly prostrate willows to send up erect shoots in that year 0.3 m (12 in). By surface age 88 years (Fig. 3E, F) the alder canopy over the plot was 4.6 m (15 ft) tall and provided a 98% cover; all the willows and the soapberry had died because they were incapable of growing as fast and tall as the alder. All the *Rhacomitrium* moss was dead beneath the dense alder leaf litter. Numerous shinleaf herbs *(Pyrola asarifolia)* had become established and were thriving, some even flowering. The scouring rushes *(Equisetum variegatum)* were thriving in spite of the dense shade and had taken on a deep bluegreen color, but bore no spore clusters (strobili). A cottonwood tree crown similar to that in Fig. 3E, right of center, stimulated to rapid growth by the alder leaf litter had surpassed the alder canopy, and had developed a trunk 7.6 cm (3 in) in diameter; it stood only 3.2 m (10.5 ft) outside the plot and must have been established as a seedling many years before and could have persisted unnoticed as a yellowish sickly nitrogen-starved prostrate individual for over 40 years. At the time of my most recent visit to the plot in August 1972 at surface age 93 years, the number of shinleaf plants had decreased markedly since 1968, probably due to shading and the alder leaf fall, which had accumulated a rich brown organic layer 8.9 cm (3.5 in) deep on top of the pebble pavement of the mineral substratum. The larger fragments of alder twig litter and the bases of the living alder stems were covered with moss. These mosses, the few remaining shinleaf plants, and the numerous wispy blue-green stems of the scouring rush, still without spore clusters, formed the only visible green below the dense alder canopy. There were many tiny fleshy fruiting bodies of ascomycetous fungi digesting the fallen alder twigs and leaves. Since it was no longer practicable to photograph the plots from above, I began in 1967 to photograph upward from the plot center with a fisheye lens camera to record changes in canopy cover.

## SECONDARY SUCCESSION AT LITUYA BAY ON PARTLY ERODED NEOGLACIAL TILL FOLLOWING DESTRUCTION OF FOREST AND PARTIAL REMOVAL OF THE SOIL BY GIANT WAVES

*Lituya Bay and its Neoglacial and giant wave history.*--This T-shaped bay (Fig. 4) was "discovered", mapped, and named "Port des Francais" by La Pérouse in July 1786 (1799). Indian fishing villages were then on the shores near the mouth of the bay. He and his crews in two vessels stayed there about a month. His excellent map of the whole bay is reproduced in Post and Streveler (1976: 113, Fig. 2). It shows that the termini of Lituya and North Crillon glaciers which lie at the heads of the bay in the transverse trench of the Fairweather Fault, had receded then farther than their present positions by about 6 km (4 mi) and 2.8 km (1 3/4 mi). Thus recession of Neoglacial ice began earlier than at Glacier Bay, probably by as much as 200 years, or about A.D. 1550 (Mark Noble, personal communication 1976, based on tree cores). The general glacial history has been worked out by Goldthwait, McKellar and Cronk (1963). The main reach of the bay extends northeast about 12.1 km (7 1/2 mi) from the mouth, and contains a single central island named Cenotaph by La Pérouse. The western slope of the Fairweather Range rises northeastward abruptly within 3.2 km (2 mi) of the fault trench to elevations of over 1829 m (6000 ft). This steep bare bedrock slope is heavily fractured and it is easy to visualize how parts of it could break off, especially at times of earthquake, and roar into the bay, setting up giant waves. Fortunately, the existence of such waves had been surmised, and a careful study of their effects had been begun by Don J. Miller in 1952, and dates of earlier giant waves had been worked out in 1952-53 by studying tree cross-sections from along the wave trimlines. The physiographic accidents occurred in 1853 or 54, about 1874, possibly in 1899, and in 1936 perhaps by some different mechanism. The most recent wave was on July 9, 1958, induced by an earthquake with horizontal slipping along the Fairweather Fault (Goldthwait personal communication 1973). This history has been beautifully documented and presented by Miller (1960). Of the three fishing boats in the bay at the time, the occupants of two survived to provide eyewitness accounts. The most recent wave seems to have been larger than the others, for it demolished the forest up to and beyond most of the earlier wave trimlines; only a portion of the forest grown up since the old 1854 wave survives as a narrow strip on the mainland




FIGURE 3. Vegetational development, primary succession on glacial till over an 88-year span at Cooper Station 26 (top photo, and A, C, E), and on his nearby Point #1 (B. D. F) following recession of Grand Pacific Glacier.

northeast of Cenotaph Island (Fig. 4, and Fig. 5B at left of center). The more numerous deciduous tree crowns of black cottonwood distinguish it from the older more exclusively conifer forest above. The cliff face from which the rockslide broke out is marked on the map (Fig. 4) by the stippled area, and in Figure 5, top photo, copied from Miller (1960), by the letter "r", and in the Figure 5A where the M-shaped snow area appropriately commemorates the name of Don J. Miller who first correctly identified giant waves as the cause of the forest destruction. The 1958 rockslide started from an elevation of about 914 m (3000 ft), struck the lower part of Lituya Glacier, sheared off about 400 m (1300 ft) of its tip, and splashed up the opposite wall of the fault trench valley to an elevation of 524 m (1720 ft)! Based on measured elevations along the forest trimline the water wave ascended with destructive force as much as 207 m (680 ft) on the south valley wall near the head of the main bay and then its crest gradually diminished down the bay, but it was still able to destroy the forest up to an elevation of 9.14 to 10.67 m (30-35 ft) near the mouth of the bay (Miller 1960: 58, Fig. 15). In the lower relatively level areas the salt water invaded the forest without destroying it but inflicted salt damage that became visible later that growing season.

*Eyewitness accounts*.--The captains of both fishing boats that survived first noticed violent vibrations about quarter past 10 local time (about sunset). Mr. and Mrs. Swanson had anchored their 40-ft boat, the *Badger* in a cove of the bay just north of the entrance. About a minute later Swanson looked toward the head of the bay past the north end of Cenotaph Island and saw that Lituya Glacier had risen up in the air, jumping and shaking, and had moved forward into view. Then the glacier dropped down out of sight and a big wall of water came over the north point at the head of the bay, crossed over and swept high up the opposite shore, then sped down the bay past Cenotaph Island. The wave reached the *Badger*, still at anchor, about 4 minutes after it was first sighted. The *Badger* was lifted by the wave and carried like a surf board, stern first, across the north spit. Swanson looked down on the trees growing on the spit from a height he estimated to be about 24 m (80 ft) above the tree tops. The wave crest broke just outside the spit and the boat hit bottom and foundered some distance from shore. The Swansons abandoned their boat in a small skiff and were picked up by another fishing boat about two hours later. The narrator of the other account, Mr. Ulrich, and his son, in their boat *Edrie*, were anchored in the bay near the south shore about 2 km (1.2 mi) from the mouth. He promptly started his engine when he felt the earthquake vibrations, and about 2 1/2 minutes later he heard a deafening crash from the head of the bay. The anchor chain snapped as the wave 15-23 m (50-75 ft) high approached, but the boat rode it out. After the giant wave passed the water returned to normal level but was very turbulent for about a half hour with much sloshing about from shore to shore with steep sharp waves up to 6 m (20 ft) high. This perhaps accounts for the parallel pair of wave-rows of logs along the denuded slopes northward from Cenotaph Island as noted by Miller (1960: 58, Fig. 15). Within an hour of the passage of the giant wave Ulrich noted that the bay near shore was filled with floating logs, but the *Edrie* passed safely out of the entrance of the bay by about 11:00 p.m.

*The secondary succession*.--We may define *secondary* succession as the re-development of ecosystems following occurrences which destroy the aerial portions but not all the soil and its living contents. Unfortunately, the opportunity which this geomorphic event provided for study of secondary succession was not taken advantage of until several years had passed. Streveler had made some preliminary observations (personal communication). But our 1973 visit of June 19-25 on the Park Service motor vessel *Nunatak* with Captain James Sanders, was an initial attempt to collect some more comprehensive information. We are grateful to Park Service Superintendent Robert E. Howe for providing the necessary transportation. Field assistance was provided by Professor Edward J. Cushing. Our major objective was to observe rates of vegetational redevelopment and the numbers and diversity of the plants involved in the *secondary* succession here for comparison with those of the *primary* succession on deglaciated surfaces already studied as mentioned above at nearby Glacier Bay. We selected an area within the 1958 wave-denuded belt along the south mainland shore directly south of Cenotaph Island (circled dot in Fig. 4, and Fig. 5 top photo) because it was convenient to the anchorage Captain Sanders had selected for the *Nunatak*. Here we found a denser stand of woody vegetation grown up within 15 years after the 1958 giant wave destruction of the previous forest cover than had developed at Glacier Bay on a surface of raw glacial till in 50 to 100 years. Not only did we study the new vegetation on the partly wave-eroded glacial till, but we examined the heaps of logs that had been assembled in giant piles and wave-rows as seen in Figure 5C and E. On the logs close to the bay shore there were only lichens, but on the south slope of the bay, near our study plot where the major wave-row of logs was piled 4.6 m (15 ft) deep against the wave trimline, young hemlock trees, which favor logs for seedling establishment, were already about 2 m (7 ft) tall. They were rooted on the crest of the wave-row, perched high above the mineral soil and presumably will be gradually lowered to the soil surface as the logs decay.

*The permanent plot*.--A large circular permanent plot of 5.18 m (17 ft) radius and 82.32 sq m (751 sq ft) was established on a level terrace of the mainland south shore (Fig. 4 and Fig. 5 top photo) the data presented below are given in terms of an area of 100 $m^2$ (1076 $ft^2$). The plot is centered on a marked dominant red alder tree *(Alnus oregona)*. It is situated about 400 m (1/4 mi) northeast of a pond (Fig. 4). This tree was estimated to be about 11.9 m (39 ft) tall, 14.6 cm (5 3/4 in) dbh (diameter at breast height) and about 12 years old. It is marked by a 1.32 m (52 in) length of galvanized steel tubing hung on the magnetic west side of the trunk with a loop of insulated copper wire coiled to allow for trunk growth. Three boulders, the largest 91 cm (3 ft) long, lie in a cluster at the west base of this tree. A marker tube 38 cm (15 in) long was driven into the soil at the magnetic S end of this largest boulder so that its top protruded 14.8 cm (5 7/8 in) above the mineral soil. Another marker tube 1.32 m long lies horizontally southward on the forest floor attached at one end to this driven marker. Both the hanging and the horizontal tubes were appropriately labeled in soft pencil, a type of label which, in Minnesota, is still legible after 20 years.

The earliest stage, beginning with willows and black cottonwoods seems to have been similar to that at Glacier Bay, but the date of the giant wave, July 9th, 1958 seems to have been too late in the season for dispersal and establishment of

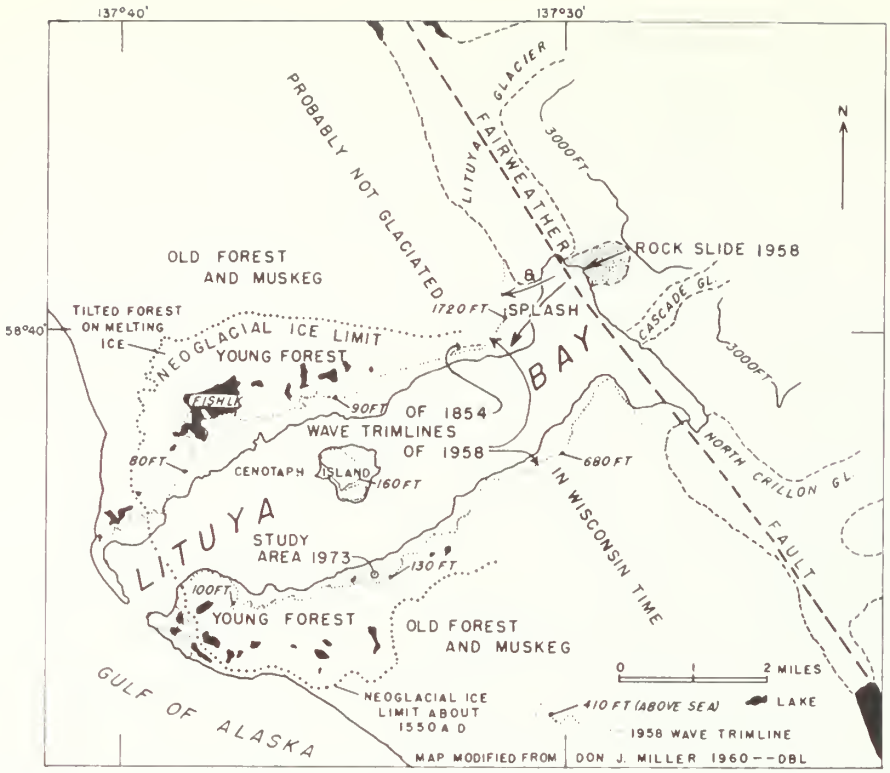



FIGURE 4. Map of Lituya Bay which had been nearly emptied of glacier ice by 1786 when La Perouse visited and mapped it. Its shores have been partly denuded by a series of giant waves, the most recent on July 9, 1958, initiated by earthquake and rockslide (strippled) falling 914 m (3000 ft). The wave splashed up to a maximum evelation of 524 m (1720 ft) and swept away forest but not all soil along the lower banks as may be seen in the top photo of Figure 5 taken a month after the event. Subsequent secondary succession on the denuded surfaces has been extremely rapid and vigorous, dominated on the south shore by tree alders grown 12 m (40 ft) tall in 15 yrs. Neoglacial maximum here was 200 years earlier than in Glacier Bay, but some of that ice is still melting from beneath a tilting spruce and hemlock forest north of Fish Lake.

these species that first year because their seeds ripen early and are very short-lived, but seeds of alders, spruce, and hemlock ripen late, so may have entered in the autumn of the same year. We have seen no evidence that Dryas has been involved at all at Lituya Bay. Although the seeds of both Sitka alder *(Alnus crispa* subsp. *sinuata)* a shrub, and red alder *(Alnus oregona)*, a tree, very likely entered the plot area in autumn of 1958, they could not have germinated until the following spring, 1959, because they needed a long cold moist period to break dormancy. Densities and heights of these various woody plants reveal important facts about the developing community, but it is unfortunate that some similar data were not collected a decade earlier. The red alder trees occurred in the plot at a density of 32 trunks per 100 $m^2$, and were 8.25 cm (3.25 in) average dbh, and up to 12 m (40 ft) tall. The capacity of this symbiotic nitrogen-fixing tree for height growth beyond that of any of its associates has resulted in deep shade below its canopy, with weakening and death of the shorter shrubs including the Sitka alder which occurred at a density of 8 shrubs per 100 $m^2$ with 2-4 per cluster, 3-5 m (10-16 ft) height and 1.5-4 cm (0.6-1.57 in) dbh. The remains of the dying and dead shrubs were still present (Fig. 5F); the only thrifty Sitka alder was in a slight canopy opening nearby. There were only 5 black cottonwoods per 100 $m^2$, averaging 3.8 m (12.5 ft) tall and 2.5 cm (1 in) dbh; most had been severely debarked by porcupines above the 1.5 m (5 ft) level presumably above the snow blanket during the previous two winters and only one seemed healthy enough to survive. But beneath the dense shade of the tree alders was a thriving population of young evergreen conifers (Fig. 5F, a photo 100 m east of the plot). There were Sitka spruces (*Picea sitchensis*) 85 per 100 $m^2$, averaging 65 cm (2.14 ft) tall and 9.7 years old (range 6-14 yrs) based on branch whorl counts. Western hemlocks occurred at a density of 18 per 100 $m^2$ averaging 37 cm (1.12 ft) tall. Associated with these most abundant woody plants were 5 other shrubs, 12 herbaceous seed plants and 5 mosses. Two of the plant species adjacent to the plot, devils club shrub *(Echinopanax horridum)* and western skunk-cabbage *(Lysochiton americanum)* occur here though I have never seen them on the deglaciated Neoglacial terrain at Glacier Bay. I believe they survived here through forest destruction and brief immersion in salt water as underground roots and stems which regenerated sprouts.

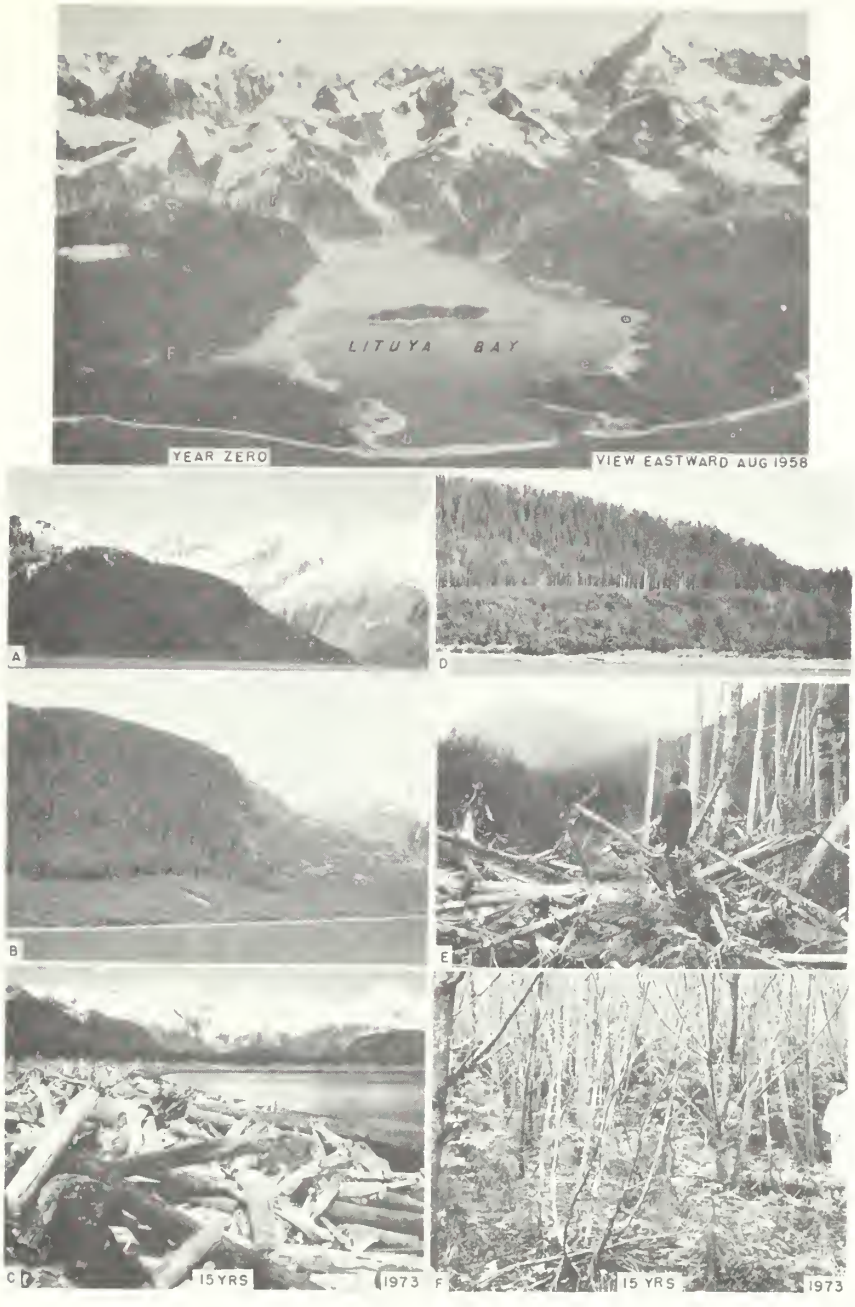



FIGURE 5. Scenes at Lituya Bay. Top, 1958, a month after the giant wave; others late June 1973, 15 yrs later. A-C on left side; D-F on right side. C and E show forest wreckage, F new red alder forest with trees 12 m (40 ft) tall, with dead Sitka alder shrub in foreground and thriving understory of Sitka spruce and western hemlock, 100 m east of Plot #73-1. Top photo Miller (1960).

This rapid development of the community, with accumulation of 4.5 cm (1 3/4 in) of organic matter, mostly alder leaf litter, on the soil but not on the boulders, has come about mainly because of the close proximity of Negolacial and pre-Wisconsin refugium forests containing the red alder, Sitka spruce and western hemlock. The accumulation of great biomass made possible by nitrogen fixed by the alder root nodule symbionts and inherent potential for attaining tree stature seems to be very large compared to that of the comparable stages in Sitka alder shrub communities 50 to 100 years following glacial recession at Glacier Bay just 60 km (37 mi) to the east. Measurements of biomass have not been done either at Glacier Bay or at Lituya Bay. Such studies would provide important contributions to our knowledge of the rate of primary and secondary ecosystem development in this maritime subarctic environment.

## LITERATURE CITED

BECKING, J. H. 1970. Plant-endophyte symbiosis in non-leguminous plants. Plant and Soil 32:611-654.

BIERHORST, D. W. 1971a. Morphology of vascular plants. New York: Macmillan.

BIERHORST, D. W. 1971b. Morphology and anatomy of new species of Schizaea and Actinostachys. Amer. J. Bot. 58:634-648.

BOHN, D. 1967. Glacier Bay: the land and the silence. San Francisco: Sierra Club. 165 p.

COOKE, W. B. and D. B. LAWRENCE. 1959. Soil mould fungi isolated from recently glaciated soils in south-eastern Alaska. J. Ecol. 47:529-549.
COOPER, W. S. 1923. The recent ecological history of Glacier Bay, Alaska. Ecology 4: 93-128, 223-246, 355-365.
COOPER, W. S. 1931. A third expedition to Glacier Bay, Alaska. Ecology 12:61-95.
COOPER, W. S. 1937. The problem of Glacier Bay, Alaska: A study of glacier variations. Geog. Rev. 27:37-62.
COOPER, W. S. 1939. A fourth expedition to Glacier Bay, Alaska. Ecology 20:130-155.
COOPER, W. S. 1942. An isolated colony of plants on a glacier-clad mountain. Bull. Torrey Bot. Club 69:429-433.
COOPER, W. S. 1956. A contribution to the history of the Glacier Bay National Monument. Minneapolis: Unviersity Minnesota, Dept. Botany. 36 p.
CROCKER, R. L. and J. MAJOR. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J. Ecol. 43:427-448.
DECKER, H. F. 1966. Pages 73-95 *In:* Goldthwait et al. (1966).
FIELD, W. O. 1947. Glacier recession in Muir Inlet, Glacier Bay, Alaska. Geog. Rev. 37:369-399.
FIELD, W. O., editor. 1975. Mountain glaciers of the Northern Hemisphere. 2 vols + atlas. Hanover, NH: US Army Corps of Engineers. Cold Regions Research and Engineering Laboratory.
GILBERT, G. K. 1904. Glacier Bay. Pages 16-39 *In:* Glaciers and glaciation. Vol. III of Alaska. Harriman Alaska Expedition. New York: Doubleday, Page. 4 vols.
GOLDTHWAIT, R. P., F. LOEWE, F. C. UGOLINI, H. F. DECKER, D. M. DELONG, M. B. TRAUTMAN, E. E. GOOD, T. R. MERRELL III, E. D. RUDOLPH. (A. Mirsky, editor) 1966. Soil development and ecological succession in a deglaciated area of Muir Inlet, southeast Alaska. Ohio State Univsty Inst. of Polar Studies, Report No. 20. 167 p.GOLDTHWAIT, R. P., I. C. MCKELLAR, and C. CRONK. 1963. Fluctuations of Crillon Glacier system, southeast Alaska. Ohio State Univ. Inst. Polar Studies, Contrib. No. 35. 11 p + 5 figs. (mimeo). Originally publ. in IUGG Internat. Assoc. Sci. Hydrol. Bull. 8, No. 2, pp 62-74.
GRIGGS, R. F. 1933. The colonization of the Katmai ash, a new and inorganic "soil." Amer. J. Bot. 20:92-113.
GRIGGS, R. F. and D. READY. 1934. Growth of liverworts from Katmai in nitrogen-free media. Amer. J. Bot. 21:265-277.
INGOLD, R. S. and A. T. NAVARRE. 1952. "Polluted" water from the leaching of igneous rock. Science 116:595-596.
LA PÉROUSE, J. F. A. 1799. A voyge 'round the world 1785-1788. Transl. from the French. London: 3 vols and folio.
LAWRENCE, D. B. 1958. Glaciers and vegetation in southeastern Alaska. Amer. Scientist 46: 89-122.
LAWRENCE, D. B., R. E. SCHOENIKE, A. QUISPEL, and G. BOND. 1967. The role of *Dryas drummondii* in vegetation development following ice recession at Glacier Bay, Alaska, with special reference to its nitrogen fixation by root nodules. J. Ecol. 55:793-813.
MILLER, D. J. 1960. Giant waves in Lituya Bay, Alaska. USGS Prof. Paper 354-C. Washington, D. C.: US Govt. Ptg. Off. pp i-iii, 51-86, 7 figs., 9 plates.
MUIR, J. 1895. The discovery of Glacier Bay. The Century Magazine 50, N.S. 28:234-247.
NOBLE, M., and C. D. SANDGREN. 1976. A floristic survey of Muir Point, Glacier Bay National Monument, Alaska. Bull. Torrey Bot. Club 103:132-136.
POST, A. and G. STREVELER. 1976. The tilted forest: glaciological-geologic implications of vegetated Neoglacial ice at Lituya Bay, Alaska. Quaternary Research 6:111-117.
REID, H. F. 1896. Glacier Bay and its glaciers. USGS 16th Annual Rept. 1894-1895.
REINERS, W. A., I. A. WORLEY, and D. B. LAWRENCE. 1971. Plant diversity in a chronosequence at Glacier Bay, Alaska. Ecology 52:55-69.
RIDLEY, H. N. 1930. The dispersal of plants throughout the world. Ashford, Kent, England: L. Reeve.
SCHOENIKE, R. E. 1958. Influence of mountain avens *(Dryas drummondii)* on growth of young cottonwoods *(Populus trichocarpa)* at Glacier Bay, Alaska. Minnesota Acad. Sci. Proc. 25-26:55-58.
SINGH, R. N. 1960. Role of blue-green algae in nitrogen economy of Indian agriculture. New Delhi: Indian Council Agric. Res.
SPRAGUE, R., and D. B. LAWRENCE. 1960. The fungi on deglaciated Alaskan terrain of known age. (Part III) Washington State Univ. (Pullman) Res. Studies 28(1):1-20.
STEWART, W. D. P. 1966. Nitrogen fixation in plants. London:Athlone.
STREVELER, G. P., and B. B. PAIGE. 1971. The history of Glacier Bay National Monument, Alaska: a survey of past research and suggestions for the future. USDI National Park Service, Glacier Bay National Monument. 89 p.
UGOLINI, F. C. 1966. Soils. Pages 29-58 *In:* Goldthwait et al. (1966).
USDI NATIONAL PARK SERVICE (no date) Glacier Bay (informational folder with map in color).
WATTS, W. A. 1967. Late-glacial plant macrofossils from Minnesota. Pages 89-97 *In:* Quaternary Paleoecology. Edited by H. W. Wright and E. J. Cushing. New Haven, CT: Yale University.
WORLEY, I. A. 1973. The "Black Crust" phenomenon in upper Glacier Bay, Alaska. Northwest Science 47:20-29.

# SEEDS IN SOILS OF FORMER EVERGLADES FARMLANDS

John Ewel and Louis Conde[1]

## INTRODUCTION

The Everglades National Park recently completed purchase of a large block of private holdings surrounded by Park lands. About 4000 ha of the purchased lands had been farmed, but will now revert to natural vegetation. Park managers are faced with a variety of questions: What kinds of ecosystems will appear on these lands? Will exotic plants be important, conspicuous components of the flora? Are seeds from the surrounding mature ecosystems getting into the abandoned farmlands? Do the species found on the farmlands pose a threat to the native, mature ecosystems which surround them? Can the new vegetation be manipulated by controlling the presence of seed sources, either through addition or extermination? Partial answers to some of these questions require knowledge of the kinds and amounts of seed present in the various successional and mature ecosystems. This study reports our findings of an inventory of the seed content of surface soils of five successional and two mature Everglades Park ecosystems. Our work was supported, in part, by U.S.F.S., Southeast Forest Exp. Station, Research Agreement 18-492.

An excellent review of the floristic role of seeds in the soil, as well as the problems involved in assaying the viable seed content of soil, was compiled by Major & Pyott (1966). They describe four main problems related to such studies: aggregation of propagules near mother plants; vegetative reproduction; sampling unknowns (depth, area, and number), and selective germination caused by the particular conditions to which the samples are subjected. In our study, conditions (well-watered flats exposed to full sun) clearly favored germination of weedy species and those which did not require partial shade or special pretreatment such as passage through an animal's digestive tract.

## SITES AND METHODS

The recently purchased farmlands are collectively referred to as the Hole-in-the-Donut because they constitute an island of former farmland completely surrounded by mature plant communities. Some parts of the Hole-in-the-Donut have been unfarmed for about 35 years, while others were farmed as recently as June 1975; most of the land has been abandoned for less than five years. About 90 percent of the Hole-in-the-Donut had been wet prairie or sawgrass glade prior to farming, while most of the remainder was pineland (Hilsenbeck 1976). Fire is important in the maintenance of both the prairie-sawgrass communities and the pinelands. The vegetation, soils, hydrology, and role of fire in these ecosystems have been described by Harshberger (1914), Davis (1943), Egler (1952), Robertson (1953), Craighead (1971), and Alexander & Crook (1973). The wet prairie and sawgrass (*Cladium jamaicensis*, a sedge) communities occupy marl soils which cover the limestone bedrock to a depth of about 10 cm. These herbaceous communities are periodically flooded between June and November. The pine community (*Pinus elliottii* var. *densa*) occupies slightly higher ground along the northern rim of the Hole-in-the-Donut; the shallow soils which cover the limestone there are loam rather than fine-textured marl and are not usually flooded during the wet season.

Everglades ecosystems are prepared for winter vegetable farming by rock plowing. This process breaks up the limestone to a depth of about 20 cm and the crushed limestone is mixed with the overlying marl; a bedding plow is then used to create alternating beds and furrows. Reclamation efforts by park managers have concentrated on mowing the successional vegetation, followed by twice disking the land to eliminate the beds and furrows. Various combinations of mowing and fire are being studied as possible tools to keep the vegetation in an early successional stage until more is learned about its probable course of succession. Without fire or mowing it appears that rock-plowed prairie and sawgrass communities develop into forests after farming stops. These new forests contain numerous tree species, but are often dominated by *Schinus terebinthifolius*, an exotic tree considered by most to be an undesirable component of the Park flora. The second-growth vegetation in the Hole-in-the-Donut and its possible management by various combinations of mowing and burning are currently the subject of a detailed study being conducted by Park personnel (see Hilsenbeck 1976 and Res. Mgt. Staff 1976).

The seven study sites were all located in, or contiguous to, the Hole-in-the-Donut. The sample areas were all within 7 km of one another and each site except the mature forest had at least one border in common with the most recently abandoned farmlands. The five successional stages of vegetation sampled were:

(i) *New field*: This site was formerly glade vegetation and is flooded from June through November. It had been farmed until June 1975 and was disked in November 1975. The site is contiguous to both the mature glade and the 35-year-old forest.

(ii) 2.5-year-old, burned in June 1975: The original vegetation was glade, near its boundary with pineland. The vegetation on the site was dominated by *Ludwigia erecta* and *L. octovalvis*, which are woody shrubs about 2 m tall. The burn (part of a Park experiment) was spotty and incomplete. The site is located near the middle of the Hole-in-the-Donut, 2.5 km from the mature glade and 4 km from site (iii).

(iii) *2.5-year-old, unburned*: The original vegetation on the site was glade. The vegetation at the time of soil sampling was similar to that of the burned site; it was dominated by the same *Ludwigia* spp. plus *Panicum bartowense*. The site

[1]Botany Department, University of Florida, Gainesville 32611

is located about 3 km from the 17-year-old woodland and 4 km from the burned site.

(iv) *17-year-old woodland:* This site was the only one located on former pinelands and was not subject to wet-season flooding. The dominant plant was *Myrica cerifera* (a native shrub about 5 m tall) but *Schinus* was also found. The site is located in the northwest part of the Hole-in-the-Donut about 3 km from the unburned site and 2.5 km from the burned site.

(v) *35-year-old forest:* This site occupies former glade and prairie. The forest is dominated by the exotic species *Schinus terebinthifolius* and is the oldest successional vegetation available within the Hole-in-the-Donut. Beds and furrows are still evident. The site is contiguous to both the new field and the mature glade.

Two mature ecosystems adjacent to the successional vegetation of the Hole-in-the-Donut were also studied: the first because it represents the original vegetation for most of the study sites, and the second because the successional vegetation seems to be developing into a forest rather than an herbaceous community.

(vi) *Mature glade:* This community consists of a diverse mixture of fire-adapted sedges, grasses, and forbs, and is flooded from June through November. The site is contiguous to both the new field and the 35-year-old forest.

(vii) *Mature forest:* This complex assemblage of more than twenty woody species is typical of the subtropical hammock forests of south Florida. It is rarely subjected to flooding, and fire is not a normal environmental factor involved in its maintenance. It is located at the northeast corner of the Hole-in-the-Donut about 1.5 km from the new field and the 35-year-old forest.

On December 14, 1975 the surface soil (c. 3 cm) was removed from three 50 cm x 50 cm plots, located at 20 m intervals along a transect, at each site. The soil was transported to Gainesville, Florida, where it was stored in covered containers at room temperature until December 24 when each soil sample was spread over a flat of sterilized greenhouse potting sand. The twenty-one flats were assigned to randomly selected locations on an unshaded greenhouse bench and watered daily. The flats were monitored for one year, during which seedlings were counted and harvested at frequent intervals to avoid mortality from crowding. Sample seedlings of each species were transplanted and grown to reproductive stages for identification (except for 19 species, representing <1 percent of the individuals, which have not yet flowered). Identifications were provided by D. Hall, FLAS Herbarium, University of Florida.

## RESULTS AND DISCUSSION

The abundance and site distribution of the species which appeared in the flats are summarized in Table 1. The total sample area of 5.25 $m^2$ yielded approximately 120 species and nearly 33,000 individuals. We suspect, but cannot prove, that four of the species (*Gnaphalium pensylvanicum, Oxalis filipes, Pteris vittata,* and *Conyza canadensis*) are greenhouse contaminants: all except *P. vittata* appeared in the flats from all sites, all are common weeds in and around our greenhouse, and none are conspicuous components of the Hole-in-the-Donut flora. Table 1 does not include a breakdown of the data among the three replicates per site, but in general, replicate samples were floristically and numerically similar, whereas among-site differences were readily apparent, even upon casual observation of the flats.

The 30,000 individuals were very unequally distributed among the 119 species (Fig. 1). Most species were represented by ten or fewer individuals, and more than 90 percent of the species were represented by less than 100 individuals. Some of the seventeen species represented by more than 100 individuals are typical invaders of old fields; they are prolific seed producers and widespread, but are short-lived and unlikely to permanently occupy the former farmlands unless these are subjected to further drastic soil disturbance. Included in this category are genera such as *Amaranthus, Ambrosia,* and *Polygonum.* Their great abundance is typical of newly abandoned farmlands, and they are likely to become less important as succession proceeds. Some of the other species which were extremely abundant, however, are more long-lived and are likely to become semi-permanent components of the successional vegetation, especially if management practices such as mowing and burning arrest succession. Representative of this category are *Baccharis, Ludwigia, Myrica,* and various grasses, including *Panicum bartowense.* These plants are almost certain to be important components of the successional vegetation in the Hole-in-the-Donut and merit special attention from Park managers.

## SEED ABUNDANCE

The numbers of seeds varied greatly among sites (Fig. 2), ranging from thousands per $m^2$ in the younger successional stages to about 500 per $m^2$ in the oldest successional forest and the two mature ecosystems. The 2.5-year-old stand which had been burned six months prior to sampling contained the most seeds: more than 30,000 per $m^2$. Of these, 84 percent were *Ludwigia octovalis + L. erecta* (two species which are inseparable in the early stages of growth). Dominance of a seed flora by very few species is a commonly reported phenomenon (e.g., Kropac 1966, Jansen 1969, Kellman 1970, 1974a).

The numbers of germinated seeds observed in soils from our youngest successional stages (i.e., c. 4500 to 30,000 per $m^2$) are similar to those reported in the literature for agricultural soils, pastures, and very early stages of succession (Kropac 1966, Jensen 1969, Feast & Roberts 1971, Kellman 1974b, Lockett & Roberts 1975). Higher seed densities have been reported in the literature, such as one of Jensen's (1969) samples which yielded 66,800 viable seeds per $m^2$, but these are usually derived from a substantially deeper soil sample than the 3 cm we used in the Everglades. Jensen (1969), for example, sampled to a depth of 20 cm.

Likewise, the lower densities of germinated seed (usually less than 500 per $m^2$) observed in our oldest successional stand and in the two mature ecosystems are consistent with values reported in the literature for old secondary and mature forests (Olmsted & Curtis 1947, Keay 1960 Kellman 1970, Guevara & Gomez-Pompa 1972, Liew 1973, Kellman 1974a, Strickler & Edgerton 1976). The drop in numbers of germinated seeds per unit area from the early stages of succession of the

TABLE 1. Numbers of seedlings harvested from soil samples taken from seven Everglades ecosystems. Each value is a total of three 0.25 $m^2$ samples. Origin: I = indigenous; X = exotic. Weediness: W = weedy or occurring on disturbed sites (Long & Lakela 1971); N = non-weedy according to Long & Lakela.

| Species | | | A | B | C | D | E | F | G |
|---|---|---|---|---|---|---|---|---|---|
| *Acrastichum aureum* L. | I | N | | 1 | | | | 3 | 8 |
| *Alternanthera romosissima (Mart.) Chodat* | I | N | 9 | 9 | 13 | | | | |
| *Amaranthus hybridus* | I | W | 338 | | 1 | 3 | | | |
| *Ambrosia artemisiifolia* L. | I | W | | | 218 | 6 | | | |
| *Ammania coccinea Rottb.* | I | N | 58 | 642 | 18 | | | | |
| *Ammania teres Raf.* | I | N | 165 | | 3 | | 28 | | 1 |
| *Aristida purpurascens Poir.* | I | N | | | | | | 2 | |
| *Ascyrum hypericoides* L. | I | N | | | | | 1 | | |
| *Aster bracei Britt.* | I | N | | | | | | 1 | |
| *Aster dumosus* L. | I | N | | | | | | 1 | |
| *Azolla caroliniana Willd.* | I | N | 1 | 1 | | | | | |
| *Baccharis halimifolia* L. | I | N | | 23 | 1 | 47 | 67 | 8 | 3 |
| *Bacopa monnieri* (L.) *Wettst.* | I | N | 1 | | | | | | |
| *Bidens pilosa* L. | I | W | | | | 35 | | | |
| *Boehmeria drummondiana Wedd.* | I | N | 3 | | | | 3 | | |
| *Borreria laevis (Lam.) Griseb.* | I | N | | | 434 | 225 | | | 1 |
| *Borreria ocimoides (Burm. f) DC.* | I | N | | | 2 | 11 | | | |
| *Centella asiatica* (L.) *Urban* | I | W | | | | | | 2 | |
| *Chamaesyce hypericifolia* (L.) *Millsp.* | I | W | 1 | 1 | 1 | 44 | 4 | 16 | |
| *Chamaesyce opthalmica (Pers.) Burch* | I | W | 2 | 4 | 2 | 26 | 1 | 11 | 2 |
| *Chenopodium album* L. | I | W | 7 | 1 | 1 | | | | |
| *Cissus Sicyoides* L. | I | N | | | | | 1 | | |
| *Colocasia esculentum* (L.) *Schott* | X | W | 2 | | | | | | |
| *Commelina diffusa Burm. f.* | I | N | 1 | 11 | | | | | |
| *Conyza bonariensis* (L.) *Cronq.* | X | W | | 1 | | | | | |
| [1]*Conyza canadensis* (L.) *Cronq.* | I | W | 6 | 6 | 8 | 24 | 8 | 3 | 18 |
| *Conyza parva Cronq.* | I | W | | | | 8 | 1 | | 1 |
| *Cuscuta campestris Yuncker* | I | N | | | | | | 1 | |
| *Cynanchum sp.* | | | | | | 1 | | | |
| *Cynoctonum mitreola* (L.) *Britt.* | I | N | 8 | | | | 4 | | |

| Species | | | A | B | C | D | E | F | G |
|---|---|---|---|---|---|---|---|---|---|
| *Cynoctonum sessilifolium (Walt.) J. F. Gmel.* | I | N | | | | | | 13 | |
| *Cyperus esculentus* L. | I | W | 8 | | 7 | | | | |
| *Cyperus iria* L. | X | W | 3 | 1 | 1 | | | | |
| *Cyperus ochraceus Vahl.* | I | N | 2 | | | | | | |
| *Cyperus polystachyos Rottb.* | I | N | 4 | | 7 | | 4 | | |
| *Cyperus surinamensis Rottb.* | I | N | 6 | 41 | 10 | 4 | | 3 | |
| *Cyperus spp. (max. 7 spp.)* | | | 36 | 1 | 45 | | 1 | | |
| *Dichromena colorata* (L.) *Hitch.* | I | N | | | | | | 1 | |
| *Digitaria adscendens (HBK.) Henr.* | X | W | | | 109 | | | | |
| *Eclipta alba* (L.) *Hassk.* | I | W | 1 | 15 | 3 | | | | |
| *Eleocharis geniculata* (L.) *R. & S.* | I | N | 3 | 1 | 1 | | | | |
| *Eleusine indica* (L.) *Gaertn.* | X | W | 4 | 138 | 13 | 5 | 1 | 15 | |
| *Eragrostis elliottii Wats.* | I | N | | | | | | 13 | |
| *Erechtites hieracifolia* (L.) *Raf.* | I | W | 1 | 1 | 3 | 7 | | 4 | 2 |
| *Erigeron quercifolius Lam.* | I | W | | | | | | 13 | |
| *Erigeron vernus* (L.) *T. & G.* | I | N | | | | | | 6 | |
| *Erysimum cheiranthoides* L. | I | W | | | 1 | | | | |
| *Eugenia sp.* | | | | | | | | | 1 |
| *Eupatorium capillifolium (Lam.) Small* | I | W | | 2 | 1 | 12 | 2 | 1 | 12 |
| *Eupatorium coelestinum* L. | I | N | | | | | | 7 | |
| *Eupatorium leptophyllum DC.* | I | W | 1 | | | 1 | 1 | 7 | |
| *Evolvulus sericeus Sw.* | I | N | | | | | | 3 | |
| *Ficus sp.* | | | | | | | | | 12 |
| *Galium obtusum Bigel.* | I | N | 1 | | | | | | |
| *Geranium carolinianum* L. | I | W | | | | 1 | | | |
| [1]*Gnaphalium pensylvanicum Wil'd.* | I | W | 25 | 49 | 53 | 97 | 86 | 44 | 101 |
| *Gnaphalium spicatum Lam.* | X | W | | 1 | | 5 | | | |
| *Heliotropium polyphyllum Lehm.* | I | N | | | | | | 17 | |
| *Hydrocotyle verticillata Thunb.* | I | N | 1 | | | | | | |
| *Hypoxis juncea Smith* | I | N | | | | | | 2 | |
| *Hyptis alata (Raf.) Shinners* | I | N | | | | | | 1 | |
| *Kosteletzkya virginica* (L.) *Presl ex Gray* | I | N | | | | | 2 | | |

| Species | | | A | B | C | D | E | F | G |
|---|---|---|---|---|---|---|---|---|---|
| *Leucospora multifida (Michx.) Nutt.* | I | W | 9 | | | | | | |
| *Linaria canadensis* (L.) *Dum.* | | | | | 2 | 2 | | | 1 |
| *Ludwigia microcarpa Michx.* | I | N | | 1 | 1 | | | 1 | |
| *Ludwigia octovalvis (Jacq.) Raven and L. erecta* (L.) *Hara* | I | N | 116 | 21498 | 3586 | 307 | 23 | 19 | 2 |
| *Ludwigia peruviana* (L.) *Hara* | I | N | 103 | | | | 34 | | |
| *Lysiloma?* | | | | | | | | | |
| *Lythrum lanceolatum Ell.* | I | N | 55 | | | | | | |
| *Mecardonia montevidensis (Spreng.) Pennell* | I | N | 1 | | | | | | |
| *Medicago lupulina* L. | X | W | | | 2 | | | | |
| *Melanthera angustifolia A. Rich* | I | N | | | | | | 11 | |
| *Melilotus alba Desr.* | X | W | | | 2 | 1 | | | |
| *Mikania scandens* (L.) *Willd.* | I | N | | | | 1 | | 42 | |
| *Mollugo verticillata* L. | I | W | 1 | | | 2 | | | |
| *Myrica cerifera* L. | I | N | | | | 181 | | 1 | 1 |
| [1]*Oxalis filipes Small* | I | W | 61 | 18 | 15 | 200 | 11 | 9 | 96 |
| *Panicum bartowense Scribn. & Merr.* | I | N | 1279 | 1 | 18 | | | | |
| *Panicum tenerum Beyer* | I | N | | | | | | 4 | |
| *Panicum?* | | | | 8 | | | | | |
| *Parthenocissus quinquefolia* (L.) *Planchon* | I | N | 1 | | | | 2 | | |
| *Paspalum conjugatum Bergius* | I | W | | | 2 | | | | 4 |
| *Paspalum setaceum Michx.* | I | N | | | | | | 5 | |
| *Physalis angulata* L. | I | N | | | | 1 | | | |
| *Pluchea purpurascens (Sw.) DC.* | I | N | | | | | 3 | 5 | |
| *Pluchea rosea R.K. Godfrey* | I | W | | | | 2 | | 6 | |
| *Polygonum lapathifolium* L. | X | W | 901 | 3 | | 1 | | | |
| *Portulaca oleracea* L. | I | W | | 6 | 7 | 3 | | | |
| [1]*Pteris vittata* (L.) *Small* | X | W | | 2 | 6 | 4 | | 9 | 26 |
| *Rhynchospora divergens Chapm.* | I | N | | | | | | 26 | |
| *Rorippa teres (Michx.) Stuckey* | I | W | | 1 | | | | | |
| *Sabatia stellaris Pursh* | I | N | | 4 | | | | 5 | |
| *Salix caroliniana Michx.* | I | N | 1 | 2 | 1 | 1 | | 5 | 1 |
| *Sambucus simpsonii Rehder* | I | W | | | 1 | 5 | | 1 | 1 |

| Species | A | | B | C | D | E | F | G | |
|---|---|---|---|---|---|---|---|---|---|
| *Schinus terebinthifolius Raddi* | X | W | | | | 3 | 33 | | |
| *Sesbania macrocarpa Muhl.* | I | W | 47 | 54 | | | | | |
| *Solanum douglasii Dun.* | I | W | | 5 | 2 | 1 | | 3 | 1 |
| *Solidago stricta Ait.* | I | N | | | | | | 1 | |
| *Sonchus asper* (L.) *Hill* | X | W | 1 | | 2 | 1 | 3 | 1 | 1 |
| *Spartina?* | | | 4 | | | | | 8 | |
| *Spermacoce tetraquetra A. Rich* | I | W | | | | 8 | | | |
| *Sporobolus poirettii (Roem. & Schult.) Hitch.* | I | W | | | | | 1 | | |
| *Tetrazygia bicolor (Mill.) Cogn.* | I | N | | | | 1 | | | 2 |
| *Thelypteris sp. 1* | | | 14 | 14 | 2 | 2 | 18 | 30 | 25 |
| *Thelypteris sp. 2* | | | | | | | 1 | | 1 |
| *Trismeria trifoliata* (L.) *Diels* | I | N | 3 | 20 | | 3 | | 3 | 3 |
| *Typha sp.* | | | 2 | 7 | 4 | 8 | 1 | | 5 |
| *Verbena scabra Vahl.* | I | N | 3 | | 2 | | 24 | | |
| *Vitis rotundifolia Michx.* | I | N | | | | 3 | | | 6 |
| unknown #1 | | | | | | | | 2 | |
| unknown #2 | | | | | | | 1 | | |
| unknown #3 | | | | | | | | 1 | |
| unknown #7 | | | | | 2 | 2 | | | 1 |
| unknown #9 | | | | | 1 | | | | |
| Total | | | 3300 | 22594 | 4611 | 1303 | 370 | 396 | 339 |

[1]Probable greenhouse contaminant

older vegetation was striking, and involved values which differed by an order of magnitude. This decrease in seed density was to be expected, based on values from agricultural studies and early stages of succession, plus values from various kinds of mature forests. Nevertheless, few investigators have measured the viable seed content of different ages of successional vegetation in the same area. Two such studies (Oosting & Humphreys 1940 and Livingston & Allessio 1968) were based on buried seed; the surface litter was cleared away before the soil was sampled. The data of Oosting & Humphreys (1940) show a general trend of decreasing numbers of seed with increasing age of vegetation, while the data of Livingston & Allessio (1968) show no clear successional trend. Guevara & Gomez-Pompa (1972) found two-to-seven times more viable seed in successional stands than in mature forest in Veracruz, Mexico.

The burned 2.5-year-old vegetation yielded about five times more seedlings per unit area than the 2.5-year-old unburned vegetation of the same age, an observation which may have important implications for the use of fire as a management tool. The burn may have increased *Ludwigia* spp. seed production, either by releasing nutrients into the soil from burned biomass or by altering the *Ludwigia* growth form, resulting in the production of more flowers and viable seed; another possibility is that burning affected the seed and/or seedbed, resulting in greater germination.

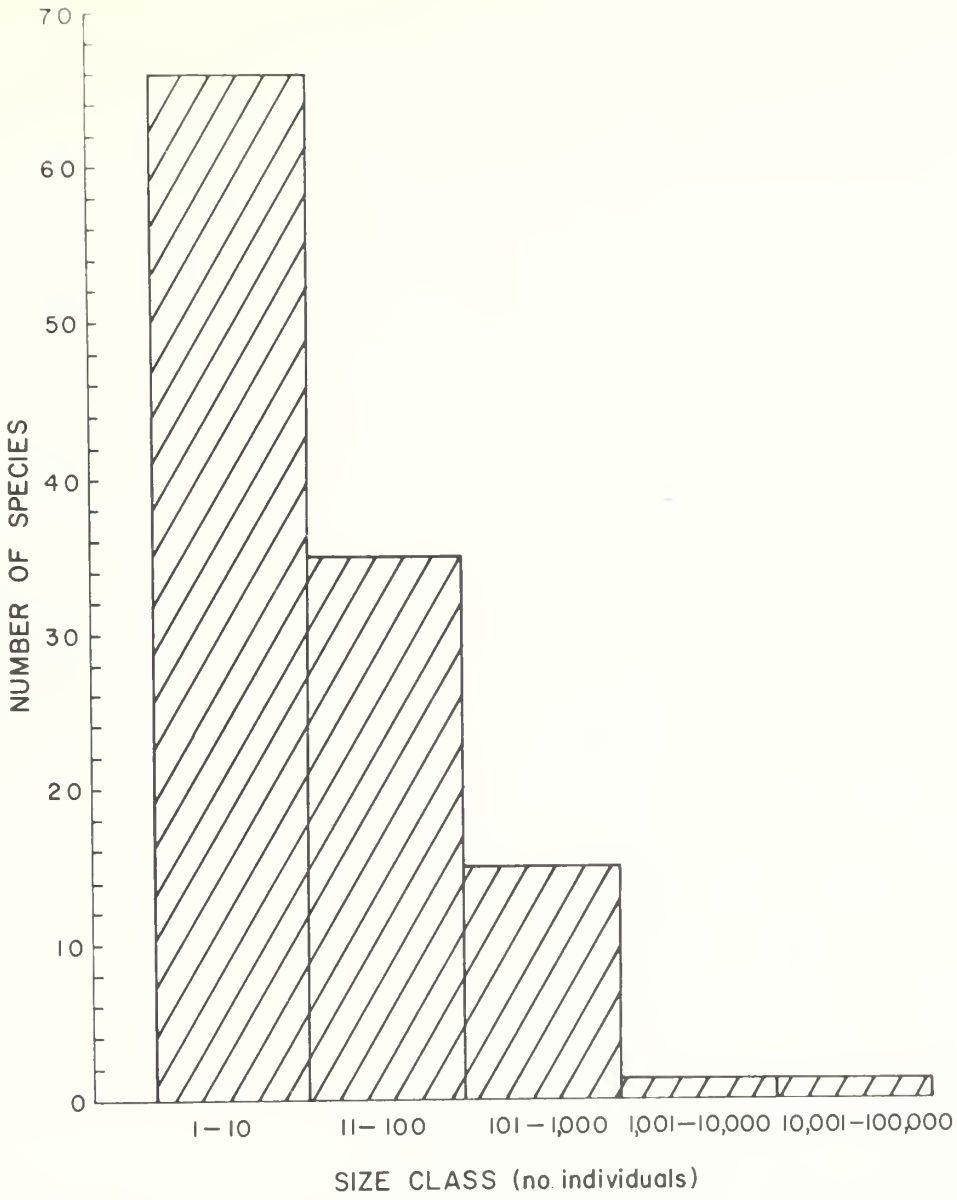



FIGURE 1. Number of species (all sites and all samples combined) in each of five logarithmically scales size classes.

## FLORISTICS

The number of species per site (Fig. 3) was much less variable than the number of individuals. Values ranged from about 30 to 50 species per site, with no clear trends in species richness reflected by successional stages. Because the older communities had far fewer individuals than the younger vegetation, yet similar numbers of species, the diversity (richness plus evenness components) of the seed flora was much greater in the older vegetation types than in the early successional stages.

Because the relationship between numbers of species encountered and area sampled is nonlinear, and because different investigators have used a wide variety of sample areas, it is difficult to compare the richness of the seed floras among studies. Our values, however, fall within the range of those reported in the literature, generally being higher than those from northern forests and somewhat lower than most values reported from the tropics. For example, Olmsted and Curtis (1947) observed zero to four species in six samples of 0.37 $m^2$ each in forests in Maine; Kellman (1970, 1974a) recorded 16 species per $m^2$ and 19 species per 2.5 $m^2$ in coniferous forests of British Columbia; and Oosting & Humphreys (1940) reported relatively rich germinated-seed floras of 29 to 47 species from samples of 0.11 $m^2$ each from ten sites in North Carolina. Liew (1973) reported a relatively depauperate seed flora of only 31 species from 20 $m^2$ of mature forest in Sabah, but most values reported from the tropics have been substantially higher. Guevara & Gomez-Pompa (1972), for example, recorded 14 to 28 species from samples of 0.51 $m^2$ in Mexico; Keay (1970) observed 42 species on 1.15 $m^2$ in Nigeria; and Kellman (1974b) reported a total of 54 species from a composite sample (78 sites) with a combined surface area of 0.23 $m^2$ in Belize. Our total flora of 119 species from a single area is higher than any reported in the literature, and is due, in part, to our relatively large total sample area of 5.25 $m^2$. The individual site values of 30 to 50 species per 0.75 $m^2$ each, however, are quite

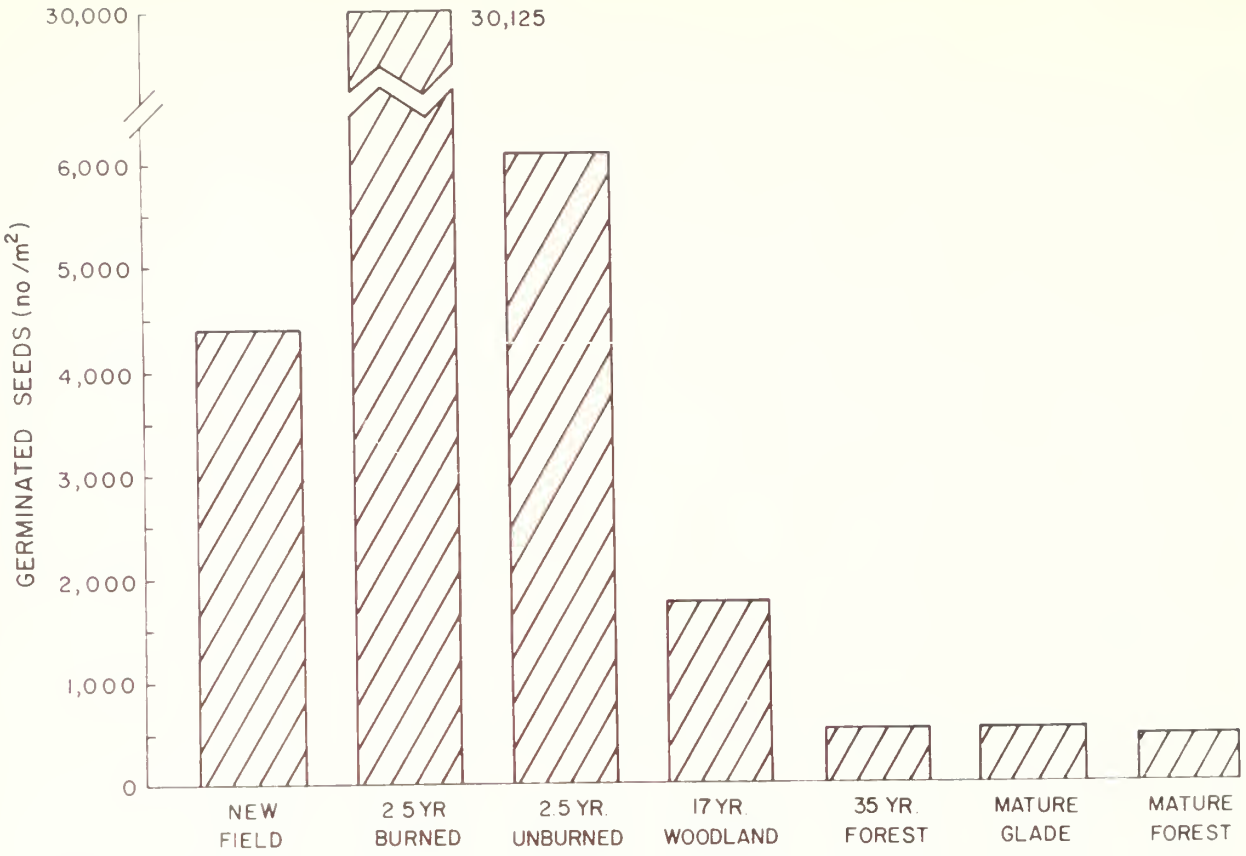



FIGURE 2. Density of germinated seeds from soils of the seven study sites after one year.

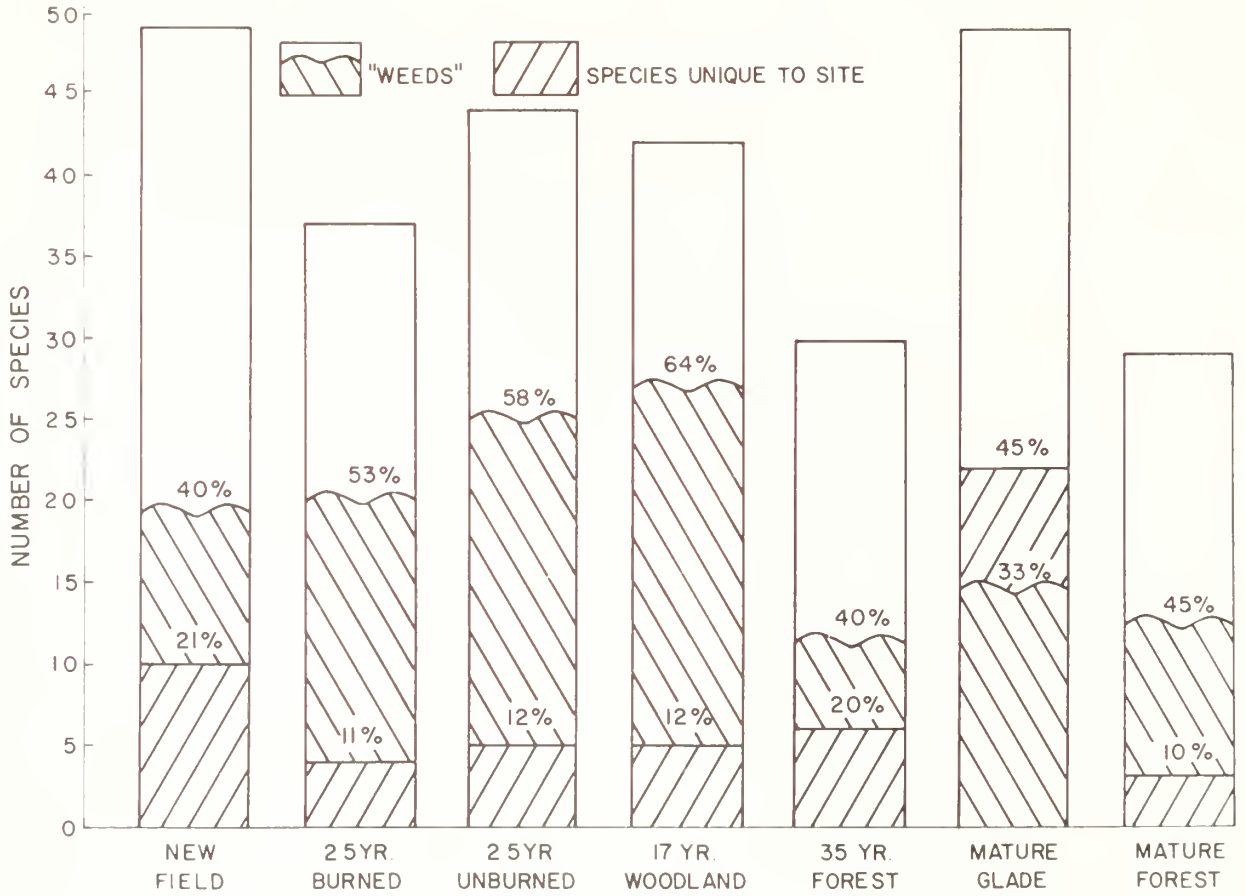



FIGURE 3. Richness, weediness, and site-uniqueness of the germinated-seed flora from soild of each of the seven study sites. Each value is the total of three 0.25 $m^2$ samples.

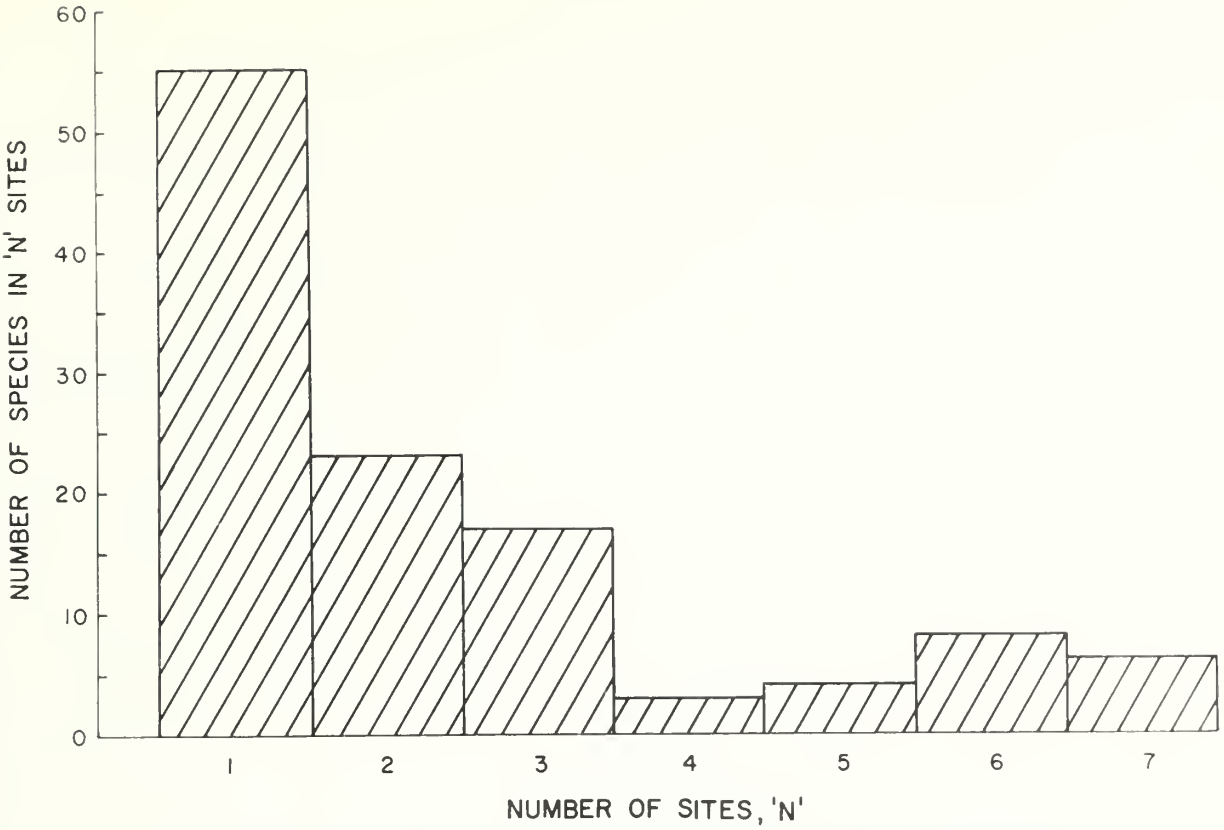



FIGURE 4. Dispersion of 119 species among the seven study sites.

high, especially considering that most of our sites are flooded for up to six months per year, which would seem to result in a great loss of viability for many species.

Figure 3 also indicates the portion of the germinated-seed flora from each site which was made up of weeds. The definition we used to classify species as weedy or non-weedy was very conservative; anything specifically described by Long & Lakela (1971) as weedy or characteristic of disturbed sites was considered to be a weed, and all other species were classified as non-weedy. Because such definitions are quite arbitrary the weed flora at each site is shown on Figure 3 as a wavy line, rather than a precise number. The conservativeness of our classification resulted in some of our most abundant and ubiquitous species (e.g., *Ludwigia* spp.) being classified as non-weedy. Only 36 percent of the seed-flora was made up of weeds, according to the criteria of Long & Lakela (1971). The number of weedy species per site ranged from 12 to 27, making up 33 to 64 percent of the species. The younger stages of succession tended to have more weedy species, and these accounted for a higher percentage of their floras: usually half or more.

Exotic species are particularly important in south Florida which, because it is a peninsula jutting into the subtropics, is potentially susceptible to species invasions from the tropics. Exotic trees such as *Schinus terebinthifolius*, *Melaleuca quinquenervia*, and *Casuarina* spp. dominate the landscape in many areas in south Florida and constitute a management problem for Everglades Park. We therefore suspected that exotics might be particularly important in the abandoned farmlands of the Hole-in-the-Donut, but were surprised to find that only about 10 percent of the species which germinated in the flats, representing less than 5 percent of the individuals identified to species, were exotics (according to Long & Lakela 1971). This is even lower than the percentage of exotics in other floras. For example, about 18 percent of the 1647 species listed for all of south Florida by Long & Lakela (1971) are designated as exotics and 20 percent of the 5523 species listed in Gray's Manual (Fernald 1950) are exotics. Thus, although exotics certainly do become readily established in south Florida and often become dominant, conspicuous features of the landscape, the seed flora of abandoned Everglades farmlands does not seem to contain an unusually high fraction of exotics, either in terms of numbers of species or numbers of individuals. Of the exotic woody species which are important in and around Everglades National Park, the only one which germinated in our flats (from the two oldest successional stands) was *Schinus terebinthifolius*, which is already a major component of the older successional vegetation in the Hole-in-the-Donut.

As shown in Figure 4, the species were unevenly distributed among the sites. Almost half of the species which germinated were found on only one of the seven sites and more than 80 percent of them were found on fewer than four sites. Propagules of many of these species are undoubtedly more widespread than indicated by our small samples, but at least they do not appear to be so widespread and abundant that they are likely to cause insurmountable management problems. Rather, management practices might better be directed toward those 22 species which were observed in soil samples from four or more of the seven sites. These are the most ubiquitous, readily dispersed species and many of them are likely to become important components of the successional flora.

On most sites, less than one-fourth of the species observed to germinate were unique to that site, as shown in Figure 3. One striking exception was the mature glade; nearly half of the species tabulated from that site were observed nowhere else, even though the number of species which germinated from the mature glade soil (49) was unusually large. Apparently, many species which grow in the mature glade produce propagules, but these are not widely dispersed. The mature-glade vegetation is of low stature (usually less than 1 m tall), so wind-mediated dispersal would be less likely to be as effective as it might from a forest. Also, many of the glade species may have propagules which are water-dispersed. Because the mature glade is at the southern border of the Hole-in-the-Donut, and because the prevailing drainage is toward the south - southwest, it is likely that water-dispersed seeds are not getting distributed into the former farmlands which lie to the north of it. Reestablishment of some glade species, therefore, may require planting and reseeding, especially in the early stages of vegetation development.

## LITERATURE CITED


ALEXANDER, T. R., & A. G. CROOK. 1973. Recent and Long-Term Vegetational Changes in South Florida. Part 1, Preliminary Report. South Florida Ecological Study. EVER-N-51, 215 p.

CRAIGHEAD, F. C. 1971. The Trees of South Florida, Vol. 1. The Natural Environments and Their Succession. Univ. of Miami Press, Coral Gables. 212 p.

DAVIS, J. H. 1943. The natural features of southern Florida, especially the vegetation and the Everglades. Geol. Bull. No. 25. Florida Department of Cons. Geol. Survey. 311 p.

EGLER, F. W. 1952. Southeast saline Everglades vegetation, Florida, and its management. Vegetatio 3:213-265.

FEAST, P. M., & H. A. ROBERTS. 1971. Weed seed populations. *In:* Annual Report, National Vegetable Research Station 1970, 21:115.

FERNALD, M. L. 1950. Gray's Manual of Botany. American Book Company, New York, 8th ed. 1632 p.

GUEVARA, S., & A. GÓMEZ-POMPA. 1972. Seeds from surface soils in a tropical region of Veracruz, Mexico. J. Arnold Arboretum, Harvard Univ. 53:312-335.

HARSHBERGER, J. W. 1914. The vegetation of south Florida. Trans. Wagner Free Inst. Sci. 7:48-189.

HILSENBECK, C. E. 1976. An Investigation of Old Field Succession in Everglades National Park, First Interim Report. Everglades National Park. Mimeo 63 p.

JENSEN, H. A. 1969. Content of buried seeds in arable soil in Denmark and its relation to the week population. Dansk. Bot. Ark. 27: 1-56.

KEAY, R. W. J. 1960. Seeds in forest soils. Nigerian Forest. Inf. Bull. (N.S.) 4:1-4.

KELLMAN, M. C. 1970. The viable seed content of some forest soil in coastal British Columbia. Can. J. Bot. 48:1383-1385.

KELLMAN, M. C. 1974a. Preliminary seed budgets for two plant communities in coastal British Columbia. J. Biogeog. 1:123-133.

KELLMAN, M. C. 1974b. The viable weed seed content of some tropical agricultural soils. J. Appl. Ecol. 11:669-678.

KROPÁC, Z. 1966. Estimation of weeds seeds in arable soil. Pedobiologia 6:105-128.

LIEW, T. C. 1973. Occurrence of seeds in virgin forest top soil with particular reference to secondary species in Sabah. Malayan Forester 36:185-193.

LIVINGSTON, R. B., & M. L. ALLESSIO. 1968. Buried viable seed in successional field and forest stands, Harvard Forest, Massachusetts. Bull. Torrey Bot. Club 95:58-69.

LOCKETT, P. M., & H. A. ROBERTS. 1975. Weed seed populations. *In:* Annual Report, National Vegetable Research Station, (Britain) 1974, 25:124.

LONG, R. W., & O. LAKELA. 1971. A Flora of Tropical Florida. University of Miami Press, Coral Gables, Florida. 962 p.

MAJOR, J., & W. PYOTT. 1966. Buried, viable seeds in two California Bunchgrass sites and their bearing on the definition of a flora. Vegetatio 13:253-282.

OLMSTED, N. W., & J. D. CURTIS. 1947. Seeds of the forest floor. Ecology 28:49-52.

OOSTING, H. J., & M. E. HUMPHREYS. 1940. Buried viable seeds in a successional series of old field and forest soils. Bull. Torrey Bot. Club. 67:253-273.

RES. MGT. STAFF. 1976. Hole-in-the-Donut Farmland Research and Management Program, Summary 1972-1976. Everglades National Park. Mimeo 51 p.

ROBERTSON, W. B. 1953. A survey of the effects of fire in Everglades National Park. U. S. Dept. of the Interior, National Park Service. 169 p.

STRICKLER, G. S., & P. J. EDGERTON. 1976. Emergent seedlings from coniferous litter and soil in eastern Oregon. Ecology 57:801-807.

# FACTORS ASSOCIATED WITH TREE FAILURE OF GIANT SEQUOIA - PATHOLOGICAL ASPECTS[1]

Douglas D. Piirto[2]

## INTRODUCTION

Giant sequoia (*Sequoia gigantea* [Lindl.] Decne.), one of the Earth's oldest and largest living organisms, with aesthetic and scientific value, is probably one of the organisms least understood. Many generalizations have been made about the giant sequoia tree, leading people to believe that it is not subject to the same natural forces that affect other tree species. Probably the most misleading generalization that has been stated since the trees were first discovered by the Joseph Walker party was by John Muir (1894) when he wrote:

> "I never saw a Bigtree (giant sequoia) that had died a natural death; barring accidents they seem to be immortal, being exempt from all diseases that afflict and kill other trees."

Hartesveldt (1962) perpetuates this misleading generalization by stating:

> "Sequoia's longevity and great size have been attributed by nearly all writers, popular and scientific, to its few insect and fungus parasites and the remarkable resistance of the older trees to damage or death by fire."

He goes on to say:

> "There is no record of an individual sequoia living in its natural range as having been killed by either fungus or insect attack."

Not pointed out, however, is the fact that this absence of reported mortality may be because few in-depth studies of the disease and insect relationships with giant sequoia have been conducted until recently.

The impact of man on forests is becoming an issue of increasing importance. With nearly four million people per year visiting Yosemite, Kings Canyon and Sequoia National Parks, considerable interest has been expressed by park managers, naturalists and the public concerning uprooting and stem failure of giant sequoia trees in areas of high recreational use. The severity of the problem is shown in the bodily and structural damage that has resulted from falling giant sequoias. A particular case in point involved the death of an elderly woman in the Hazelwood Grove of Sequoia-Kings Canyon National Park. As she was picnicking with some friends, a giant sequoia fell, striking another tree which in turn fell and struck her as she tried to run out from under it. Several hours later another large old-growth giant sequoia fell within the same area. At the time of the Hazelwood incident, Mr. Jack Hickey, a naturalist with the National Park Service, initially suggested that carpenter ant excavation may be a principal factor associated with failure of old-growth giant sequoia trees.

The Hazelwood case raised three very important points:

1. The potential hazard of falling giant sequoias to unsuspecting tourists.

2. The loss of giant sequoia trees that required centuries to grow.

3. The lack of sufficient information to describe the factors associated with tree failure of giant sequoia.

These three points along with the controversy generated by Mr. Hickey's hypothesis were the impetus for a project designed to determine the underlying causes of uprooting and stem failure in giant sequoia trees.

The information generated from this study will, hopefully, be of value to park managers when making decisions concerning:

1. The development of recreational facilities around giant sequoia trees and

2. The development of innovative forest management practices which will preserve, protect and perpetuate for future generations the giant sequoia forest.

## SCOPE

Uncertainty as to the factors associated with tree failure of old-growth giant sequoia required a broad research approach. Within this broad approach, however, the following objectives were established:

1. To identify the factors associated with tree failure of old-growth giant sequoia by:

   a) Surveying recently fallen trees to determine similarities in their history that might account for failure.

---

[1]University of California Forest Products Laboratory Internal Report No. 36.01.90, Progress Report No. 5. This paper is based on research work of a Ph.D. dissertation submitted to the University of California, Berkeley (Pirrto, 1976). Acknowledgments are made to: the National Park Service for financial and logistical support; Ph.D. Thesis Committee, Drs. W. Wayne Wilcox (Chairman), John R. Parmeter and David Wood; the many other too numerous to list here who have helped at various stages of this work. In particular, I would like to acknowledge my parents, Mr. and Mrs. R. A. Pirrto for their constant encouragement and financial support.

[2]Forest Products Laboratory, University of California, Richmond.

b) Determining the important wood decay fungi of old-growth giant sequoia.

c) Conducting exploratory tests on carpenter ant-fungus interaction.

d) Investigating the wood properties of giant sequoia.

2. To evaluate techniques for detection of potential giant sequoia tree failures.

3. To review the significant literature pertaining to giant sequoia and tree failure.

4. To discuss the implications of the research results to management of giant sequoia groves.

5. To make recommendations for needed research on subjects related to tree failure of giant sequoias.

This paper will report the results of several studies conducted to accomplish the above stated general objectives.

## FACTORS ASSOCIATED WITH TREE FAILURE OF GIANT SEQUOIA

Giant sequoia trees are subject to the same natural forces as other tree species. Field studies have shown that a complex of factors may be involved, depending upon the type of tree failure (e.g., root failure, stem failure or earth failure). However, advanced decay and fire scars were the most frequently observed and the most significant factors associated with tree failure of old-growth giant sequoia trees found in the study. In 21 of the 33 study trees (64%), and in 19 of the 22 root failure trees (86%), one-third or more of the failure zone was not structurally functional because of advanced decay. Of the 27 trees containing fire scars, 26 fell toward the scarred side. Nine Basidiomycetes (*Armillaria mellea, Fomes annosus, Naematoloma capnoides, Polyporus schweinitzii, Polyporus versicolor, Poria albipellucida, Poria incrassata, Stereum hirsutum* and Unknown No. 23B) were associated with decayed giant sequoia wood, several of which have the reputation or potential for being very serious forest pests. Carpenter ant galleries were found in or near the failure zone in 16 of the 33 study trees. However, only six of these 16 study trees contained carpenter ant galleries immediately in the failure zone. Microscopic examination of discolored wood associated with carpenter ant galleries revealed the presence of an early to moderate stage of decay. These studies indicate that carpenter ants are not directly responsible for tree failure. Exploratory tests demonstrated a preference by carpenter ants to excavate decayed wood substantiating field observations and previous reports. A range in excavation activity was noted. Attempts to isolate decay fungi from carpenter ants were not successful and, therefore, it is not yet clear if carpenter ants play any role in vectoring decay fungi or in facilitating their spread within wood. Both decay and carpenter ant galleries were frequently associated with fire scars. Although physical disturbances ( e.g., roads, trails, streams) were associated with 22 of the 33 study trees, their role in initiating premature failure of giant sequoia trees requires further elucidation. The fact that large portions of the root system and butt have been found to be no longer structurally functional suggests that trails, roads and similar improvements should be kept away from giant sequoias to the maximum extent possible. Such improvements may result in damage to roots and the lower bole allowing the entrance of fungi.

It was shown that measurement of changes in rate of stem growth may not be an appropriate method for assessing the long-term effects of stress conditions, such as attack by fungi and insects, or of physical disturbances on old-growth giant sequoia trees; or at least such changes had no apparent relationship with tree failure.

Whereas the "Shigometer" was effective in detecting decay in white fir, only a limited capability for detecting decay in giant sequoia heartwood was demonstrated in the laboratory. Various factors make the meter in its present form unattractive for field applications.

## PROPERTIES OF THE WOOD OF GIANT SEQUOIA RELATED TO DECAY AS FACTORS IN TREE FAILURE

These studies have shown:

1. Toughness values for discolored wood and non-discolored wood adjacent to carpenter ant galleries and to advanced decay were not significantly different. More extensive sampling may be required to accurately explore the relationship between the presence of decay fungi and toughness in this normally low-toughness species (old-growth).

2. Charring had little, if any, effect on decay resistance of sequoia heartwood and sapwood and white fir sapwood. Because many previous workers have reported fire scars as entrance courts for decay fungi, it was expected that this tissue might be substantially more susceptible to decay. Further study of this relationship should explore the significance of the slight differences found here and more carefully examine the role of fire scars as entrance courts for decay fungi.

3. Significant differences existed in the total number of rings present in sapwood between old-growth and young-growth giant sequoia trees; however, no significant difference existed in the total width of the sapwood, suggesting that this feature is independent of age.

4. Rings per inch, average growth ring width, average percent latewood, specific gravity, and extractive content (expressed as a percent of moisture-free, extracted wood) were significantly different between outer heartwood of old-growth and young-growth trees. No significant differences existed in extractive concentration (grams of oven-dry extract per cubic centimeter of green wood) and in decay resistance of outer heartwood between old-growth and young-growth trees.

5. Diameter inside bark, average-growth ring width, water extract concentration and total extract concentration were significantly correlated with decay resistance of young-growth sequoia outer heartwood. No correlation between any of the measured properties and decay resistance was found in old-growth giant sequoia outer heartwood.

6. Outer heartwood of both old- and young-growth giant sequoia trees was classified as resistant to *Poria monticola* and highly resistant to *Lenzites trabea* and *Stereum hirsutum*. However, large variability between trees in resistance of these fungi was noted. This variability was most likely the result of differences between trees in the nature, quantity and distribution of extractives. In young-growth trees it was

directly correlated with water-soluble and total extract concentration.

7. Removal of the extractives, both water-soluble and alcohol-soluble, lowered the decay resistance of giant sequoia heartwood markedly.

8. Treating giant sequoia sapwood blocks with either water- or alcohol-soluble extractives, in concentrations approximately equivalent to half of the concentration in heartwood, imparted resistance to decay by *Poria monticola* comparable to that by heartwood.

## IMPLICATIONS FOR MANAGEMENT OF GIANT SEQUOIA

A. Giant sequoia trees are subject to the same natural forces (such as disease and insect attack) as other tree species and thus must be managed accordingly. The fact that potentially dangerous forest diseases have been found associated with recent old-growth tree failures is cause for considerable concern. Of particular interest are *Fomes annosus, Poria incrassata* and *Poria albipellucida*. Continued research should be focused on establishing the role of these diseases in tree failure.

B. Because large areas of the root system and lower stem of old-growth giant sequoias may not be structurally functional as a result of fire scars and extensive decay, buildings, roads, trails, etc., should not be constructed around them. These studies indicate that many of these old trees must be considered a hazard to humans and property.

C. Investigations to develop a method of estimating the degree of soundness or decadence in the root systems and butts of old-growth giant sequoias should be continued.

D. Many previous workers have reported a significant role of fire scars as entrance courts for decay fungi. For this reason care should be taken to protect the base and roots of valuable giant sequoias from scarring during prescribed burning operations.

E. Carpenter ants do not appear to be directly responsible for tree failure. However, carpenter ants might still play an important role in vectoring decay fungi or making wood more susceptible to decay. Continued research on the relationship between carpenter ants and decay fungi is recommended.

F. Wood properties of young-growth giant sequoia are comparable to those of young-growth coast redwood, suggesting that giant sequoia should be considered for planting stock in managed production forests.

## RECOMMENDATION

It is recommended to personnel responsible for managing giant sequoia stands that an interdisciplinary team of specialists be formed to:

1. Develop long-term forest management practices which will preserve, protect and perpetuate for future generations the giant sequoia forest and

2. Point out areas for needed research.

## RECOMMENDATION FOR CONTINUED RESEARCH

These results have helped focus attention on the areas where additional information is most needed to gain a better understanding of the factors associated with mortality and failure of giant sequoia trees. This information is considered necessary in order to:

1. Minimize the conditions which are not natural to giant sequoia groves, thereby possibly increasing the longevity of the old giant sequoia trees.

2. Classify areas according to hazard and risk of failure.

3. Provide a scientific data base from which resource managers can develop long-term management plans for giant sequoia both within and outside of its native range.

Recommended areas for continued research into the nature and possible causes of giant sequoia tree failure include:

*Site Classification*

1. To characterize through more detailed studies the site conditions in the areas of fallen giant sequoias in comparison with those of standing giant sequoias, with respect to soil type, soil saturation, site class, slope, terrain, drainage patterns, stocking levels, age class distribution, debris accumulation, climatic conditions and human and physical disturbances such as roads, trails and streams.

*Pathology*

1. To elucidate the role of *Fomes annosus, Poria incrassata, Poria albipellucida* and other known and unknown organisms as pathogens to giant sequoia (e.g., is *Fomes annosus* killing giant sequoias in the Redwood Mountain area of Sequoia-Kings Canyon National Park? Is a forest disease buildup occurring in the redwood mountain area?).

*Ecological Interrelationships*

1. To determine what effect, if any, an increase in stocking level of white fir in sequoia groves has on populations of decay fungi, aphids and carpenter ants in and around giant sequoias.

2. To define more completely the relationship between decay and carpenter ants (e.g., Do carpenter ant galleries in the base of old trees indicate that decayed wood is also present? If so, what tree species containing decayed wood as well as what stage of decay do carpenter ants prefer? What role does wood moisture content play in attracting carpenter ants. Can carpenter ants vector and/or facilitate the spread of wood decay fungi?).

3. To determine the influence of fire of various intensities on levels of disease and insect attack within the giant sequoia ecosystem.

4. To examine more comprehensively the role of fire scars on structural stability and as entrance courts for decay fungi and insects.

5. To characterize the within-tree ecological relationships of wood decay fungi and

associated microorganisms (e.g., Can bacterial and fungal association predispose giant sequoia heartwood to attack by decay fungi?).

*Detection Methods*

1. To develop techniques for detecting hazardous giant sequoia trees (e.g., Can aerial color photography be utilized to detect giant sequoia trees subject to failure? Are easy techniques for detection and assessment of root and butt rot in individual trees available and can such results be correlated with subsequent tree failure?).

LITERATURE CITED

HARTESVELDT, R. J. 1962. The effects of human impact upon *Sequoia gigantea* and its environment in the Mariposa Grove, Yosemite National Park, California. Ph.D. Dissertation. Univ. of Michigan.

MUIR, J. 1894 (1961). The Mountains of California. Published in cooperation with the American Museum of Natural History, The Natural History Library, Anchor Booles, Doubleday and Co., Inc., Garden City, New York.

PIIRTO, D. D. 1976. Factors associated with tree failure of giant sequoia. Ph.D. Dissertation. Univ. of California, Berkeley (Parts to be published in the Journal of Forestry, Wood and Fiber, Forest Products Journal and Plant Disease Reporter).

# FACTORS ASSOCIATED WITH TREE FAILURE OF GIANT SEQUOIA - ENTOMOLOGICAL ASPECTS

C. T. David, D. A. Tilles, and D. L. Wood[1]

During the early 1970's, failure of giant sequoia (*Sequoisdendron giganteum*) was attributed by some park personnel to be a result of damaging excavations by the carpenter ant, *Camponotus modoc* Wheeler. It had been hypothesized that carpenter ant populations had reached abnormally high levels in areas of high visitor use, thus intensifying their destructive impact upon the ancient trees. These high ant populations were proposed to be a result of increased availability of food, primarily garbage left by park visitors.

Research to determine the validity of these hypotheses was carried out between the years 1972-1976. The objectives of this study were to determine: 1) if carpenter ants were the primary agent causing failure of giant sequoia, 2) if ants were present in greater numbers in areas of high human use than in areas of low use, 3) if park management practices (i.e., garbage disposal, controlled burning) significantly influenced ant population dynamics, and 4) the biology of *Camponotus modoc*, the most abundant ant species associated with giant sequoia.

Two methods were used to estimate ant population levels: 1) hectare plots (100 x 100 m) were constructed in areas of high and low visitor use. All carpenter ant nests and foraging trails within the plots were mapped and population estimates were made for each nest; 2) transects, 100 m in length, were established at random in high and low use areas. Estimates of ant numbers were made for the area 10 m on both sides of the transect. Ant population levels were somewhat higher in only 1-2 areas of high human use; however, high ant populations were also observed in areas of low human use.

A collection of materials carried by foraging ants returning to their nest was made. It was determined that ants fed almost exclusively on other arthropods; about 90% of this food consisting of the aphid, *Cinara occidentalis*, and its honeydew. Garbage was found to be an insignificant component of their total food resources.

The effect of fire on carpenter ant populations was studied before and after controlled burns in the Redwood Mtn. area of Kings Canyon National Park. Fire had a devastating effect on ant colonies located in relatively unprotected areas (i.e. incense cedar or sugar pine stumps) whereas those colonies located deep within living or dead giant sequoia were generally unharmed by the burning.

In summary, carpenter ants were not found to be of primary importance in the failure of giant sequoia (see conclusions of preceding paper, which discusses Pathological aspects) and thus park management practices (with the exception of controlled burning) did not greatly influence the population dynamics of these animals.

As the aphid, *Cinara occidentalis*, was found to be the most significant component of the ant's food resources, a project was initiated to study aspects of the ant-aphid relationship. The primary objectives of this study were: 1) to obtain a more detailed account of the aphid's contribution to the ant's diet, 2) to determine in what ways the ant influenced the aphid's population dynamics and 3) to describe *Camponotus* behavior while foraging on *C. occidentalis*.

During the summers 1974 and 1975, it was determined that prolonged survival of aphid colonies was largely dependent upon the continued attendance of the carpenter ant, *C. modoc*. Of 22 aphid colonies observed during 1974, 10 were unattended by ants and survived no longer than 3 weeks; however 10 out of the 12 attended colonies were still present at this time. Experiments in which ants were conducted during 1975 and 1976. In all cases, excluded aphid colonies disappeared while most of the attended colonies survived for a longer period of time.

The ant played an important role in the protection of the aphid from predators. During 1975, ladybird larvae were 50 times more abundant on naturally occurring, unattended colonies than on attended colonies. During August 1976, 286 mirids (aphid predators) and 25 spiders were collected from aphid colonies excluded from ants, while only 2 mirids and 1 spider were found on a similar number of attended, control colonies.

Diurnal ant attendance was very low during mid-summer 1975 (about 0.5 ants per aphid colony), while during mid-summer 1976, attendance was very high (about 13 ants per aphid colony). Aphid population levels were very high during 1975 (.61 branches with aphids) and very low during 1976 (.01 branches with aphids). Apparently there was an abundance of honeydew available for food which resulted in the low diurnal ant attendance in 1975. The increased attendance during 1976 provided an important source of protection to the aphid which would have been otherwise available as food for the large number of predators that had overwintered from the previous season.

About 11% of the ants returning down fir trees were found carrying aphids back to their nest during periods of high aphid populations in 1975. This behavior was not observed during 1976 when aphid populations were very low.

Ant attendance was found to suppress the development of alatae, the dispersal form of the aphid. During 1975, both naturally unattended and attended aphid colonies were collected each week and analyzed in the laboratory. Twice as many alatae were found in the unattended colonies than in the attended colonies. During 1976, no naturally unattended colonies were found and only 3/408 aphids collected were alatiform.

A marked division of labor was observed among *C. modoc* workers. Minor workers (pronotal width less than 1.3 mm) were most intimately associated with the aphids, apparently collecting honeydew and often found in the vicinity of the nest and were involved in gallery excavation and nest defense.

[1]Department of Forestry and Entomology, University of California, Berkeley 94530.

# PROBLEMS OF REVEGETATION OF ALPINE TUNDRA

David R. Stevens[1]

## INTRODUCTION

The Alpine tundra was one of the primary reasons for establishment of Rocky Mountain National Park. The unique character of this resource continues to attract millions of people to the park. Easily accessible by automobile on Trail Ridge Road since 1932, the average park visitor has been able to actually experience the character of the alpine. To many visitors, a trip to Rocky Mountain is not complete without a walk on the tundra.

The attractiveness of the resource, however, may be the cause for its destruction. As described by Willard and Marr (1970), "visitors to the tundra are affecting its survival in many ways incidental to its use."

The activity that has had the greatest effect is trampling. Low intensity, widely distributed use has little or no impact; however, visitors following the same path day after day soon kill the vegetation, leaving the soil to be eroded away by wind and water. Vehicles driving or parking on the tundra have the same effect if allowed to continue over time.

Historic uses of the area such as the effects of early road construction, in most cases have not been properly restored and still affect the esthetics of the alpine. Several buildings have also recently been removed, leaving scars on the landscape which need to be revegetated. Even in relatively recent development and construction, the effects on adjacent tundra have not received the consideration needed.

The result of these disturbances has been the loss of ground cover and valuable topsoil. The problems of wind and water erosion that plague restoration projects at lower elevations, appear to be considerably more severe over 11,000 feet.

The objective of this paper is to review past restoration efforts, examine the critical environmental factors, and report on studies of what appear to be the most feasible techniques, using modern technology to restore the disturbed sites.

## THE STUDY AREA

Rocky Mountain National Park, 412 square miles, lies along the Continental Divide in northcentral Colorado. Elevations range from 7,600 feet to 14,255 feet with about one-third of the total area over 11,000 feet above sea level. Mountains are formed by a series of granitic batholiths intruded into pre-Cambrian mica-schists and pegmatites. The physiography of the east slope is characterized by steep cliffs and U-shapped valleys as altered by local Pleistocene glaciation. The generally more level rolling alpine tundra areas were apparently not glaciated. On the west side, the mountains fall off less steeply to the Colorado River valley at about 9000 feet elevation.

Numerous studies have described the alpine tundra including Kiener (1939), Griggs (1956), and Willard (1963). A good description of the trail ridge is given by Marr and Willard (1971).

The tundra vegetation is characterized by a complex mosaic of vegetation communities related to physiography, snow accumulation, moisture availability, exposure, temperature, and substrate. Forces of cryopedology as well as other environmental factors also shape the landscape.

The fellfield ecosystem occupies the windiest sites where the soil is coarse, rocks are abundant, and there is no snow cover. The cushion plant fellfield is characterized by plants such as moss campion (*Silene acaulis*) plant sandwort (*Arenaria obtusiloba*), Rocky Mountain nailwort (*Paronychia sessiliflora*) and dwarf clover (*Trifolium nanum*). On sites with less rock and some snow cover will be the alpine clover fellfield which is characterized by alpine clover (*Trifolium dasyphyllum*) along with the cushion plants mentioned above. The mountain dryad fellfield is best developed on gravel sites where mountain dryad (*Dryas octopetala*) is dominant.

Snowbed ecosystems occur on sites where the snow accumulates for sixty to ninety percent of the year. Vegetation types on these sites include the hairgrass meadow, characterized by hairgrass (*Deschampsia caespitosa*). The toninia-sibbaldia type is dominated by (*Toninia cumulata*) and sibbaldia (*Sibbaldia procumbens*). Another vegetation type common in snow accumulation sites is the Drummond rush type which is characterized by Drummond's rush (*Juncus drummondiana*).

On sites of high moisture levels such as solifluction terraces, the Rocky Mountain sedge ecosystem is dominant. Characteristic plants are Rocky Mountain sedge (*Carex scopulorum*), marsh marigold (*Caltha leptosepala*), and Perry primrose (*Primula parryii*). On some of these sites a willow type has developed with characteristic willow species of (*Salix planifolia*), (*Salix brachycarpa*) and (*Salix glauca*).

Alpine turf ecosystems are present as persistent vegetation on upland dry sites with good soil formation. They are characterized by Kobresia (*Kobresia myosuroides*), alpine avens (*Geum rossii*), sedge (*Carex rupestris*), and bistort (*Polygonum bistortoides*).

On zootic ecosystems the characteristic plants are controlled by the activities of small mammals including the pocket gopher (*Thomomys talpoides*), and voles (*Microtus* spp.).

The tundra environment is cold, windy, and highly variable. Winters are long and cold, summers are short--averaging 40 to 70 days of growing season with hail, sleet, and snow possible year round.

Rocky Mountain National Park is managed as a natural area. Natural resources and processes must remain essentially unaltered. Revegetation projects, therefore, are directed toward

[1]Rocky Mountain National Park, Estes Park, Colorado 80517.

duplicating or restoring the natural vegetation composition and structure. The constraints in a natural area mean artificiality should be kept to a minimum. Manipulation of the terrain and vegetation, however, may be carried out to encourage, simulate, or restore natural conditions on lands altered by human activities.

## HISTORY

Attempts at restoration and revegetation were initiated as early as 1933 in Rocky Mountain National Park. The construction of Trail Ridge Road presented a need for control of erosion along the new route and restoration of the site of the Fall River Road on the west side of the park where it was to be abandoned. The availability of labor from the Civilian Conservation Corps provided manpower for the project. The early efforts were almost entirely a transplanting program. At lower elevations this included shrubs and trees.

In August 1938, native seeds were collected under the supervision of Dr. H. D. Harrington of Colorado State University. The seeds were planted in plots along Trail Ridge Road from 9500 feet at Hidden Valley to 11,800 feet on twenty two plots in September and October. When reported on by Harrington (1946), the experiment was considered a success. Of twenty four species tested, fifteen seemed to offer particular promise. It was concluded that in this experiment, the seeding of denuded areas with native species did help in initiating natural succession of vegetation.

In 1941 one of the most revealing experiments was made in revegetation of the alpine tundra. Approximately 21,000 square yards (two-thirds of the back slope of Trail Ridge) were "spot sodded." Records show 8700 mandays of CCC labor were used to lay tundra sod in spots and strips along Trail Ridge Road. The records are unclear as to the exact technique but vegetative reproduction was expected to fill in the spaces between the spots. Today, however, both the spots and the strips can be seen essentially as they were laid.

In 1958 a study was initiated on the ecosystems of the park to determine the nature and degree of effect of visitors (Marr and Willard, 1970; Willard and Marr, 1970). The five-year study emphasized the alpine tundra. Besides providing excellent data on where and what impact visitors were having, specific data on recovery rates of the tundra without man's aid were obtained. For this purpose two sites, damaged by human use, were fenced to human trespass in order to prevent further disturbance and allow natural recovery.

Studies by Greller (1974) of road cuts and slopes were made to identify plants most successful in occupying newly exposed sites to determine species that provide maximum coverage in the briefest time and to indicate patterns of succession and the extent to which these can be relied upon to repair damaged tundra. His findings indicated extensive human assistance was necessary if road cuts were to be revegetated.

In 1965 the landscaping around the Alpine Visitor Center at Fall River Pass was accomplished by transplanting tundra from areas disturbed by the enlargement of the parking area. This project was very successful and today provides an adequate replica of the undisturbed tundra on similar sites.

Two other studies on lower elevation sites also provided data applicable to the alpine.

In 1969 a short area of cut slope in subalpine zone above Hidden Valley was restored with two treatments in an attempt to determine a technique to stabilize these areas. One site was laid back to the angle of repose at 1 1/4:1. This required considerable cutting of trees above the slope and removal of fill material. The other treatment built up the slope by using wire gabions to a 1/2:1 slope. Both areas were topsoiled and seeded in the fall. No effort was made to hold the soil against winter winds and, therefore, by spring most of the topsoil was gone along with the seed. Vegetation establishment has been very slow, and today some vegetation is developing at the low edge of both sites.

Another study in 1968 by Gary Jollif attempted to determine techniques of revegetation of deteriorated sites on three roadside campgrounds in the upper montane and subalpine zones. His findings showed that the critical factors to plant establishment were available nitrogen and soil moisture.

## CRITICAL FACTORS

The preceding studies, among others, indicated certain environmental factors that must be considered or compensated for in order for restoration efforts to be successful. These environmental factors do not act independently; they are all interrelated.

Generally, the extreme variability of the alpine environment in almost all aspects is the major difference from lower elevations. This is illustrated by the large number of vegetation types, associations, and stands that are described by most investigators for relatively small areas of tundra (Marr, 1962). Each site is unique, based on geologic substrate, exposure, slope, elevation, and glacial history, and how these factors effect other environmental characteristics.

Soil on the alpine varies from large rocks to fine silty clay. The need of soil for plant growth is well established and is no different for the alpine tundra. Usually soil is lost through wind and water erosion on disturbed sites. The primary consideration in relation to soil is its stability. Plants cannot be established if the substrate is constantly moving or eroded away. The depth of the organically rich layer must be maintained to at least what would be naturally present at the site. Willard (1976) estimated 500 to 1000 years to build an inch of topsoil. This is related to the slow breakdown of organic matter because of the low temperatures in the alpine (Holch *et al*, 1941). Greller (1970) stated that stabilization, increased soil moisture, and increased organic matter greatly facilitated colonization of denuded sites. This was also confirmed by Brown (1976). The water holding capability of the soil is also improved by adding organic matter as mulch.

Soil fertility can also be limiting under alpine conditions. Nishimura (1974) stated that "nitrogen can be limiting in the alpine environment and that cold soils were found to inhibit the absorption of phosphorus." He recommended a soil survey be made to determine the need for fertilization. Brown (1976) found productivity 100 times greater where fertilized over a three year period.

The effects of wind may be the most important factor that needs to be considered. Glidden (1974) showed that Trail Ridge may have some of

the most extreme wind conditions known. During the period January to May 1974, 44% of the days had winds greater than 74 miles per hour (hurrican force), and 14% had over 100 miles per hour. The top wind speed recorded was 155 miles per hour. The summers are considerably less windy. Marr and Willard (1971) measured mean wind speeds of 26 mph in December but only 10 mph in July. These effects must be compensated for in restoration projects in order to hold the soil, seed, mulch, and protect from mechanical damage. Wind blown snow and sand can be especially damaging to vegetation. Desiccation from the wind also reduces the effective moisture level and dries out denuded soil rapidly. In winter it lowers the ambient temperature generally maintained by soil radiation.

Wind in relation to physiography of the terrain is responsible for snow accumulation. The distribution and depth of snow in accumulation areas is the factor primarily responsible for the mosaic of vegetation types. The depth of snow cover on the vegetation provides different micro-environments, shortens the growing season, and provides a source of moisture as it melts. Snow also moderates the winter temperature extremes.

Moisture comes to the alpine in the form of snow in the winter and generally thunderstorms in the summer. Summer thunderstorms can be especially severe, causing soil movement and erosion. Marr and Willard (1970) measured a mean annual precipitation of 25 inches with the maximum mean of 3 inches in August. The driest month was October. Bell (1975) reported drouth conditions in June and stated that soil moisture may be limiting at any season.

Some of the most important factors to restoration are the relation of soil moisture and temperature. The formation of "needle ice" as described by Marr (1962) may be an important factor in seedling establishment. As the subsurface moisture freezes on bare areas, it forms long ice crystals that force the surface up. This action disturbs or breaks off the fragile roots of seedlings, causing them to die when the ice melts. Frost heaving can also disturb established vegetation, but it apparently is not as severe because of the insulation provided by the plants themselves.

Temperature extremes are common on the tundra, especially in summer. Bell (1975) measured a maximum change of 14°F in two minutes. These changes may be even more extreme on the surface of organically rich black soil which is open to radiation (Willard and Marr, 1971). They found that bare humus soil of the A horizon supported the fewest seedlings when compared to the B and C horizons and concluded that this was because of needle ice activity in the spring and fall and desiccation under higher summer temperatures. The growing season on the tundra is as short as 45 days (Marr, 1961) with snow possible any day of the year.

The source of seed for restoration efforts is important. If seeds are available, the native alpine plants have evolved over millions of years and should be better adapted to the environment. Brown (1976) results confirmed this on the bear-tooth plateau. Reports by Cox (1933), Griggs (1956), Osburn (1961), Greller (1974) and Willard (1971) would indicate that seeds are present in sufficient numbers on the alpine to revegetate disturbed sites. Holch *et al* (1941) and Bell (1975), however, indicate that this may not be the case with at least some species. Brown stated that of the 200 plant species found, less than 10% were active colonizers.

Plant succession, if it occurs at all, must be very slow on the alpine. As stated by Willard (1971), "secondary succession back to a climax kobresia stand is tediously slow; there are no precise data on time intervals, but our joint studies and those of Griggs (1956) Osburn (1958) and Willard (1960-63) all indicate it will take at least several hundred and possibly even a thousand years for ecological processes to produce a persistent (climax) ecosystem." Greller (1975) indicated that plant succession plays a minor role on the road slopes. He also emphasized the importance of stabilization to the establishment of early successional plants.

## PRESENT STUDIES

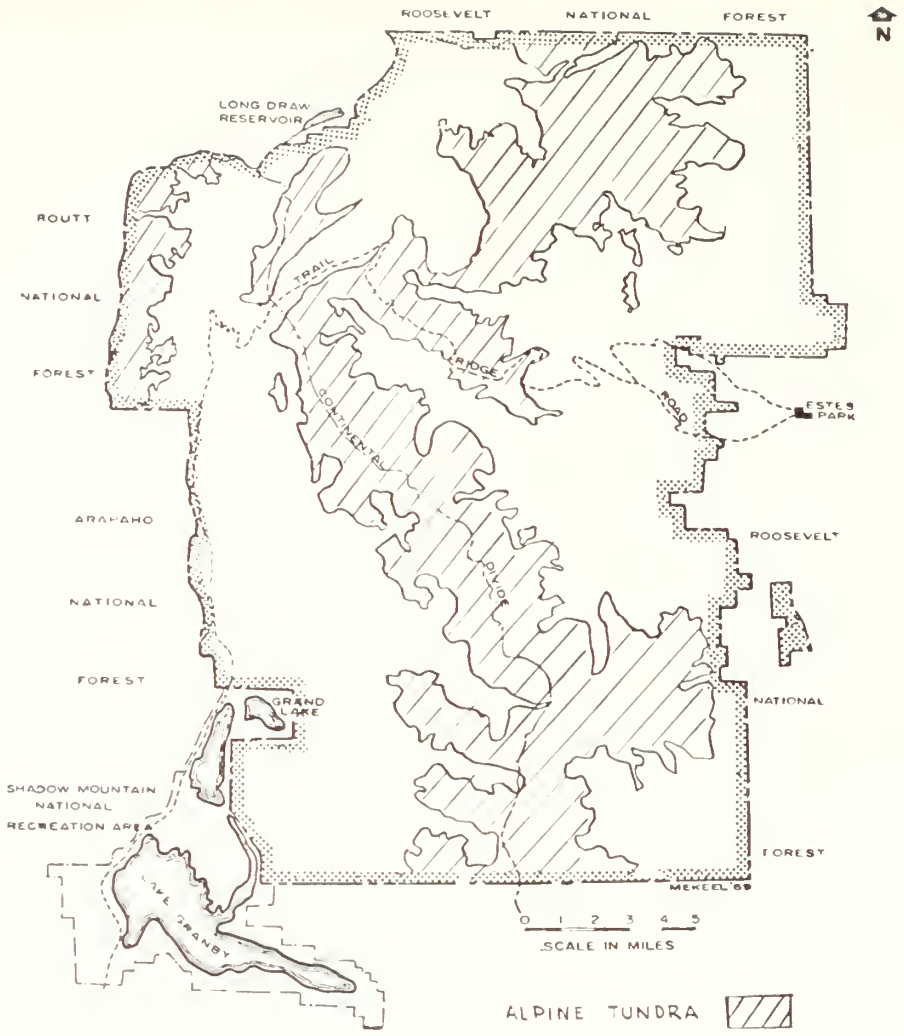
In 1975, on the site where several buildings were removed from the tundra, a study of restoration techniques was initiated. The site is essentially a fellfield ecosystem. Using results from the aforementioned studies and revegetation efforts, a plan of experimental plots was worked out. The primary objective of the project was to test various techniques which appeared to offer some solution to the previously mentioned problems essentially unique to the alpine environment. A secondary objective was to develop a vegetation cover on the site which resembled, at least superficially, the undisturbed tundra. The adverse effects of water and wind erosion, along with temperature extremes, are being reduced through snow fences, burlap mat, and aspen mat. Topsoil was added on several plots, with and without mulch. Mulch was cut from similar sites of alpine tundra in an attempt to include some native plant seeds. No other seeds were planted, assuming the seeds would be available. Fertilizer, mostly nitrogen, was added to some plots. All were treated in September 1975 and water was added initially.

Initial results are encouraging. There was no lack of seedlings the first summer. Many, however, were normal invaders from lower elevations such as *Rumex* spp. and *Chenopodium* spp., and may have been imported with the topsoil. Survival of these in succeeding growing seasons will be measured.

This year another site disturbed by vehicle encroachment at Fall River Pass was treated using similar techniques. This site is primarily alpine turf with considerable kobresia. Based on one year's data, the use of burlap to control erosion was not duplicated, but a jute mesh was used instead. The progress of both plots will be monitored both photographically and quantitatively. These studies, however, are considered to be long term with no meaningful results expected for several years.

## CONCLUSIONS

One of the conclusions of about 40 years of revegetation efforts in Rocky Mountain National Park is that to restore high elevation alpine tundra land requires considerable effort and assistance by man. We find that the best management is protection of the resource before damage exceeds what is naturally repairable. As stated by Bell (1975), "It seems prudent to consider kobresia meadow effectively irreplaceable and to preserve them intact." In the case of visitor trampling, this is being accomplished by channeling the visitor activities with fences, paved walkways, and trails. Education programs also




ROCKY MOUNTAIN NATIONAL PARK

must be utilized to inform the visitor of the seriousness of the loss of tundra vegetation. However, we realize some damage is still going to occur and periodically restoration, if possible, will be necessary.

Experience has demonstrated that transplanting natural tundra turf (from a similar site) is the most successful technique to restore damaged sites. The major problem is that there is usually no source of tundra turf for transplanting purposes without damaging other areas. Without tundra for transplanting, a technique to regenerate alpine tundra must still be developed. This is the major challenge in the management of alpine tundra today. Results of the present studies take time, and tundra revegetation, even with the best assistance available, is going to be a slow, tedious process.

LITERATURE CITED

BELL, K. L. 1974. Autecology of *Kobresia bellardii*. Ph.D. thesis, University of Alberta, Edmonton, Alberta. 167 pp.

BROWN, R. W., R. S. JOHNSTON, B. Z. RICHARDSON, and E. E. FARMER. 1976. Rehabilitation of Alpine Disturbances: Beartooth Pleateau, Montana. Proceedings of the High Altitude Revegetation Workshop, No. 2, Environmental Resources Center, Information Series No. 21, Colorado State University, Fort Collins, pp. 58-73.

COX, F. 1933. Alpine Plant Succession on James Peak, Colorado, Ecological Monographs 3:299-372.

GLIDDEN, E. E. 1974. Analysis of Alpine and Subalpine Wind Conditions in Winter in Rocky Mountains National Park, 91 pp.

GRELLER, A. M. 1974. Vegetation of Road Cut Slope in the Tundra of Rocky Mountain National Park, Colorado. Biological Conservation. 6(2):84-93.

GRIGGS, R. F. 1956. Competition and Succession on a Rocky Mountain Fellfield. Ecology 37(1): 8-20.

HARRINGTON, H. D. 1946. Results of a Seeding Experiment at High Altitudes in Rocky Mountain National Park. Ecology 27(4):375-377.

HOLCH, A. E., E. W. HERTEL, W. O. OAKES, and H. W. WHITWELL. 1941. Root Habits of Certain Plants of the Foothills and Alpine Belt of Rocky Mountain National Park. Ecological Monographs 11:327-345.

JOLLIF, G. D. 1969. Campground Site Vegetation Relationships. Ph.D. thesis, Colorado State University, Fort Collins. 139 pp.

KIENER, W. 1967. Sociological Studies of the Alpine Vegetation on Longs Peak. University of Nebraska Studies, Series No. 34.

MARR, J. W. 1961. Ecosystems of the Front Range, Colorado. University of Colorado Studies, Series in Biology No. 8. 134 pp.

MARR, J. W. 1964. Utilization of the Front Range Tundra, Colorado, Pages 109-118. Grazing in Terrestrial and Marine Environments, Editor D. J. Crisp. Blackwell Scientific Publications, Oxford, England. 332 pp.

MARR, J. W. and WILLARD, B. E. 1970. Persisting vegetation in an Alpine Recreation Area, in Southern Rocky Mountains, Colorado. Biological Conservation 2(2):97-104.

NISHIMURA, J. Y. 1974. Soils and Soil Problems at High Altitudes. Proceedings of a Workshop on Revegetation of High Altitude Disturbed Land. Environmental Resources Center, Colorado State University. Information Series No. 10. Pages 5-9.

OSBURN, W. S. 1958. Ecology of Winter Snow-Free Areas of the Alpine Tundra of Niwot Ridge, Boulder County, Colorado. Ph.D. thesis, University of Colorado. 77 pp.

OSBURN, W. S. 1961. Successional Potential Resulting from Differential Seedling Establishment in Alpine Tundra Stands. Bulletin of the Ecological Society of America. 42:146-147.

WILLARD, B. E. 1960. Ecology and Phytosociology of the Tundra Curves Area, Trail Ridge, Colorado. MS thesis. University of Colorado. 144 pp.

WILLARD, B. E. 1963. Phytosociology of the Alpine Tundra of Trail Ridge, Rocky Mountain National Park, Colorado. Ph.D. thesis. University of Colorado. 243 pp.

WILLARD, B. E. 1976. High Elevation Reclamation Nuts and Bolts. Proceedings of the High Altitude Revegetation Workshop No. 2, Environmental Research Center. Information Series No. 21. Colorado State University, Fort Collins. Pages 1-3.

WILLARD, B. E. and J. W. MARR. 1970. Effects of Human Activities on Alpine Tundra Ecosystems in Rocky Mountain National Park, Colorado. Biological Conservation 2(4):257-265.

WILLARD, B. E. and J. W. MARR. 1971. Recovery of Alpine Tundra under Protection after Damage by Human Activities in Rocky Mountain National Park. Biological Conservation 3(3):181-190.

# ECOLOGY OF SHORELINE VEGETATION, LAKE POWELL

Loren D. Potter[1]

## INTRODUCTION

Lake Powell is a man-made reservoir created by the construction of Glen Canyon Dam at Page, Arizona. The lake occupies the stretch of the Colorado River formerly called Glen Canyon and extends from the dam to Cataract Canyon. The lake and surrounding area have been set aside under the National Park Service as the Glen Canyon Recreation Area. The control of water levels and power production at the dam are under the jurisdiction of the Bureau of Reclamation. Because of the aridity of the region there is a close correlation between geological formations and the development of vegetation. The emphasis here is on neither the aquatic ecosystem nor on the terrestrial ecosystem, but on the transition between the two--the interface of land and water which makes up the shoreline.

Research was supported by grants NSF-RANN GI-34831 and NSF-AEN 72-03462 A03 to the Shoreline Ecology Subproject. This is Contribution No. 45 of the Lake Powell Research Project Contribution Series.

## SETTING

The general course of the Colorado River and tributaries was established by Miocene time across the uplifting, folding, and faulting of sedimentary strata. The early Miocene channel today is the broad upper gorge. A second cutting cycle in Pliocene-Pleistocene carved an inner gorge through the Carmel, leaving it as a broad platform, and through the Glen Canyon group of Navajo, Kayenta, and Wingate sandstones leaving steep cliffs and talus slopes. Because of the net dip slope to the west, the upper end of the reservoir is on exposures of the oldest formations down to Pennsylvanian Hermosa limestone. The low average gradient of the riverbed in Glen Canyon of 2 feet per mile passes in and out of varying strata because of the uplift and dip of strata caused by the adjacent uplifts of the Henry Mountains, the Kaiparowits Plateau, the Circle Cliffs, the Monument upwarp, and the laccolithic Navajo Mountain. Into the Glen Canyon area steep-walled, deeply incised tributary canyons had formed.

In the Lake Powell area expanses are vast, desolate, and relatively uninhabited. Plateaus are deeply incised into vertical-walled gorges. The sparseness of vegetation, the erodability of the sandstone, and the intensity of summer thunderstorms result in rapid run-off, scouring of surfaces to form "slickrock", and the accumulation of eroded sand into shallow basins. Run-off down steep canyons causes erosional pits or splash pools, which are now the most mesic sites of the area. Penetration of moisture through porous sandstone to a limestone layer results in lateral movement and emergence at cliff faces as calcium-enriched seepwater and the development of a calciphilous vegetation. The general regional vegetation is dominated by blackbrush (*Coleogyne*) and Mormon tea (*Ephedra*). Stream riparian stands of sedge, willow, cottonwood, and oak are now limited to the upper reaches of side canyons, where the steep gradient makes them sparse or absent, and to unflooded tributaries such as the Escalante, San Juan, and Dirty Devil rivers.

[1]Biology Department, University of New Mexico, Albuquerque.

## RIVER TO A LAKE

Cataract Canyon, unchanged by the reservoir, is a steep-gradient rushing, aerated river desired for boat trips and which in comparison causes disappointment on reaching the quiet waters of Lake Powell. Below the lake is a river greatly changed by the reservoir. Now the scouring and depositions of spring floods have yielded to controlled releases; clear, cold water; no scouring; no deposition; dense algal growths; and maturing river terrace forests of tamarisk.

Behind Glen Canyon Dam is a reservoir 565 feet deep, 186 miles long, with a volume of 28 million acre feet, and area of 164,000 acres, backing up the San Juan River for 75 miles, and a total shoreline of 1800 miles--the equivalent of the entire Pacific coastline from Tihuana, Mexico, to the Olympic Peninsula. The many aspects of Glen Canyon prior to flooding have been excellently summarized by Jennings (1966).

Where the river flows into the lake, changes are variable. A new seasonal cycle of flooding of shoreline vegetation is determined by controlled releases at the dam superimposed upon natural inflow rates and evaporational losses. The impact of rushing floodwaters changes to that of the impact of wave action. On entering the lake, river water current diminishes, silt load gradually settles, and turbid, cold, saline water tends to sink. In spite of the great length and volume of the lake, it exhibits lateral transport and mixing features typical of a river and affecting its biological and physical properties (Standiford, Potter, and Kidd 1973; Reynolds and Johnson 1975; Jacoby, Jr. 1975; Kidd 1976; and Reynolds 1976). The general aspects of the shoreline ecology of Lake Powell have been published by Potter (1976).

## SHORELINE SURFACE MATERIALS

Because of the close correlation of geological strata, physiography, and shoreline surface materials to the development of vegetation, to siltation into the reservoir, vegetational succession, recreational use of the shoreline, and management of the reservoir, one research effort was to map the shoreline. This was done for the entire 1800 miles at a scale of 13 inches/mile (1 inch = 400 feet) at four contour levels from 3620-3700 feet. Although folds and uplifts result in variations of strata along the shoreline, these balance out to provide a remarkable consistency from 3620 to 3700 feet. The percentage of each classification of shoreline surface materials and mileages at four contour levels are given in Table 1.

TABLE 1. The percentage and total mileage of shoreline surface materials.

| Type | Elevation (ft) 3620 | 3660 | 3680 | 3700 | Av. |
|---|---|---|---|---|---|
| Cliff | 53 | 53 | 54 | 54 | 54 |
| Domed terrace | 22 | 21 | 21 | 21 | 21 |
| Talus | 18 | 17 | 19 | 19 | 18 |
| Sand | 3 | 3 | 2 | 2 | 3 |
| Shelfy terrace | 2 | 2 | 2 | 2 | 2 |
| Alluvium | 1 | 3 | 1 | 1 | 1 |
| Rock slide | 1 | 1 | 1 | 1 | 1 |
| Miles | 1472 | 1638 | 1733 | 1823 | |

Since 1974 the reservoir has been in the process of filling. Although there have been interruptions, the normal pattern of filling is to reach peak levels in July and then drawdown to low levels in January or February. These fluctuations will continue after the reservoir has been filled to maximal level. Therefore, there is an important effect of the drawdown on the physical-biological features of the several shoreline surface materials which affect the quality of the lake, aesthetic aspects, and recreational use of the shoreline.

Cliff walls, too steep on which to land a boat, vertical or overhanging, dominate the shoreline and provide the unusual beauty of Lake Powell. In alcoves vertical bare walls are broken by seepline vegetation and sometimes mesic woody groves below with species equivalent to a moist deciduous forest. Large rock spalls have broken off. A principal result of exposure during drawdown is a white "bathtub ring" composed of precipitated minerals from the rock plus the dried remains of algae and diatoms.

Domed terrace areas of smoothly rounded contours with curved basins between provide excellent, clean, rock campsites and are little affected by the drawdown process. Local pockets of sand, often the "garden spots" of the shoreline are highly impacted areas because of their use for toiletry.

Talus slopes vary from mixtures of coarse and fine materials to mostly sand blown off the adjacent plateau forming "fallen dunes". Slopes may be hundreds of feet high and are precarious areas for shoreline use because of slumping and falling rocks. Submergence and then drawdown result in removal of fine-textured particles leaving coarse boulder shorelines and a weakening of the base which often results in talus slumps.

Sand deposits, often as dunes, represent only 3 percent of the shoreline. These areas, and the alluvium, have the richest vegetation both in species diversity and foliar coverage. Submergence destroys the vegetation but upon exposure as a drawdown zone provides the most favorable seed bed for plant reinvasion. It quickly recovers its vegetational cover but with a definite decrease in diversity of species.

Shelfy terraces result from tilted, finely cross-bedded sandstone, particularly of the upper Navajo sandstone. It poses some difficulty in landing a boat and finding a level place on which to sleep. Submergence tends to soften its sharp edges to some extent.

Alluvial covered terraces are a very minor (1%) part of the shoreline now found only up the major tributary rivers and near the heads of a few broad canyons. Upon flooding, these deposits add the most nutrients and organic matter to the lake. Many areas support groves of trees, heavily used for campsites. Upon flooding, most alluvial terraces slump into the bottom sediments. Where remnants remain they become covered with silt and remnant driftwood. Plant succession is diverse and rapid after exposure.

Rock slide areas occur principally where Wingate sandstone overlies the softening Chinle formation allowing massive collapse of the blocky, fractured sandstone. These areas are minimally affected by submergence and re-exposure and are unfit for shoreline use at any time.

On sandy shores and alluvial terraces there is a lateral movement of water from the contour of maximal water level which results in a zone of growth stimulation of vegetation. Native species such as Indian ricegrass (*Oryzopsis hymenoides*), blackbrush (*Coleogyne ramosissima*), sacred datura (*Datura meteloides*) and evening-primrose (*Oenothera* spp.) proliferate vegetatively and develop masses of flowers and fruits.

## VEGETATIONAL BIOMASS

By the use of clip plots and species separations, evaluations of the standing vegetational biomass foliage cover, and species composition for each of the major shoreline types were obtained. Some of this information is summarized in Table 2.

Noteworthy is the relatively high biomass and coverage in the sandy shoreline. However, after submergence and re-exposure for one year to plant invasion, the foliage cover of the original native vegetation is nearly equaled; but a major change occurs in species composition--which is the emphasis of the balance of this paper.

## VEGETATIONAL INVASION OF DRAWDOWN ZONE

The dominant plant of the sand and alluvial drawdown zones is tamarisk (*Tamarisk pentandra*), an introduced Eurasian exotic which has been successful in spreading throughout the Southwest. Its light, air and water borne seeds allow for discontinuous distribution. It is favored by a moist, sandy seedbed and is tolerant of the common alkaline conditions; it flowers and matures fruit over a long period; it germinates quickly after dispersal; it produces a rapid growing taproot; it has a favorable root:shoot ratio; it develops lateral roots, root sprouts and a bushy growth form; it is resistant to burial or submergence; it remains evergreen the first year for seedling growth and after that becomes winter deciduous; and it can flower, fruit, and produce vegetative root sprouts within a year. Its list of attributes as a pioneer invader is astounding!

As the water level is lowered from its peak level in July the sandy shores are receptive seedbeds to water-washed tamarisk seeds. Germination occurs and seedlings are repeatedly moistened by wave action. In a few weeks rows of tamarisk seedlings appear on contour lines and continue to appear on successive recessional levels in the period from July to mid-August after seedlings are scarce until the first week in September, Figure 1.

TABLE 2. Summary of the dominant species, total standing biomass, and total foliage cover in several vegetational types on shoreline surface materials.

| Species (over 10% biomass) | Domed terrace | | Shelfy terrace | | Dune sand | | Sandy drawdown | | Talus | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Rel. wt. % | Rel. cover % | Rel. wt. % | Rel. Cover % | Rel. wt. % | Rel. cover % | Rel. wt. % | Rel. cover % | Rel. wt. % | Rel. cover % |
| *Coleogyne ramosissima* | 29.2 | 13.0 | 40.0 | 17.0 | 35.4 | 19.7 | | | 19.5 | 11.7 |
| *Gutierrezia microcephala* | 15.7 | 28.8 | 16.9 | 20.3 | | | | | | |
| *Ephedra torreyana* | 11.9 | 4.8 | 8.8 | 12.7 | | | | | | |
| *Oryzopsis hymenoides* | | | | | 13.7 | 24.6 | | | | |
| *Ephedra viridis* | | | | 11.0 | 11.7 | | | | | |
| *Tamarix pentandra* | | | | | | 66.0 | 55.5 | | | |
| *Oenothera pallida* | | | | | | 24.0 | 19.8 | | | |
| *Haplopappus drummondii* | | | | | | | | 30.2 | 30.9 | |
| *Atriplex confertifolia* | | | | | | | | 27.4 | 22.4 | |
| Total biomass (oven-dry g/M$^2$) | 13.8 | | 11.7 | | 86.5 | | 13.3 | | 45.2 | |
| Total foliage cover % | 1.5 | | 1.4 | | 5.0 | | 4.5 | | 5.0 | |

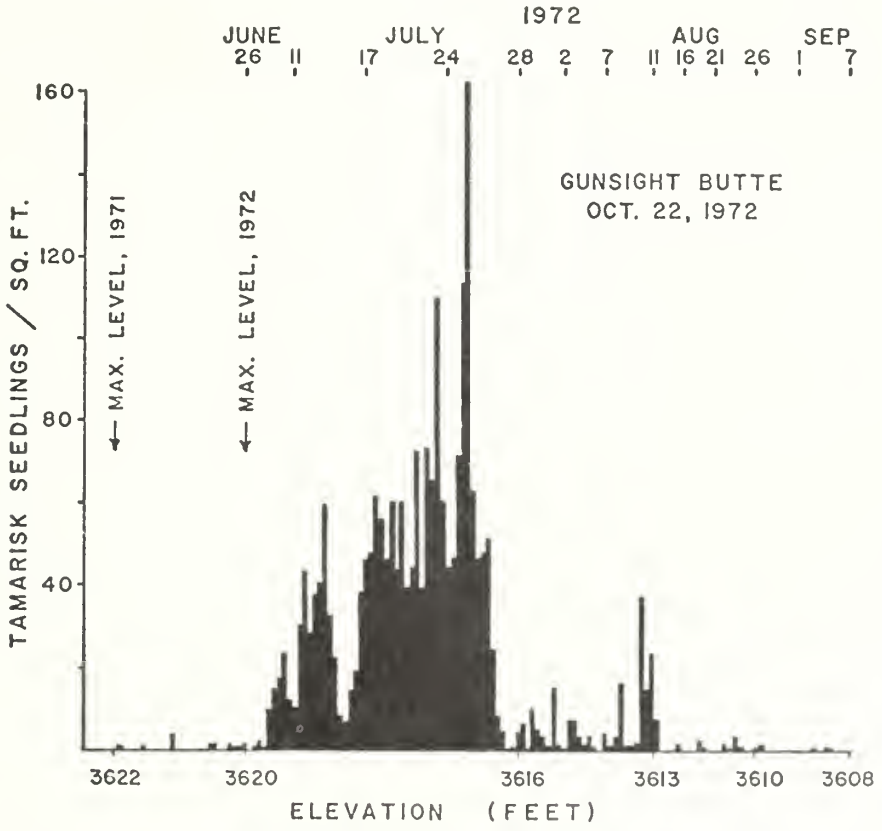



FIGURE 1. Tamarisk seedling establishment along sandy shore of drawndown zone from late June to September.

Where the shoreline is gently sloping vast acreages of the upper drawdown zone may become a verdant meadow of tamarisk seedlings, as may also occur on lower sandy river terraces along the Colorado River. The contours exposed after early September are either barren or dominated by Russian thistle (*Salsola kali*), another introduced, exotic invader.

By the following May or June, tamarisk plants may be a meter or more tall. If July peak water levels do not exceed those of the previous year tamarisk plants continue and reach heights of 2 to 3 meters. During stages of filling a reservoir, peak levels normally continue to be higher each year so that shorelines during the summer recreational period are along recently flooded and original climax vegetation. When the reservoir reaches full pool, or when July levels are less than the year before, the successional vegetation of the upper drawdown zone remains exposed and continues to grow. Examination of the dense thickets of tamarisk along the Colorado River terraces is indicative of what can be expected to happen along the alluvial and sandy shores of Lake Powell. Tamarisk stands and reinvasion have not been eliminated during the filling years of the reservoir.

## SUBMERGENCE EFFECTS

The rate of physical breakdown and biological decomposition varies greatly among species depending on anatomical structure and chemical composition. Among trees, the more resistant are single-leaf ash (*Fraxinus anomala*), Gambel oak (*Quercus gambelii*), and netleaf hackberry (*Celtis reticulata*). Among the shrubs, the most common and resistant is blackbrush (*Coleogyne ramosissima*) followed by Mormon tea (*Ephedra* spp). Spanish bayonet (*Yucca* spp.) remains green for several weeks then undergoes retting until it becomes a rosette-like mass of fibers. Forbs and grass quickly decompose. The decomposition of flooded vegetation is important in adding nutrients to the lake and the release of polyphenols which are inhibitors to calcite precipitation (Reynolds, 1976).

The submerged vegetation also provides a substrate for the growth of periphyton and invertebrates. Mantles of growth develop amazingly fast, within a week or two, providing a mantle of bacteria, blue-green and green algae, diatoms, and macro- and micro-invertebrates. These are important as a basic food supply to fish populations but become highly undesirable when they form mats of organic material off sandy shorelines used for swimming and water recreation.

Simultaneous with periphyton development has been a rapid development of benthic organisms on the bottom substrates. A granular, highly flocculated complex of silt and organisms of olive-green color covers many offshore areas. Below the mineral surface of submerged shorelines a zone of chemical reduction quickly develops which becomes blackened and omits an odor of hydrogen sulphide. The more organic matter which is added, the greater this effect becomes.

The greatest potential addition of organic matter to submerged sandy and alluvial shorelines is tamarisk. Based on the data of tamarisk seedling establishment during the period of July to September, an experiment was conducted to test the possibility of control of seedlings by water manipulation. If the water level was lowered from the peak level and held until seedlings were established in the narrow zone, then raised to flood the seedlings and subject them to wave action and sand abrasion, the tamarisk seedlings might be eliminated or reduced. The water level could then be lowered during the time after which seedling establishment does not occur. Known numbers of 1, 2, and 3-months-old seedlings in fiberglass containers were submerged off a sandy shoreline in Wahweap Bay so that the soil level was covered by 50 centimeters of water. At appropriate intervals, containers of plants of each age were removed and partially buried in the sandy shore just above the waterline. Several days after removal surviving plants were counted. Figure 2 is based on the data obtained. Three days of submergence resulted in 50% mortality of 1-month seedlings-a degree of elimination not reached until about 6 days for 2-month-old seedlings and not until more than 24 days for 3-month-old seedlings. About 95% mortality was attained for 1-month-old seedlings at 12 days and 100% elimination for both 1-and 2-month-old seedlings after 24 days.

The increased resistance of tamarisk with age was illustrated in a stand at Wahweap Bay which was established in July to September 1974. Plants were 1 to 2 meters tall by the time the bases were flooded June 26, 1975. The water rose to a new peak level in 1975 and completely covered the tops of 2-meter-tall tamarisk plants for a period of 34 days. During the submergence, many twigs and leaves stayed alive; adventitious roots were developed from submerged stems and functioned as aquatic absorptive roots. Upon emergence with the drawdown in August to October many shoots increased their chlorophyll in existing leaves and others produced new shoots. Within a month's time after exposure of upper twigs some plants were in flower and even fruit. As the water retreated to the base of the plants, adventitious stem roots (now aerial) became nonfunctional and growth was dependent on the original root system in the sand. During submergence, the sandy substratum had become so low in oxygen as to produce a zone of reduction, black in color and 7 centimeters deep in which the roots had sloughed off. Roots below were still functional. Lateral shoots soon developed from root sprouts.

The tremendous adaptability of this riparian species to flooding after plants reach several months of age and its many mechanisms for rapid recovery upon emergence are aided by the flooding death of most other species which remove them from interspecific competition.

## SHORELINE PREDICTIONS

Within several years full pool level at 3700 feet should be reached and then it can be expected that the level will be lowered to about 3660 with seasonal water level fluctuations. The 54% of cliff shoreline will have a visual "bathtub ring" which can be expected to endure for several decades. Slightly affected will be the 21% of domed terrace shoreline except that pockets of silt and sand will be reinvaded by pioneer vegetation including tamarisk which will endure as long as there is a moisture supply. Talus slopes and rock slides (19 and 1%) will show slumping, some will completely disappear. The sand and alluvium shorelines (each 3%) will be smoothed in contour and have increased concentrations of silt and organic matter. This 6% of shoreline receives almost all of the impact of recreational shoreline use. These areas are gently sloping; they are safe shores on which to

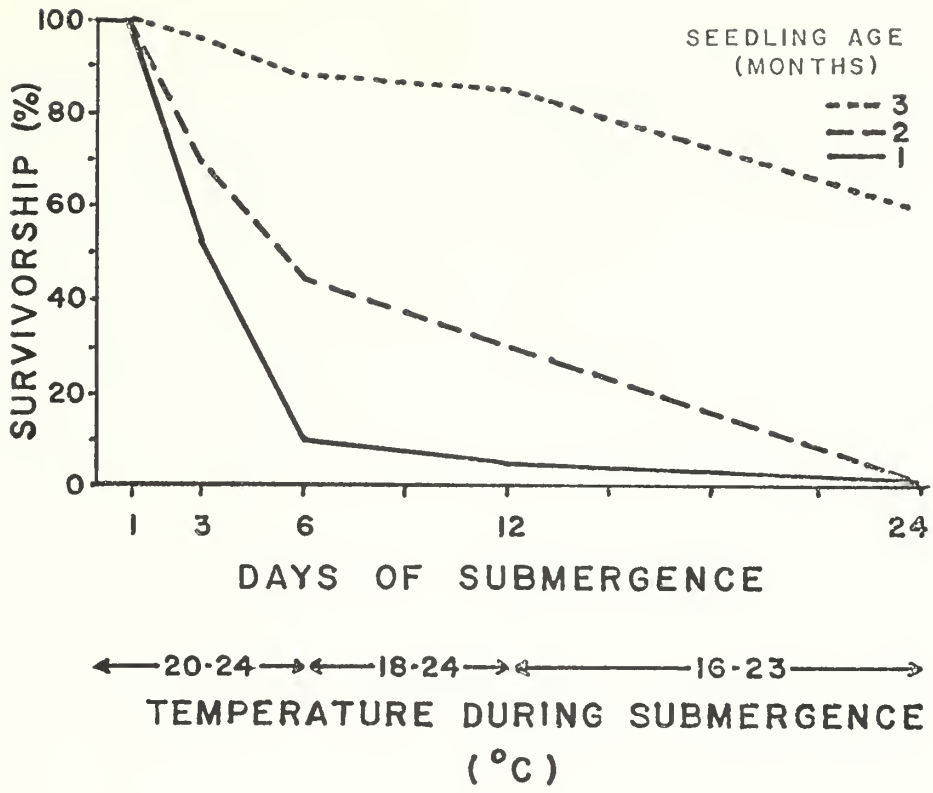



FIGURE 2. Survivorship curves for several ages of tamarisk seedlings submerged in Lake Powell in October.

land a boat; they provide a means of safely tying a boat; it is possible to pitch a tent in the sand; areas are level enough on which to sleep; and for those not using portable toilets the sandy areas are most frequently used for toiletry. Swimming and water sports commonly demand a sloping sandy shoreline, especially for children. Finally, there is a common attitude that a lake vacation means camping and playing on a sandy shore. The minority--those who sleep on boats, swim only in deep water, or prefer slickrock surfaces, is recognized.

The limited sand and alluvium shores--focal points of recreational use--are also the sites most susceptible to the greatest change in vegetation after flooding. Tamarisk invasion can quickly lead to dense thickets. Growths of 1 to 2 meters per year are attained. Unlike river terrace stands which are scoured by floodwaters, lake margin stands will endure flooding, become covered with silt and periphyton, add to submerged organic material, and rapidly change the nature of a formerly clean, sandy bottom. Observation of tamarisk patches in densely used recreational areas shows an avoidance of these shores even with one year's growth of tamarisk. Bringing a boat to shore through a dense tamarisk thicket, swimming in algal-covered submerged stands with mucky-covered bottom, and camping in tamarisk thickets with accompanying populations of noxious insects will not be an enriching, aesthetically pleasing experience.

As the water level is lowered from full pool, one can expect tamarisk to advance down slope on sandy shores. Where soils are deep tamarisk stands will survive and provide a seed source; where shallow they may die. Approximately 294 miles of shoreline are susceptible to tamarisk invasion. The acreage between 3700 and 3660 feet has been computed to be 10,414 acres, equivalent to 16 square miles. At a conservative figure of 4 feet of water-loss per season by evapotranspiration of tamarisk, the potential loss would represent 41,600 acre-feet per year.

Because of the importance of the limited sandy shoreline for recreational use in Glen Canyon National Recreation Area, it is recommended that some control measures for tamarisk be instigated as soon as full pool level is reached. The cost is least and the effectiveness greatest when control is started with seedling or young-aged stands. There is no way to completely eliminate the species and control, like maintenance, is a continuing process. Some priority ranking based on scarcity and need for sandy shorelines should be a basis for selection of areas to manage and the degree of expenditure to invest. In limited areas it may be advisable to use either herbicides or mechanical control.

There is some evidence of both cottonwood (*Populus* spp.) and Russian olive (*Elaeagnus angustifolia*) successfully rooting and establishing themselves along the same sandy shores. Their

shade provides some competiton against tamarisk development and they are much more desirable for shoreline campsites. Plantings in dispersed clumps may be advisable.

There is a need for continued research on the ecology of tamarisk in relation to its invasion of both river and reservoir shorelines to determine acceptable ways to lessen its deleterious effect on critical recreational areas.

## LITERATURE CITED


JACOBY, G. C., JR. 1975. An overview of the effect of Lake Powell on Colorado River Basin Water Supply and Environment. Lake Powell Research Project Bulletin No. 14, Institute of Geophysics and Planetary Physics, UCLA, Los Angeles.

JENNINGS, J. D., 1966. Glen Canyon: A Summary. Univ. of Utah Anthro. Papers, No. 81, Glen Canyon Ser., No. 31. 84 p.

KIDD, D. E., 1976. Bacterial Contamination of Lake Powell Waters: An assessment of the problem. Lake Powell Research Project Bulletin No. 16., Institute of Geophysics and Planetary Physics, UCLA, Los Angeles.

POTTER, L. D., D. KIDD, and D. STANDIFORD. 1975. Mercury levels in Lake Powell-Bioamplification of mercury in a man-made desert reservoir. Environ. Sci. and Technol. 9:41-46.

POTTER, L. D., 1976. Shoreline Ecology of Lake Powell. Lake Powell Research Project Bulletin No. 29, Institute of Geophysics and Planetary Physics, UCLA, Los Angeles.

REYNOLDS, R. C., JR. and N. M. JOHNSON. 1975. Major Element Geochemistry of Lake Powell. Lake Powell Research Project Bulletin No. 5, Institute of Geophysics and Planetary Physics, UCLA, Los Angeles.

REYNOLDS, R. C., JR. 1976. Inhibition of calcite precipitation by polyphenols. Lake Powell Research Project Bulletin No. 35, Institute of Geophysics and Planetary Physics, UCLA, Los Angeles.

# NATURAL RESOURCES, WHITE WATER RECREATION, AND RIVER MANAGEMENT ALTERNATIVES ON THE COLORADO RIVER, GRAND CANYON NATIONAL PARK, ARIZONA[1]

Steven W. Carothers[2], Stewart W. Aitchison[2] and R. Roy Johnson[3]

## INTRODUCTION

The Colorado River, as it flows through Grand Canyon National Park, is not a free river - it has been contained, tamed and changed by two man-made structures, 350 miles apart, Glen Canyon and Hoover dams. Any discussion or investigation dealing with biotic resources and management decisions must take into consideration the effects these dams have had on the natural system.

Prior to the early 1960's, resource managers at Grand Canyon National Park were virtually unaware of or unconcerned with resource management problems along the Colorado River. Most of the Park visitors were concentrated on the south rim of the Canyon, and to a lesser extent, the north rim. Relatively few visitors entered the Canyon, and when they did it was usually on the well maintained trails of the inner canyon corridor. Back country hiking and river running were rare and management attention to these activities was minimal.

In 1963 the gates of Glen Canyon Dam were closed, forming Lake Powell. Beginning then, we entered an era beset with problems for the resource managers of Grand Canyon National Park.[4] The effects of Glen Canyon Dam on the downstream resources have been dramatic.

Prior to the construction of Glen Canyon Dam, the Colorado River was a silt-laden river, warm in summer and cold in winter; the river's flow could fluctuate anywhere from almost no flow during dry summers to an excess of 200,000 cubic feet/second during spring floods (Fenneman, 1931). Now the river, as it originates from the bottom of Lake Powell, is clear and perpetually cold (45-50°F), diurnally tidal as water releases are based on power demands; and rarely does the flow fluctuate outside a range from 5,000 cfs to 35,000 cfs. From a resource management standpoint, the result of these changes in the character of the Colorado River has been twofold:

1. The predictable flows and clear water have resulted in the Colorado River below Glen Canyon Dam becoming one of the most sought-after white water recreation rivers in the Western Hemisphere.
2. The natural biotic system of portions of the riparian (stream-side) zone of the river has been destroyed and subsequently replaced by a new "exotic" system.

## THE MANAGEMENT PROBLEM

By late 1969 the Park managers were astonished at the annual increase in river running enthusiasts. Before 1963 fewer than 100 people had run the Colorado River through the Grand Canyon (Johnson and Martin, 1976). By 1967 the annual number of river runners had reached 2100, and river running was becoming a thriving business on the Colorado Plateau. Incredibly, by 1973 over 21 commercial boating companies and private outfitters carried over 15,000 people down the river, an increase of almost 700 percent in six years (see Figure 1). The Park Service could not ignore the fact that the high numbers of annual users were causing impact on the riparian resources of the Colorado River. Thus, during the summer of 1970 the National Park Service began the first of several research expeditions down the Colorado from Lee's Ferry to Diamond Creek, a distance of 225 river miles. Participating in these expeditions were several scientists from a variety of disciplines and institutions. The Park Service was interested in having the scientists view the river system first hand so that they could participate in the formulation of a meaningful and productive research/management plan. Then, early in 1973, the NPS initiated a large scale research project (see Johnson and Martin, 1976) designed to obtain sufficient data whereby a river management plan could be developed and implemented in consonance with a NPS natural areas philosophy.

The purpose of this paper is to describe the pre- and post-dam riparian resources from Lee's Ferry (Mile 0) to the Grand Wash Cliffs (Mile 280) on Lake Mead, to identify some of the man-related impacts on the resources and to offer some suggestions for the mitigation of these impacts.

## THE PRE- AND POST-DAM RIPARIAN RESOURCES

Prior to and during the construction of Glen Canyon Dam, numerous studies were undertaken that were designed to provide a data base on what resources would be lost by the inundation of Glen Canyon (see Woodbury et al., 1959, for biological studies). Unfortunately, there were no studies undertaken on what change would occur below the Glen Canyon Dam site in the Grand Canyon. Evidently, it did not occur to anyone that Glen Canyon Dam would cause significant modifications in the downstream ecology. We have been able to reconstruct the pre-dam vegetative conditions through analysis of pre-dam photographs (see Karpiscak, 1976) and the published account of a brief botancial survey of the Colorado River from Green River, Utah, to Lake Mead (Clover and Jotter, 1944).

---

[1] Grand Canyon National Park, Colorado Research Series Contribution #22.

[2] Museum of Northern Arizona, Route 4, Box 720, Flagstaff, Arizona 86001.

[3] National Park Service, Grand Canyon, AZ 86023.

[4] In 1935, 350 miles downstream from Glen Canyon Dam, the gates of Hoover Dam were closed, forming Lake Mead. The inundation of the lower section of the Colorado River has also had an effect on the river regime from Mile 240 to the Dam site at Mile 350.

*Pre-Dam Riparian Vegetation.* Prior to the construction of Hoover and Glen Canyon Dams, there existed three distinct zones of vegetation which paralleled the river from Lee's Ferry to the Grand Wash Cliffs (see Figure 2). The zone closest to the river (Zone 3) and hence subjected to annual flooding, was composed partially of many ephemeral herbaceous species that were adapted to habitats subjected to periodic disturbance, and partially of some mesophytic woody plants such as seep willow and desert broom, *Baccharis* spp., and the true willows, *Salix* spp., that would make a futile attempt to become established before the next scouring flood. Above the ephemeral zone was a belt of vegetation whose lower boundaries were delineated by the high water line of major floods which would periodically scour away all vegetation growing below this zone. Typical plant species of this high water line zone (Zone 2) were Apache plume (*Fallugia paradoza*), redbud (*Cercis occidentalis*), hackberry (*Celtis reticulata*), mesquite *(Prosopis juliflora)*and acacia (*Acacia greggii*). On the talus slopes (Zone 1) above this zone lived desert species that were not influenced by the river environment below (e.g., brittle bush, *Encelia farinosa;* various cacti, *Opuntia* spp., creosote bush, *Larrea tridentata;* Mormon tea, *Ephedra* spp., etc.).

The construction of Hoover Dam inundated the two lower vegetational zones and much of the desert vegetation of the upper zone upstream from the Dam to Mile 240. Within a matter of a few years, however, a new zone consisting almost exclusively of salt cedar (*Tamarix chinensis*) appeared at the water's edge.

*Post-Dam Vegetation.* The significant reduction in high flood waters in the Colorado River below Glen Canyon Dam has permitted the development of a new riparian community that extends from Lee's Ferry (Mile 0) to the backwaters of Lake Mead (Mile 240, see Figure 3). This rapidly proliferating community (Zone 4) is composed of salt cedar, arrowweed (*Pluchea sericea*), coyote willow *(Salix exigua)*, four species of *Baccharis*, and hundreds of species of herbaceous plants. In most areas, this new community occupies all of the former ephemeral zone (Pre dam Zone 3, see Figure 2), while in other locations, particularly where the bedrock has always been close to the river, there are no discernible changes between the pre- and post-dam vegetational patterns. Above the new riparian community and below the high water line community we now find another distinct zone (Zone 3) of ephemeral plants, e.g., red brome (*Bromus rubens*), tansy mustard (*Descurainia pinnata*), fescue (*Festuca octoflora*) and *Chaenactis fremontii*, to mention only a few. Two very noxious exotic species, Russian thistle (*Salsola kali*) and camelthorn (*Alhagi camelorum*) also proliferate in this zone. Interestingly, it is this zone wherein the majority of campable beaches are contained and many of the species typical of this zone are indicators of disturbed areas.

Preliminary investigations indicate that the woody vegetation of Zone 2 (see Figure 3) is beginning to die back. Although the high water floods of pre-dam days only rarely reached the lower limit of this vegetation zone, it may have been of sufficient frequency to provide some required nourishment for this vegetative community. The high water flows now never approach the lower limits of this community, and each year more and more of the plants in this zone appear to be dying.

*Animal Communities.* The rapid proliferation of the new riparian habitat has resulted in a concomitant increase in the density and diversity of animal life along the Colorado River. Although virtually no information is available on the animal communities of the riparian habitats of the pre-dam regime our data indicate that each of the post-dam vegetation zones has a characteristic complement of both invertebrate and vertebrate species.

During blooming periods, the new riparian community supports almost three times the density of insects that are found in Zone 2. Although the species diversity data are as yet unanalyzed, significantly more families of insects are also found in the new riparian growth. It is interesting, however, that the insect productivity through an annual cycle is more stable in the Zone 2 terrace community (Stevens, 1976). This is partially explained by the fact that the dominant plant of Zone 4 is the exotic salt cedar, which attracts large numbers of pollinators when blooming, but supports only a very limited insect community when not blooming. The temporal sequence of salt cedar blooming, however, is concomitant with the reproductive activity of a host of vertebrate species that have begun to utilize the new riparian growth. Some lizard species, especially the western whiptail, *Cnemidophorus tigris,* and the desert spiny lizard, *Sceloporus magister,* have moved downward from their native habitat of Zone 2 and invaded the new riparian growth of Zone 4. Although these species are presently common in both habitat types, they reach their highest densities in the new riparian growth, particularly where very dense stands of salt cedar occur. In addition, the diurnal tidal flow provides a new feeding area for some reptiles. At least one species, the whiptail, has learned to feed on small crustaceans (Amphipoda) at the water's edge as the "tide" goes out. To our knowledge, this is a totally new behavioral pattern and feeding zone for this reptile.

Mammalian responses to the new habitat of Zone 4 have also been noted. Prior to 1969 the white-footed deer mouse (*Peromyscus maniculatus*) was not known to occur along the banks of the Colorado River. Its distribution was limited to the forested areas of the south and north canyon rims. In 1969, however, we began occasionally encountering this species in the new riparian growth. By 1976 the species had become a common mouse on some beach areas, and in general distributed throughout the Grand Canyon area, but only in Zone 4. Two other species of cricetid rodents, the brush mouse (*Peromyscus boylii*) and the pinyon mouse (*Peromyscus truei*) have also recently been discovered in this new zone. They, too, are out of their normal range of habitat distribution and like the white-footed deer mouse may simply be colonizers in a previously unexploited habitat.

The most notable vertebrate responses to the new habitat are exemplified by the patterns of avian use. The Colorado River drainage is a well known migratory corridor for transient bird species. Once the rapidly growing vegetation of the new riparian habitat provided adequate breeding cover for some migratory species, we feel that many of them remained to breed. This is especially true for the small insectivorous species such as the Willow Flycatcher (*Empidonax traillii*) and the Bell's Vireo (*Vireo bellii*). Prior to 1963 the flycatcher was known only from one locale in the Grand Canyon and the vireo did not occur as a breeding resident (Phillips et al., 1964). Now the Bell's Vireo is one of

the most common breeding species of Zone 4 and the flycatcher, although not as common, is well represented. Other species that are either new breeding residents to the streamside habitats of the Colorado River or experiencing rapid population increases are as follows: Yellow Warbler (*Dendroica petechia*), Yellowthroat (*Geothlypis trichas*), Yellow-breasted Chat (*Icteria virens*), Northern Oriole (*Icterus galbula*) and Blue Grosbeak (*Guiraca caerulea*) (see also Carothers and Johnson, 1975). We have determined (see Carothers and Sharber, 1976) that at the present time these small insectivorous colonizers make up about 15 percent of the total avian population of the inner canyon area. As the new riparian growth continues to proliferate, not only should these relative density figures increase, but absolute density and species diversity should also increase.

The changes caused by the Glen Canyon Dam in the terrestrial flora and fauna are no more dramatic than the changes in the aquatic life of the river itself. The entire native fish fauna of the river has been dramatically reduced and an indigenous race and endangered fish species, the humpback chub (*Gila cypha*), has all but been extirpated, solely as a result of the changes in water temperature and turbidity (Suttkus et al., 1976). Additional changes from pre- to post-dam river regimes are summarized by Czarnecki et al., 1976; Sommerfeld et al., 1976; and Cole and Kulby, 1976.

All of these data serve to demonstrate that the biotic resources of the post-dam regime are substantially different from those of the pre-dam days. The riparian vegetation and the river itself have been significantly changed as a result of Glen Canyon Dam, and the biotic resources that are now present can only remain as long as Glen Canyon Dam remains. Thus, from a natural resources point of view, much of the recently invaded biota is as exotic to the system as the Dam itself. These considerations are extremely important to the resource manager. The managerial constraints for allowing park visitors to utilize man-created habitats, such as Zone 3 and 4 on the Colorado River, must be different from the constraints for allowing use of relict or unique habitats such as Zones 1 and 2. In other words, if man-related impact must be inflicted on the Colorado River riparian habitat, it is better to concentrate this impact in Zones 3 and 4 than in the native habitats of Zones 1 and 2.

## HUMAN IMPACT

Throughout this research project, the biological inventories have provided a baseline description of the resource. The Park Manager should realize now that some of the riparian habitats of the Colorado River are in a state of dynamic flux, changing rapidly with each passing year. Decisions on resource protection, use, and/or manipulation can, and should be founded now on a better understanding of their ecological consequences. Thus, this is the justification of scientific research in our National Parks.

Of equal importance to the manager, however, is information relating to the interrelationships between people as river recreationists and the biotic resources. That is, what kinds of impacts on the biota are inflicted by the thousands of people that run the Colorado River annually?

Clearly, if the river recreationists did not debark from the launching point of their river trip until the terminal destination was reached, the resource manager would have little cause for concern. This, however, is not the case. Most Colorado River excursions average 10 days in length. This means at least 9 campsites, 10 lunch stops, and numerous stops at attraction sites (Indian ruins, waterfalls, etc.) and hiking areas. Resource impacts by river runners are virtually negligible until they get off the boat and invade the riparian or desert ecosystems.

The impacts on the biological resources that we have found to be associated with human activity are as follows:

1. Habitat destruction
    a. Fire (wildfire and removal of driftwood for cooking fires)
    b. Trampling (soil compaction, vegetation removal)
2. Incorporation of inorganic and organic wastes in beaches
    a. Charcoal
    b. Litter (including organic garbage)
    c. Feces and urine
3. Interruption of "normal" patterns of wildlife densities and distributions
    a. Proliferation of exotic plants and animals
    b. Proliferation of native animals

*Habitat Destruction.* Although fire is an important feature in most natural terrestrial ecosystems, man-caused blazes are generally detrimental. Impacts may range from small sand-scarred fire rings to entire stands of riparian vegetation being consumed in holocausts. We have documented at least 10 man-caused blazes along the Colorado River in the past three years. Virtually all of the fires were caused by the careless incineration of toilet tissue. The short term impacts of wildfires may include elimination of actual or potential wildlife nesting sites, foraging sites and display sites. Large burns may kill or force movement of certain animal species and may result in the invasion of non-native pioneer plant species.

Perhaps the most serious impact caused by the river recreationist has been habitat destruction through soil and vegetation trampling. This is especially true in vegetation Zones 1 and 2 (see Figure 3), the native desert and high water line woody vegetation communities. In many area, multiple trails, all with the same ending and beginning place, are maintained through large numbers of people trampling the vegetation. This condition invites accelerated soil erosion and dramatically changes the flora of these areas. Much of the native riparian growth in the larger tributaries (e.g., Clear Creek, Hermit Creek, Tapeats Creek, and Havasu Canyon) also show a heavy amount of damage due to foot traffic. This problem has resulted from the lack of any organized trail system designed to accomodate the number of park visitors in these areas.

Vegetation trampling in the new ephemeral riparian community, Zone 3, may have the effect of keeping much of the rapidly growing salt cedar from invading the campable areas. As stated before, the plants typical of this zone are

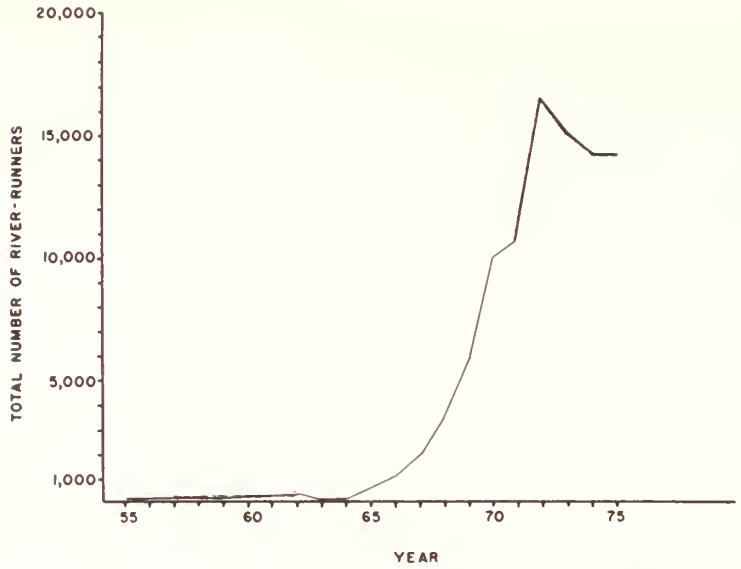



FIGURE 1. The annual number of river runners on the Colorado River from 1955 to 1975.

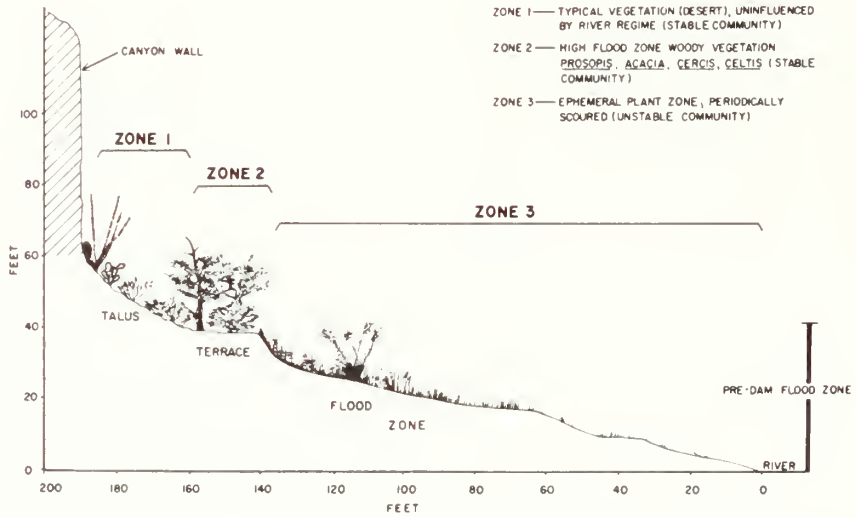



FIGURE 2. A profile of the vegetative zones of the Colorado River floodplain in the Grand Canyon prior to the construction of Glen Canyon Dam.

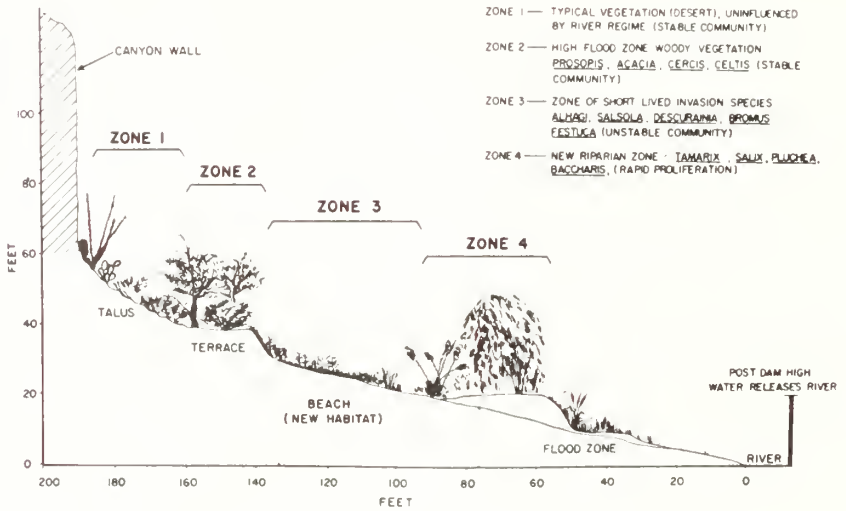



FIGURE 3. A profile of the vegetative zones of the Colorado River floodplain in the Grand Canyon 13 years after the impoundment of Colorado River waters by Glen Canyon Dam.

species that usually proliferate in disturbed areas. Where there is no foot traffic, this zone has been overgrown by the salt cedar and other species more typical of Zone 4. Thus, in many beach areas, human activity may be functioning to keep campsites free of encroachment by perennial plant species.

*Incorporation of Human Wastes into Beaches.* Dolan et al. (this symposium) have demonstrated how cooking fires, improper garbage disposal, and general littering are contributing to the "sand-box" condition on most campable beaches. Another very serious problem is the rapid accumulation of raw feces and urine into and on the campable beach areas. Although NPS regulations require that the fecal wastes from all river groups be contained and buried, the number of dumps in many areas has probably exceeded the capacity of the natural purging processes. At the more heavily used campsites, it is not uncommon for a boatman to unearth the remains of the previous group's fecal dump site when attempting to bury the wastes from his group. Many of these campsites, for example the Deer Creek Camp (Mile 136, left), are receiving up to 100 separate dumps per river season in an area that does not exceed 5 acres. We also know that this area has been receiving heavy use for at least 4 years. Four hundred dumps in four years in a 5 acre sand-box is probably too much. A study recently completed (Knudsen, 1976) demonstrated that some of the fecal pathogens remain infectious even after having been buried in beach sand for a year or more. Where heavy use is common, (e.g., Deer Creek Camp), raw feces has erupted to the surface. Not only does this result in certain aesthetic displeasure, but a potential health hazard exists as well.

*Interruption of "Normal" Wildlife Patterns.* The improper disposal of organic garbage and the intentional feeding of some "wild" animals have resulted in some striking changes in animal population densities and behavioral patterns. Heavily used campsites have higher densities of harvester ants (*Pogonomyrex californicus*) than lightly and moderately used campsites. Because of their painful and toxic sting this species presents a source of great discomfort and a potential health hazard. The flesh fly (Sarcophagidae) and blow fly (Calliphoridae) populations show corresponding population increases at heavily used camping areas. Not only a source of discomfort and annoyance, but these species could become a source of fly-vectored disease. Increases in these insect populations have also resulted in increases in certain vertebrates, such as some species of lizards which are found in unusually high densities near dirty campgrounds. One of the more interesting consequences of human occupancy of the wilderness beaches of the Grand Canyon is that at two of the most heavily used beach areas, House Sparrows (*Passer domesticus*) have taken up residence. This species does not normally occur outside of urban areas, as it seems to need the presence of man as part of its habitat requirements. Four species of native mammals, spotted skunk (*Spilogale putorius*), ringtails (*Bassariscus astutus*), rock squirrels (*Spermophilus variegatus*), and mule deer (*Odocoileus hemionus*) and one species of bird, the Raven (*Corvus corax*) have experienced either increases in densities or demonstrated significant shifts in their behavioral patterns as a result of being purposely fed by river runners or hikers. In some cases, particularly with the deer and rock squirrel, the increased and easily available low quality food supply has resulted in population explosions which have left these animals in poor health. As a result, Park Managers are now finding it necessary to discuss control programs for tame squirrels and deer.

## MANAGEMENT ALTERNATIVES ON THE COLORADO RIVER

If the resource managers of 15 years ago had today's information regarding the effects of Glen Canyon Dam on downstream ecology and the associated management problems, Lake Powell might not be where it is. Although this is a topic for interesting conjecture, the fact remains that Grand Canyon Park Managers must contend with the problems created by Glen Canyon Dam. To begin solving the problems, the Park Service must pursue one of two major alternatives: one, lobby for the removal of Glen Canyon Dam, or two, manage the existing riverine environment as if it were the natural condition. At the present time, alternative one is politically unrealistic. Thus, native or not, the new riparian regime of the Colorado River must, by default, become the new natural system. The ecological research has demonstrated that this new habitat is tremendously productive in terms of wildlife resources, and if for no other reason, it should then be managed with the conservation goals of the National Park Service Act of 1916 in mind. A clear distinction should be made, however, and that is that the zones of vegetation representing "the way it was" (i.e., Zones 1 and 2) be given relatively more protection from impacts and use than the new riparian vegetation of the lower zones.

Having thus established a profile of the resource, a description of the human related impacts on that resource, and a possible management philosophy that is in consonance with NPS objectives, what then are some mitigating measures for reducing human impact?

Throughout our investigation, we were continually impressed by the fact that the *activities* of people are more important in terms of causing impacts than the absolute *numbers* of people. That is, the amount of damage a given number of users inflict on the environment is a function of how those users treat the resource. Ten people with no feeling or understanding of the conservation or wilderness ethic can cause infinitely more damage than 100 conscientious and knowledgeable users. The key word in the above passage is *knowledgeable*. If we are to allow use of the back country in our National Parks, then we must insure for the lasting quality of the resource by insisting that the visitors *know* how not to destroy that resource. On the Colorado River, at least 90 percent of the total users are commercial passengers. The National Park Service has total control of the outfitters in that the permit system for allowing river operations is governed by the NPS. The outfitter and guide have total control of their passengers. It is the responsibility of the Park Service to educate the outfitter and the guides regarding the sound reasoning behind the rules and regulations and, most importantly, to decisively enforce these regulations. In addition to educating the user, another impact-mitigating measure would possibly be to reduce the total area and certain types of areas now subjected to human impact.

Very early in our investigation, through a postage-paid visitor usage questionnaire, we began censusing both commercial and private river groups as to the location of their nightly camps. By the end of the 1974 river season, we had established that over 300 separate campsites were

in use along the 300 miles of river (Aitchison, 1976). This number of campsites agreed with a separate study on the physical carrying capacity of the system (cf. Weeden et al., 1975). During 1974 and 1975, approximately 75 percent of all visitors were accommodated by only 100 of the available campsites. The beach soils and vegetation have a very low stability threshold; that is, the first few footsteps on the beaches and especially in the fragile desert ecosystem cause the most disturbance. After the initial disturbance, each succeeding footstep causes less and less relative damage. Not all of the available campsites are of the same quality in terms of potential or realized impact. Many camps have low Biotic Resource Ratings (BRR, see Aitchison, 1976) which means simply that the relative density and diversity of biotic resources is low. These are camps that consist mainly of sand and rock, and with the exception of mass wasting of the sand (see Dolan et al., this symposium) and various forms of littering, little ecological damage can be done by the visitor. Since we have demonstrated that as few as 1/3 of the total available campsites are consistently used perhaps the manager, with the assistance of the ecologist, could pick out 150 campsites, evenly distributed throughout the system, with the lowest BRR's and only allow human acitivites in these areas.

Although it is not the task of the researcher to make management decisions, we have determined that there are three critical problems that must be taken care of above all other human related impacts and they are as follows:

1. Establish trail systems at points along river and in tributaries that can accommodate the amount of foot traffic that is presently destroying the soil and vegetation of these areas.

2. Disallow the disposal of any and all human wastes in the beach soils.

3. Educate the wilderness user in the proper behavior necessary to insure a lasting quality resource.

If immediate attention were given to the above items, human related impacts on the riparian resources of the Colorado River would most assuredly be reduced on a significant scale.

In conclusion, we find it necessary to make one final recommendation. In addition to educating the park visitor, perhaps we should look to the internal education system of the National Park Service and reevaluate the training of the resource managers themselves. It seems to us that the emphasis of many management goals is on the accommodation of the visitor rather than on the protection of the resource. The National Park Service is the only federal agency that can guarantee the preservation of natural landscapes for the generations of the future. If we cannot look to the Park Service for example of proper conservation of these resources, where can we look?

## LITERATURE CITED


AITCHISON, S. W. 1976. Campsite usage and impact. *In*: Carothers, S. W. and S. W. Aitchison, (eds.), An ecological survey of the riparian zone of the Colorado River between Lee's Ferry and the Grand Wash Cliffs, Arizona. Final Report, Colorado River Research Program, Contract No. CX82150007, Grand Canyon National Park.

CAROTHERS, S. W. and R. R. JOHNSON. 1975. Recent observations on the status and distribution of some birds of the Grand Canyon Region. Plateau 47(4):140-153.

CAROTHERS, S. W. and N. J. SHARBER. 1976. Birds of the Colorado River. *In:* Carothers, S. W. and S. W. Aitchison (eds.), An ecological survey of the riparian zone of the Colorado River between Lee's Ferry and the Grand Wash Cliffs, Arizona. Final Report, Colorado River Research Program, Contract No. CX82150007, Grand Canyon National Park.

CAROTHERS, S. W. and N. J. SHARBER. 1976. Birds of the Colorado River. *In:* Carothers, S. W. and S. W. Aitchison, (eds.), An ecological survey of the riparian zone of the Colorado River between Lee's Ferry and the Grand Wash Cliffs, Arizona. Final Report, Colorado River Research Program, Contract No. CX82150007, Grand Canyon National Park.

CLOVER, E. U. and L. JOTTER. 1944. Exceprts from floristic studies in the canyon of the Colorado and tributaries. American Midland Naturalist 32(3):591-642.

COLE, G. A. and D. M. KUBLY. 1976. Recommendations following a limnologic study of the Colorado River and its major tributaries in the Grand Canyon. Final Report, Colorado River Research Program, Contract No. PX821060-263, Grand Canyon National Park.

CZARNECKI, D. B., D. W. BLINN, and T. TOMPKINS. 1976. A periphytic microflora analysis of the Colorado River and major tributaries in Grand Canyon National Park and vicinity. Final Report, Colorado River Research Program, Contract No. CX821060008, Grand Canyon National Park.

DOLAN, R., B. HAYDEN, A. HOWARD, and R. R. JOHNSON. (In press). Man's impact on Colorado River fluvial deposits within the Grand Canyon. *In:* Proceedings of the First Conference on Scientific Research in the National Parks, 9-13 November, 1976, New Orleans, Louisiana.

FENNEMAN, N. M. 1931. Physiography of Western United States. New York and London, McGraw-Hill.

JOHNSON, R. R. and S. P. MARTIN. 1976. The Colorado River research project: a National Park Service multidisciplinary, interdisciplinary research project. In the Proceedings of the 3rd Resources Management Conference, NPS, April 29-30, 1976. Fort Worth, Texas.

KARPISCAK, M. 1976. Vegetational changes along the Colorado River. *In:* Carothers, S. W. and S. W. Aitchison (eds.), An ecological survey of the riparian zone of the Colorado River between Lee's Ferry and the Grand Wash Cliffs, Arizona. Final Report, Colorado River Research Program, Contract No. CX82150007, Grand Canyon National Park.

KNUDSEN, A. B. (In press). A bacteriological analysis of portable toilet effluent at selected beaches along the Colorado River, Grand Canyon National Park, Arizona. Symposium on River Management and Research, January 25-27, 1977, Minneapolis, Minnesota.

PHILLIPS, A., J. MARSHALL, and G. MONSON. 1964. The Birds of Arizona. University of Arizona Press, Tucson.

SOMMERFELD, M. R., W. M. CRAYTON, N. L. CRANE. 1976. Survey of bacteria, phytoplankton, and trace chemistry of the lower Colorado River and tributaries in the Grand Canyon National Park. Final Report, Colorado River Research Program, Contract No. CX821060007, Grand Canyon National Park.

STEVENS, L. E. 1976. Insect production of native and introduced dominant plant species. *In:* Carothers, S. W. and S. W. Aitchison (eds.), An ecological survey of the riparian zone of

the Colorado River between Lee's Ferry and the Grand Wash Cliffs, Arizona. Final Report, Colorado River Research Program Contract No. CX82150007, Grand Canyon National Park.

SUTTKUS, R. D., G. H. CLEMMER, C. JONES, C. R. STOOP. 1976. Survey of fishes, mammals and herpetofauna of the Colorado River and adjacent riparian areas of the Grand Canyon National Park. Final Report, Colorado River Research Program, Contract No. CX821060006, Grand Canyon National Park.

WEEDEN, H. A., F. Y. BORDEN, B. J. TURNER, D. N. THOMPSON, C. H. STRAUSS and R. R. JOHNSON. 1975. Grand Canyon National Park Campsite Inventory. Progress Report, Colorado River Research Program, Contract No. CX0001-3-0061, Grand Canyon National Park.

WOODBURY, A. M., S. FLOWERS, D. W. LINDSAY, S. P. DURRANT, N. K. DEAN, A. W. GRUNDMANN, J. R. CROOK, W. H. BEHLE, H. G. HIGGENS, G. R. SMITH, G. G. MUSSER, D. B. MCDONALD. 1959. Ecological studies of the flora and fauna in Glen Canyon. Anthropological Papers, No. 40, University of Utah, Salt Lake City.

# INTER-RELATIONSHIPS AMONG VISITOR USAGE, HUMAN IMPACT, AND THE BIOTIC RESOURCES OF THE RIPARIAN ECOSYSTEM IN BIG BEND NATIONAL PARK

David J. Schmidly, Robert B. Ditton, William J. Boeer, Alan R. Graefe[1]

## INTRODUCTION

In recent years, the Rio Grande of Big Bend National Park (BBNP) has experienced dramatic increases in recreational usage. The primary goal of this research project has been to secure detailed information concerning the actual and potential impact on the Rio Grande in BBNP and on associated land area ecosystems resulting from present levels of recreational usage.

Any study of human impact on an area must ultimately concern itself with four factors. These are (1) the natural resources of the area; (2) the users of this resource; (3) the impacts of the user upon the resource; and (4) the necessary management decisions needed to modify and control the impact in order to preserve the resource. This paper is concerned with the first three of these factors and their inter-relationships. Management implications resulting from data analysis have been dealt with elsewhere (see Ditton et al., 1976 a, b; and Schmidly et al., 1976).

## APPROACH

The project was multidisciplinary in that both biological and social science skills were involved and interdisciplinary in that we were in coordinated communication. The initial stage of the project involved an effort to locate all major riparian vegetative communities along the Rio Grande in BBNP. Sixty-four major riparian sites were identified and for purposes of statistical analysis each was treated as a distinct sampling entity, although in practicality the riparian communities tend to form a continuum along the river (Figure 1). Most of the riparian areas are accessible only by floating the river. However, 26 riparian sites are accessible via roads; 18 of these may be reached via a dirt road called the River Road, which becomes impassable during rainy weather. These 18 sites have been given names by park management and designated as primitive campsites. There are also eight sites that are accessible via paved roads; two of these (Cottonwood and Santa Elena Picnic Area) are small campgrounds and another (Rio Grande Village) is a major campground.

For purposes of analyzing visitor usage data, the river was divided into five sections based on the location of the three major canyons (see Figure 1). These are: section I, from Lajitas to the mouth of Santa Elena Canyon (including the canyon itself); section II, from Cottonwood campground to Talley; section III, from Talley to Solis (including Mariscal Canyon); section IV, from Solis to Rio Grande Village; and section V, from Rio Grande Village to the eastern border of the park (including Boquillas Canyon).

Of the 64 riparian sites, quantitative data concerning visitor usage was available only for those sites accessible via the River Road. Consequently, these same sites were used to measure biological resources (i.e., rodent fauna and vegetation). Impact analysis was conducted at each of the 64 riparian sites, but this paper will focus primarily on those sites where biological and user data were also available.

## RIVER USE

Because almost all of the river corridor lies in the backcountry, analysis of visitor user patterns focused on backcountry use. The existing BBNP backcountry permit system was used as the data base for establishing the extent, character, and patterns of Rio Grande Corridor use. The data base was differentiated into distinct categories as follows (for a detailed explanation see Ditton et al., 1976a). First, backcountry use of the river was separated from backcountry use of other areas of the park. Then, river use was divided into float trips and nature road (River Road) use. Within these two major categories, further analysis yielded user-group-, time- and place-specific information. Use data were recorded using three units of measure: 1) number of parties, 2) numbers of individuals, and 3) number of man-days. The latter category was considered the best measure of weighted use distribution and related impact on the river corridor because both the actual number of visitors and the time they spent on the river are reflected in this measure.

The distribution of backcountry use across the three major categories is presented in Table 1A. From a parkwide perspective, it can be seen that the Rio Grande attracts approximately 40% of total backcountry use (parties) while the desert and mountains account for nearly 60%. Using the man-days measure, which weights use in terms of length of stay and party size, the amount of river-oriented backcountry use (categories 1 and 2) is almost equal to the non-river-oriented camping category.

Float trip and River Road camping patterns were analyzed further because these activities account for nearly all of the recreational use that is associated with the Rio Grande corridor in BBNP. Float trip activity was broken down according to the functional river subsystems (Figure 1). The distribution of float trips across the five river subsystems in 1975 is given in Table 1B. In terms of the number of parties accommodated, the three canyons account for 69% of the total float trip use. The 25% figure for Section IV can be explained largely by short day-floats. Using the man-days measure, the three canyons collectively account for 81% of all float trips within BBNP.

A breakdown (in man-days) of total River Road camping by individual designated sites is presented in Table 2. These data reveal that camping at designated primitive River Road campsites in Section II and IV was concentrated at a very few sites. Two River Road sites (Gravel Pit and Solis) accounted for 39% (in man-days) of total annual River Road use. Four more sites (San Vicente

[1]Contribution of the Texas Agricultural Experiment Station (Depts. of Wildlife and Fisheries Sciences, and Recreation Parks), Texas A&M University, College Station, Texas 77843.

Crossing, Talley, Black Dike, and Johnson Ranch) accounted for an additional 32% (man-days) of total annual River Road site use. Thus, in terms of man-days of camping provided, six sites account for 71% of the total annual River Road use. Alternatively, eight of the remote River Road sites received less than 2% each of the total river oriented backcountry camping. These data suggest that, for most sites at most times, use is extremely low.

Up to this point, Float Trips and River Road Camping have been discussed individually. This is appropriate because these two activities are largely separated spatially, with Float Trips occurring mainly in Sections I, III and V and River Road Camping limited to designated areas in Sections II and IV. An important exception to this general trend should be noted, though. Two of the more popular River Road campsites, Talley and Solis, also serve as the put-in and take-out points, respectively, for the popular Mariscal Canyon Float Trip. Thus, these sites are the most heavily used areas of the entire backcountry riparian corridor. In addition, they are areas where floating and car camping activities overlap. Consequently, these particular sites have the greatest potential for visitor overuse problems and conflicts.

## SUBJECTIVE SITE EVALUATION

A requisite of this entire project was the need to assess the extent of human impact along the riparian corridor of BBNP. Impact measurement and analysis are done according to an ordinal scale and are similar to work undertaken by Leopold et al. (1971) and Sorenson (1971) who measured magnitude and importance of environmental impacts. This research, however, deals only with magnitude of impact. To accomplish this, a subjective site evaluation sheet was developed which included four basic parameters and 15 different variables (Figure 2). The four basic categories are: human impact (six different variables); livestock impact (two variables); site description (three variables); and wildlife characteristics (four variables). Each of the 15 variables is rated on a scale from 1 to 5, with 1 representing the most desirable condition and 5 the least desirable condition. For example, a score of 1 is assigned for human litter if no litter is present at a particular site; a score of 3 is assigned if litter is apparent upon inspection; and a score of 5 is assigned if litter is obvious everywhere. Scores of 2 and 4 are also possible. Totals were obtained for each of the four major categories. Thus, the total score for the human impact parameter could range from 6 to 30, with 6 indicating no human impact and 30 very heavy impact.

Data were obtained by visiting and completing a subjective site evaluation sheet for each of the 64 riparian sites. Sites were visited either by floating or by automobile via the River Road. The number of visits per site varied from one to four and the number of persons filling out the impact forms varied from two to six. Scientists, students, and park personnel filled out the impact forms separately. The data were then tabulated and the median for each variable per site was calculated. This paper is concerned only with human impact and median scores for this parameter for each of the 18 sites with user and biological data are given with the user data in Table 2. Tabulation of the site evaluation sheets resulted in a large data base in the form of a 64 X 6 matrix (64 sites, 6 human impact variables) that are closely connected by some relationship and are separated from other such groups by gaps. The cluster analysis of the human impact data (see Figure 3) reveals three major clusters, A, B, and C. Cluster A includes those sites with high impact values; cluster B, those with intermediate impact values; and cluster C, those with low impact values. Of the 64 sites, 15 (or 23%) fall within cluster A; 10 (16%) within cluster B; and 39 (61%) within cluster C. Of the 15 sites in cluster A (heavily impacted sites), 11 (70%) can be reached by the River Road; whereas of the 39 sites in the least impacted cluster (C), only 7 (18.0%) are accessible by the River Road. So the cluster analysis reveals that (1) very few of the riparian sites may be considered heavily impacted and (2) the majority of the heavily impacted sites are those that may be reached via the River Road. In fact, of the 17 River Road sites for which use data are available, 10 (59%) fall within the heavily impacted cluster.

## BIOLOGICAL RESOURCES

Two biotic components, the small terrestrial rodent fauna and vegetation, were monitored in the riparian ecosystem of BBNP. Neither the rodent fauna nor the vegetation of the riparian habitat of BBNP has been studied intensively. These components were selected because both should be reliable indicators of human impacts serious enough to detrimentally affect the riparian ecosystem. Rodent densities are strongly influenced by vegetative "cover" (i.e., the spacing and size of plants). Cover is important to small rodents because it provides them a source of food as well as protection from predators. Many types of human and livestock impact (such as trampling) tend to reduce cover and, hence, if severe enough, they could greatly influence the diversity and density of rodents. Rodent trapping and analysis of vegetative cover were concentrated only at those sites where use data (in man-days) were available.

*Vegetation.* Denyes (1956) recognized three plant associations along the Rio Grande floodplain: (1) the riverbank association, consisting of mesquite (*Prosopis juliflora*). seep willow (*Baccharis* sp.), willow (*Salix gooddingi*), or cottonwood (*Populus palmeri*), located adjacent to areas of exposed silt and coarse gravel at the waters edge; (2) the *Baccharis* association, composed of dense stands of seep willow; and (3) the mesquite association, consisting of a thin line of extensive mesquite trees or an extensive area of several different plant forms. We have found these three associations to be somewhat altered from Denyes' description and, although difficult to document, our general impression is that significant vegetation changes have occurred on the riparian habitats of BBNP over the past 30 years. The major change is associated with the tremendous increase of salt cedar (*Tamarix gallica*) along the river. The *Baccharis* association, mentioned by Denyes (1956) as common in the fine sandyloam soils along the river, is recognizable today only at a few places (for example, Black Dike) and appears to have been replaced by a mixed mesquite-salt cedar-bermuda grass (*Cynodon dactylon*) association. Similarly, salt cedar also appears to be replacing native cottonwood and willow trees at many places.

Early accounts (Taylor et al., 144; Sperry, 1938) describe the vegetation along the river as open and severely over-grazed. However, since ranching activities ceased at the inception of the park, plant densities seem to have increased greatly so that at several places (for example,

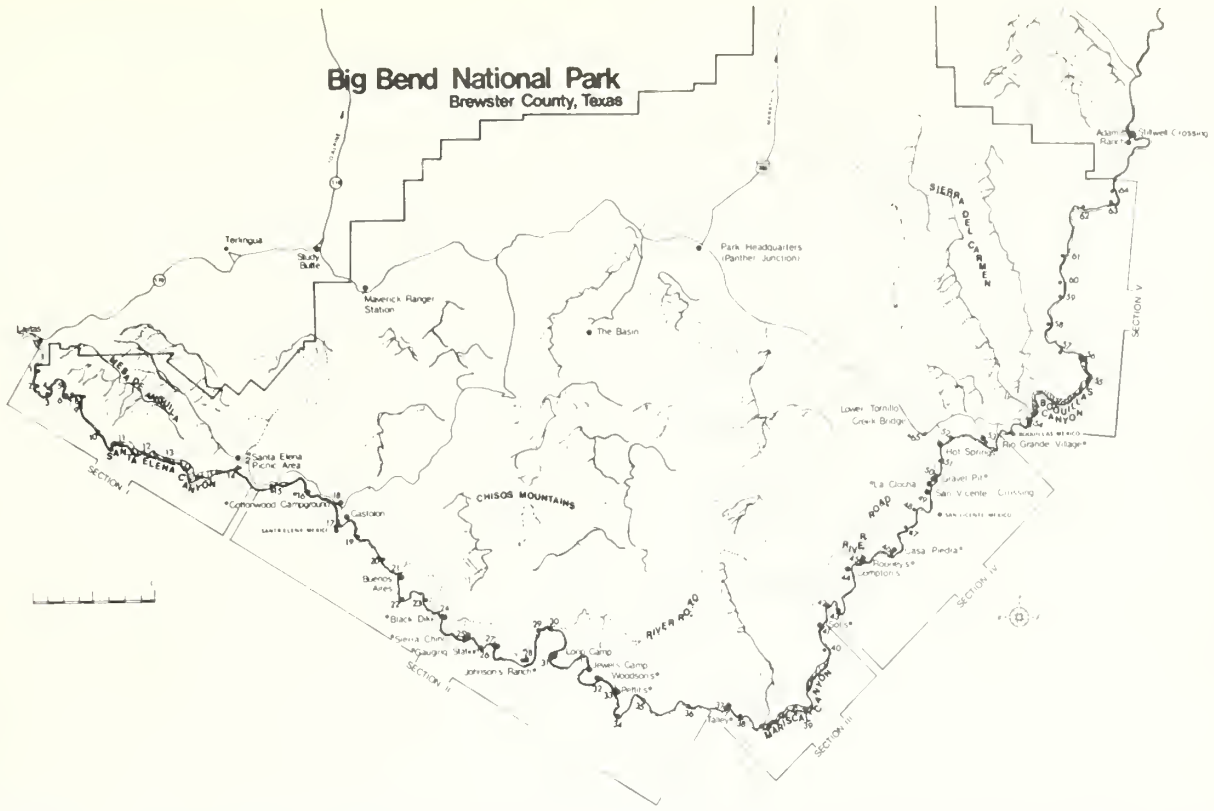



FIGURE 1. Map of the Rio Grande corridor in BBNP showing the 64 riparian sites and five river sections. Named places along the river represent backcountry campsites as designated by park officials. Sites with start represent places where the rodent fauna and vegetation were sampled.

TABLE 1. Analysis of user data for Big Bend National Park. (A) Distribution of backcountry use across three major categories; (B) Distribution of float trips across the five river subsystems.

| A. | User Categories | # of parties | % | # of man-days | % |
|---|---|---|---|---|---|
| | 1) Float Trip | 727 | 18.7 | 7,405.5 | 25.0 |
| | 2) River Road Camping | 849 | 21.8 | 7,151.0 | 24.1 |
| | 3) Non-river-oriented camping | 2,318 | 59.5 | 15,124.5 | 50.9 |
| | Total | 3,894 | 100.0 | 29,681.0 | 100.0 |

| B. | Section | # of Parties | % | % of man-days | % |
|---|---|---|---|---|---|
| | I Santa Elena Canyon | 186 | 22.1 | 1,637.7 | 22.1 |
| | II (between canyons) | 50 | 5.9 | 278.7 | 3.7 |
| | III (Mariscal Canyon | 258 | 30.7 | 2,464.5 | 33.3 |
| | IV (between canyons) | 210 | 25.0 | 1,130.4 | 15.3 |
| | V Boquillas Canyon | 137 | 16.3 | 1,894.5 | 25.6 |
| | Total | 841 | 100.0 | 7,405.5 | 100.0 |

TABLE 2. Annual River Road campsite use, percentage use, and total human impact by campsite. Numbers in parentheses represent site designation number in Figure 1.

| River Road Site | Use in Man-Days | Percentage Use | Total Human Impact[1] |
|---|---|---|---|
| Gravel Pit (5) | 1,426.5 | 20.0 | 16.0 |
| Solis (41) | 1,377.7 | 19.3 | 18.0 |
| San Vicente Crossing (48) | 677.9 | 9.5 | 16.0 |
| Talley (37) | 577.3 | 8.1 | 17.0 |
| Johnson Ranch (28) | 545.9 | 7.6 | 18.0 |
| Black Dike (24) | 475.5 | 6.6 | 28.0 |
| La Clocha (49) | 273.0 | 3.8 | 20.0 |
| Woodson's (32) | 264.8 | 3.7 | 14.5 |
| Rooneys (45) | 229.7 | 3.2 | 9.5 |
| Buenas Aires (21) | 224.0 | 3.1 | 6.0 |
| Casa Piedra (46) | 167.7 | 2.3 | 14.5 |
| Other | 164.7 | 2.3 | - |
| Pettit's (33) | 136.7 | 1.9 | 8.5 |
| Ganging Station (27) | 120.2 | 1.7 | 14.0 |
| Smokey Creek (23) | 118.0 | 1.6 | 9.5 |
| Jewel's Camp | 105.7 | 1.5 | - |
| Comptom's (44) | 98.0 | 1.4 | 7.5 |
| Loop Camp | 76.7 | 1.1 | 8.0 |
| Sierra Chiro (25) | 65.6 | 0.9 | 7.0 |
| Hot Springs | 26.0 | 0.4 | - |
| | | 100.0 | |

[1]Calculated as median value of man's impact parameter in Figure 2.

Johnson Ranch) mesquite forests now occur where the river bottom was once open and sparsely vegetated. Extensive fields of grass also occur today at sites (for example, Smoky Creek and Coyote) which formerly were cultivated and farmed.

Total percent cover (based on the Daubenmire method, 1959) for the categories trees, shrubs, and grasses at 18 riparian sites is presented in Table 3. The values were lower than expected for trees except for site 16 which had a value of 33 percent. The lower values were due to the fact that the "trees" were usually confined to a narrow area along the river and the rest of the area was somewhat open. The values for "shrubs" were small but this was expected since most plants in this category (*i.e.*, composites, weeds, and cactus) had little canopy cover. The only site with extensive shrub cover was La Clocha (site 49) where a thick cover of fleabane was present.

*Rodents.* Table 3 presents the results of 12,960 trap nights of collecting small rodents at 18 different riparian sites (720 trap nights per site) along the Rio Grande. The riparian rodent fauna of BBNP is less diverse than that of the desert-shrub, grassland, or woodland habitats. Eight species of small terrestrial rodents occupy riparian habitats in BBNP. Four of these (*Perognathus penicillatus, P. nelsoni, P. flavus,* and *Dipodomys merriami*) are members of the family Heteromyidae and four (*Peromyscus leucopus, P. eremicus, Sigmodon hispidus,* and *Neotoma micropus*) belong to the family Cricetidae. *Perognathus penicillatus* is overwhelmingly the most abundant small rodent in the riparian habitat and, for this reason, the total density of heteromyid rodents is greater than that of cricetid rodents. The three other heteromyid species are relatively rare along the river, although *D. merriami* is common at a few sites.

Densities of the four species of cricetid rodents are more similar to one another than the densities of the heteromyid species. *Peromyscus leucopus* is the most common cricetid and *P. eremicus* the least common; *Sigmodon hispidus* and *Neotoma micropus* occur in about equal numbers. Generally, heteromyid rodents prefer open and sparsely vegetated habitats, whereas cricetid rodents prefer habitats with considerably more ground cover. Long term trends toward increasing density and cover of vegetation along the riparian corridor, as a result of the cessation of ranching activities, may eventually result in an increase of the density of cricetid species and a decrease in the density of heteromyid species.

## RELATIONSHIPS AMONG USAGE, SUBJECTIVE IMPACTS, AND BIOLOGICAL PARAMETERS

We determined the extent of correlation among human impacts, useage, and biological resources by using Kendall's coefficient of rank correlation (t, tau; for a complete discussion of this method see Sokal and Rohlf, 1969). This approach was used instead of the Pearson product-moment correlation statistic (r) because our data are known not to be bivariate normally distributed. Values of t for the correlations of user and biological parameters with human impact data are as follows (probability of statistical significance given in parentheses; asterisks indicate those values that are statistically different from zero):

Observer: _____ Profession: _____

Date: __ __/ __ __/ __ __ (day / month / year)

River site (no.): _____

River side: M or A

Size class: A, B, C

| PARAMETER | RATING | COMMENTS |
|---|---|---|
| A. MAN'S IMPACT | | |
| Litter | | |
| Trampling | | |
| Rock moving | | |
| Campfire | | |
| Human waste | | |
| Wood cutting | | |
| TOTAL | | |
| B. LIVESTOCK IMPACT | | |
| Trampling | | |
| Waste | | |
| TOTAL | | |
| C. SITE DESCRIPTION | | |
| Access | | |
| Shoreline vegetation | | |
| Campsite potential | | |
| TOTAL | | |

D. HABITAT TYPES (check those present)

_____riparian
_____dune
_____gravel beach
_____bench
_____talus slope

E. WILDLIFE CHARACTERISTICS

| | |
|---|---|
| Habitats | |
| Unique combinations | |
| Modifications | |
| Values and needs | |
| TOTAL | |

FIGURE 2. Rio Grande ecological survey riparian community evaluation sheet.

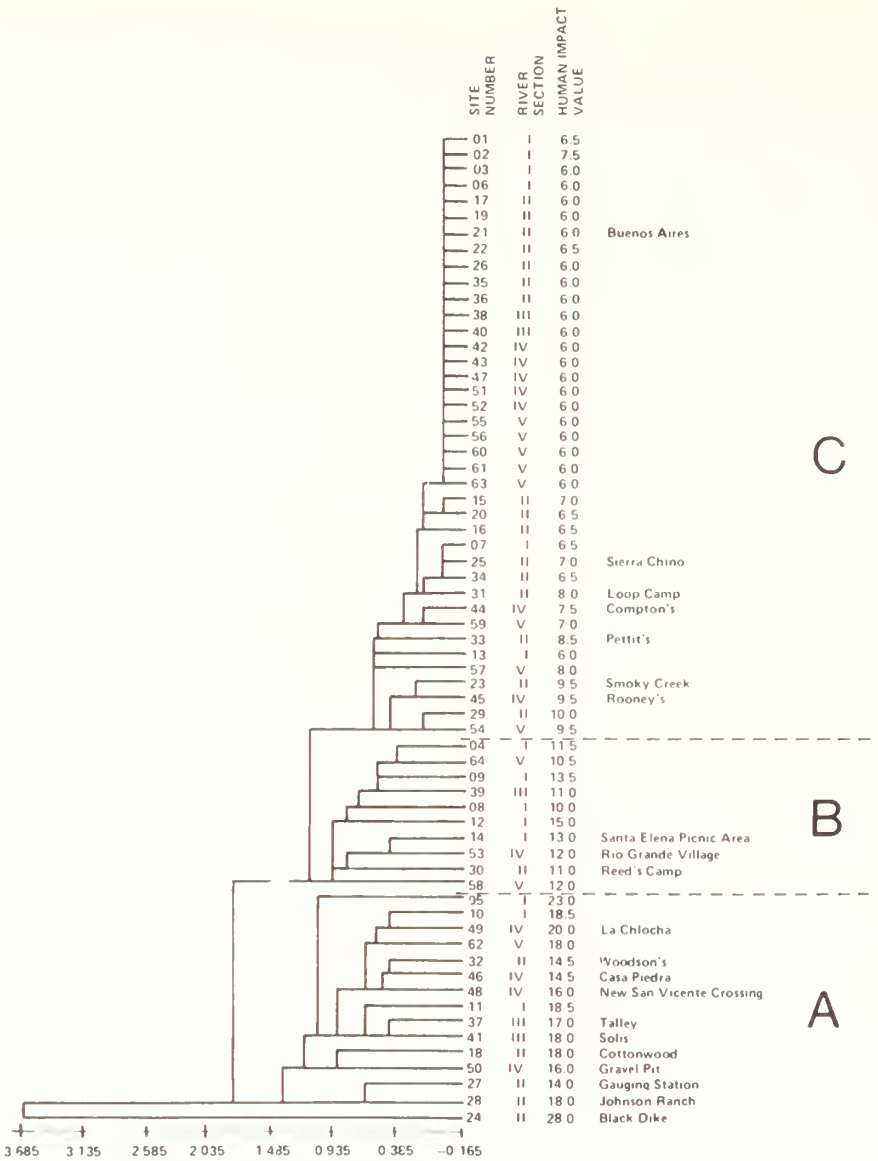



FIGURE 3. Dendrogram of numbered riparian sites based on human impact variables.

| | Human Impact |
|---|---|
| Use in Man-Days | .5822 (.0012)* |
| Total Rodent Catch | .0620 (.6966) |
| Total Cricetid Catch | .1705 (.2758) |
| Total Heteromyid Catch | .0615 (.7874) |
| Shrubs | .1302 (.4066) |
| Grasses | .1102 (.4842) |
| Trees | -.3609 (.0214)* |

Several important points are evident from these data. First, with the exception of the vegetative category "trees," neither vegetative or rodent densities correlates significantly with human impact. Trees are negatively and significantly correlated with human impact, indicating that as impact increases the frequency of trees decreases. Aside from this rather obvious conclusion, the data suggest that the extent of human impact along the Rio Grande has not been great enough to significantly affect the rodent or vegetative components of the riparian ecosystem. Second, correlation analysis reveals a positive and significant relationship between total subjective human impact ratings and annual camping use by site (man-days). This verifies that as use increases, subjectively evaluated impact increases.

The upshot of these two correlation analyses taken together is that site impacts have occurred as a result of recreational use, but not to the point where ecological conditions, as indicated by the biological health of rodent fauna and vegetation, are in jeopardy. This suggests viewing these correlations in the context of "change" rather than "impact" (which implies damage). Any recreational use of a resource will result in some change in resource conditions. The critical task for management is to decide what is the acceptable level of physical-biological change.

TABLE 3. Total rodent catch and percent vegetative cover (based on the Daubenmire 1959 method) of trees, shrubs, and grasses for 18 riparian sites along the Rio Grande in BBNP. See Figure 1 for the location of sites.

| Species | Sampling Sites 14 | 15 | 16 | 18 | 24 | 25 | 27 | 28 | 32 | 33 | 37 | 41 | 45 | 46 | 49 | 50 | 53 | 65 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Perognathus flavus | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Perognathus penicillatus | 62 | 74 | 29 | 36 | 21 | 40 | 64 | 68 | 40 | 47 | 74 | 56 | 35 | 40 | 44 | 45 | 64 | 57 |
| Perognathus nelsoni | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| Dipodomys merriami | 3 | 0 | 1 | 0 | 0 | 0 | 15 | 2 | 3 | 8 | 0 | 10 | 0 | 2 | 2 | 5 | 0 | 16 |
| Peromyscus eremicus | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 3 | 5 | 0 | 0 | 1 | 1 | 0 | 0 | 4 | 1 |
| Peromyscus leucopus | 16 | 9 | 5 | 1 | 7 | 10 | 7 | 16 | 14 | 11 | 44 | 7 | 4 | 4 | 3 | 2 | 2 | 0 |
| Sigmodon hispidus | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 5 | 3 | 6 | 4 | 0 | 0 | 26 | 9 | 11 | 0 |
| Neotoma micropus | 3 | 6 | 8 | 1 | 3 | 5 | 1 | 18 | 8 | 8 | 8 | 4 | 0 | 1 | 4 | 1 | 1 | 3 |
| Total Catch Heteromyid | 65 | 74 | 33 | 36 | 21 | 41 | 79 | 70 | 43 | 55 | 74 | 67 | 37 | 42 | 46 | 50 | 64 | 73 |
| Total Catch Cricetid | 19 | 16 | 15 | 2 | 12 | 16 | 10 | 36 | 30 | 27 | 58 | 15 | 5 | 6 | 23 | 12 | 18 | 4 |
| Todal Rodent Catch | 84 | 90 | 48 | 38 | 33 | 57 | 89 | 106 | 73 | 82 | 132 | 82 | 42 | 48 | 69 | 62 | 82 | 77 |
| Trees | 8.0 | 6.0 | 33.5 | 3.5 | 6.0 | 9.8 | 9.8 | 12.0 | 9.8 | 4.7 | 8.0 | 9.8 | 9.8 | 8.0 | 12.0 | 14.0 | 4.1 | 4.7 |
| Shrubs | 4.1 | 1.8 | 1.8 | 4.1 | 3.0 | 1.8 | 2.4 | 1.2 | 2.4 | 1.2 | 3.0 | 5.3 | 3.0 | 2.4 | 21.9 | 4.7 | 3.5 | 3.0 |
| Grasses | 4.7 | 8.0 | 36.0 | 21.9 | 5.3 | 3.5 | 16.0 | 12.0 | 16.0 | 18.0 | 21.9 | 14.0 | 8.0 | 4.7 | 19.9 | 16.0 | 14.0 | 0.0 |

This requires a value judgment as to the *desirability* of changes that are anticipated or have already occurred; i.e., is there excessive deviation from the accepted standard of resource quality? And this acceptable level of change depends on the management objectives of the area.

When viewed from a National Park Service-wide perspective, the total recreational use of BBNP and the Rio Grande appears very low. This might lead one to the casual and incorrect conclusion that recreational impact on the river corridor is not really a problem. This study disaggregates possibly misleading current park use figures into area-specific and time specific data sets that indicate when and where changes exist within the river system and how serious the changes are. While it appears that existing changes have not yet reached the point of constituting serious ecological damage, the changes have been measured in terms of parameters that can be readily perceived by visitors and that are amenable to management. Hence, the observed changes, if deemed undesirable or excessive by management, can be reversed before they lead to serious damage.

Earlier, when total subjective impact scores for 64 river sites were clustered, 49 sites or 77% were in the moderately and lightly impacted clusters. Looking at the River Road sites (remember, these are the only river sites we have specific use data for), it is revealing to note that 10 of 18 are shown in the heavy impact cluster. These 10 are all generally related to convenient access, i.e., close proximity to a paved park road or special attractions like the entrance to Santa Elena, Johnson's Ranch, and Mariscal Canyon. Access can therefore be verified as the major component in explaining variation in human impact. While this verification should not be too surprising, it does emphasize the role access plays in distributing human impact. Likewise, since access can be easily manipulated, so too can these impacts be controlled, shaped or mitigated.

Because study findings are based on data collected during only one year, further efforts need to be made to monitor user-resource relationships in BBNP. Impact and use analyses completed for this study are replicable by park personnel and should be carried forward.

## LITERATURE CITED

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science, 33:43-64.

DENYES, H. 1956. Natural terrestrial communities of Brewster Co., Texas, with special reference to the distribution of the mammals. Amer. Mid. Nat., 55:289-320.

DITTON, R. B., D. J. SCHMIDLY, W. J. BOEER, and A. R. GRAEFE. 1976a. Data needs and analysis for evaluating human impact on the Rio Grande Corridor fo Big Bend National Park. Proceedings of the 3rd Resources Mgmt. Conf., Southwest Region, National Park Service, :1-26.

DITTON, R. B., D. J. SCHMIDLY, W. J. BOEER, A. R. GRAEFE. 1976b. A survey and analysis of recreational and livestock impact on the riparian zone of the Rio Grande in Big Bend National Park. A paper to be presented at the River Recreation Management and Research Symposium, Minneapolis, Minnesota.

LEOPOLD, L. B., F. E. CLARKE, B. B. HANSHAW, and J. B. BALSLEY. 1971. A procedure for evaluating environmental impact, geological survey circular 645. U. S. Dept. Interior, Geological Survey, Washington, D. C.

SCHMIDLY, D. J., and R. D. DITTON. 1976. A survey and analysis of recreational and livestock impacts on the riparian zone of the Rio Grande in Big Bend National Park. Report prepared for the Office of Natural Resources, Southwest Region, National Park Service, Santa Fe, New Mexico (Contract No. CX70050442), 160 pp.

SOKAL, R. R., and F. J. ROHLF. 1969. Biometry. W. H. Freeman and Company, San Francisco, 776 pp.

SORENSON, J. C. 1971. A framework for identification and control of resource degradation and conflict in the multiple use of the coastal zone. Publ. Dept. Landscape Architecture, College of Environmental Design, Univ. Calif.-Berkeley.

SPERRY, O. E. 1938. A checklist of the ferns, gymnosperms, and flowering plants of the proposed Big Bend National Park. Sull Ross State Teachers College Bull., 19(4):10-98.

TAYLOR, W. P., W. B. MCDOUGALL, and W. B. DAVIS. 1944. Preliminary report of an ecological survey of Big Bend National Park. Report of work accomplished March-June, 1944. Administrative report submitted by the Fish and Wildlife Service to the National Park Service, 9:55p (mimeo).

# OZARK RIVER-USE INVESTIGATIONS

Leo F. Marnell[1]

## INTRODUCTION

Ozark National Scenic Riverways (ONSR) was designated the Nation's first National Scenic River on August 27, 1964. The Riverways is situated in the southern Missouri Ozarks and includes approximately 140 miles of the Current River and its principal tributary, the Jacks Fork (Figure 1). The National Park Service (NPS) administers Ozark Riverways as a National Recreation Area.

### *Statement of Problem*

A controversial issue at ONSR is alleged "overuse" of the Current and Jacks Fork rivers by recreational floaters, primarily canoeists. Concerned environmentalists feel that the area's natural resources are being damaged and contend that visitor enjoyment is suffering due to overcrowding. An opposing view is held by commercial interests who have sought vigorously to expand recreational use of the river. Riparian users tend to view all outside attitudes as a threat to their traditional freedoms. The controversy has been highlighted by the usual forms of notoriety, including criticism from the media, political pressure tactics, harassment by special interest groups, and court litigation. The dilemma is a familiar one to the National Park Service, an agency historically plagued by its accountability to diverse and often conflicting ideologies.

### *Interim Management Actions*

Concerns were felt within the NPS nearly a decade ago about possible environmental and sociological impacts accompanying floater use of these rivers. In 1971 when the first accurate count was made, 12,600 canoes were recorded on one 11-mile section of the upper Current River. That year the NPS imposed a moratorium to curb the growth of commercial canoe outfitters, who collectively accounted for 90 percent of the floater traffic on the Riverways. Permits were issued to established business operators in the surrounding counties and canoe inventories were stabilized. No permits have been issued since that time.

In spite of this action river-use has continued to rise, mainly due to increased weekday use during the summer. A contributing factor has been the proliferation of car-top canoe rental businesses throughout the region. In 1975, 36,100 canoes floated the section of river cited earlier, representing nearly a two fold increase over the five year period. Approximately 49,000 people floated this section between Memorial Day and Labor Day last year (Figure 2).

### *The Legal Complex*

The NPS has been in court on several occasions during the past three years to confront the growing problem of unauthorized commercial operations within the Riverways. Illicit operators have organized to challenge the Service's authority to regulate canoe rental enterprises inside the boundary. A court ruling in November 1975 weakened the authority contained in Title 36, Section 5.3 of the *Code of Federal Regulations*, which the NPS had been relying upon to deal with these activities. The Service subsequently promulgated a Special Regulation applicable specifically to Ozark Riverways, which defined "commercial operations" more explicitly. The new regulation was recently challenged and litigation was again unfavorable to the NPS position. Loss of control over commercial canoe operations within the boundary of ONSR continues to hang in balance.

At no time has the NPS contended that the actions taken reflect an attempt to establish a "carrying capacity" for recreation use of the rivers. The objective, instead, has been to preserve the *status quo* to allow time for the Service to make an assessment of the situation and formulate a plan for managing river-use.

## THE RESEARCH PROGRAM

A research program was initiated in October 1971 to secure facts on river-use at ONSR. A holistic approach was favored over a strategy giving excessive attention to only one or two selected aspects of the problem. The principal tradeoff of this approach was that data pertaining to any one concern would be less than comprehensive. University and interagency assistance supplemented expertise on the Park staff. The NPS scientist at ONSR assumed the role of program coordinator as well as principal investigator for several field studies.

### *Elements of the Program and Research Methods*

The research effort at ONSR focused attention on five areas of concern: (1) Water Quality, (2) River-Use Monitoring, (3) Sociological Studies, (4) Safety Concerns, and (5) Environmental Impacts.

*Water Quality.* Because the Current River and Jacks Fork constitute the principal resource of Ozark Riverways, high priority was given to the establishment of safeguards for preserving the quality of these rivers. A contract was awarded to the U.S. Geological Survey in 1972 for a three-year baseline study, after which a continuing water quality monitoring program was undertaken. The U.S.G.S. established permanent sampling stations and made comprehensive tests of all major physical and chemical parameters, selected nutrients, bacteria, and trace elements. Special emphasis was given to the measurement of nutrient and bacterial levels in the water on sections experiencing heavy recreational use. Additonal short-term studies were made to assess the impacts of specific types of recreation on water quality (*i.e.*, swimming, horseback riding, etc.)

[1]National Park Service, Ozark National Scenic Riverways, Van Buren, Missouri 63965. Current address: Glacier National Park, West Glacier Montana 59936.

*River-Use Monitoring*. Future management of river-use at ONSR will very likely be based to some extent on established use-patterns. For this reason, and also because a meaningful interpretation of other studies requires a knowledge of basic use-parameters, an important part of the research effort has been to document the volume, composition, and distribution of recreational use on the Current and Jacks Fork Rivers. This project focused on the peak-use season between Memorial Day and Labor Day.

Super-8 mm time-lapse movie photography evolved as the most practical means for direct monitoring of river traffic (Marnell, 1975). Five camera systems were placed alternately at ten surveillance locations to record the kinds and number of watercraft operating on ten designated river zones (Figure 3). A voluntary Floater Information Card Survey was administered in cooperation with canoe rental businesses to obtain supplemental information which was processed by computer. Origin-destination data obtained from the Card Survey were used to resolve the problem of duplicate counts of watercraft made by the cameras (i.e., many float trips span several river zones). Park Rangers were also asked to record observations of float traffic on their daily boat patrols. Collectively, these methods of data collection provided information describing the volume and spatial distribution of floater traffic on all river zones, traffic separation in time (i.e., peak-use days and hours on each zone), traffic composition (watercraft types and ownership categories), floater origin-destination patterns, access-use, floater camping trends, trip duration (days and nights out), floater group sizes, and floater residence. Cross variable analyses were performed by computer to reveal additional parameters. For example, it was found that large groups tended to prefer certain accesses. The quantitative river-use data will make an important contribution to the data base and will be especially valuable should use-allocation become necessary at ONSR at some future date.

*Sociological Studies*. Investigations were undertaken to probe important social aspects of river-use. Initial concern focused on the expectations of recreational floaters coming to the Riverways and their positive and negative perceptions (Gisi, 1971). An effort was also made to assess floater perceptions of crowding (Habermehl, 1973). The latter study attempted to define specific conditions which contributed to the illusion of crowding among canoeists. An extensive study was made of the social structure of large-group floaters (Wehrung, 1975); group cohesiveness and social interactions with other floaters were investigated. In 1975 a study was undertaken on the lower Current River to assess the potential for user-group conflicts which conceivably could result from management options aimed at redistributing use. Special attention was given to the attitudes of local fishermen toward canoeists (Brown, 1975). Also, a study was made to determine whether canoeists floating on the lesser-used downstreams sections were fundamentally different (i.e., motivated by a different set of values) than their counterparts on intensive-use zones (Chilman, 1976). An investigation is currently planned to evaluate floater reactions to different strategies which could be applied for manipulating river-use at ONSR.

*Safety Concerns*. Although the safety of visitors in the national parks has always been an important concern, added emphasis has recently been given to this matter. A safety investigation was contracted at ONSR during the summer of 1975 with the focus on hazards associated with river-use. Special consideration was given to problems occurring at major access points and along the river corridor, and accident statistics for the period 1968-75 were thoroughly audited (Weaver, 1976).

*Environmental Impacts*. Environmental interests feel that present levels of river-use at Ozark Riverways are having a detrimental effect on the environment. In an effort to address this concern, the NPS contracted with the University of Missouri to assess environmental impacts, document the extent of resource alteration, and to make recommendations for corrective actions. Impacted areas were selected for examination and compared with non-impacted (i.e., control) sites. Bank and trail erosion was studied and soil compaction was measured with special instruments. Photo-documentation and transect analyses were performed to evaluate changes in vegetation resulting from recreational uses along the river corridor (Sutton, 1976).

## RESULTS AND DISCUSSION

There is no evidence that present levels of recreation use are producing significant adverse effects on the water quality of the Current and Jacks Fork rivers. Temporary increases in bacteria levels were noted as a result of large groups of horses fording the Jacks Fork River; however, the influence on water quality was undetectable two miles downstream. Concentrated peak-day uses, including swimming and bathing at popular access points, does not significantly influence water quality. It is concluded that the aquatic system is adequately buffered and capable of sustaining present use-levels (Barks, 1977). The most serious long-term threat to water quality at ONSR is the potential for contaminated groundwater to enter the system through springs discharging water from extensive areas outside the Riverways boundary (Aley, 1976).

An esthetic problem exists at ONSR in relation to human sanitation, although a health hazard is not presently indicated. The problem is most pronounced on the section from Cedargrove to Round Spring during July and August. Sanitary facilities are inadequate to accommodate the levels of use occurring on this section of the river corridor. Climatic conditions and the character of floodplain substrates cause rapid breakdown of human wastes. Another mitigating factor is that flooding periodically flushes the system.

There is visible resource damage at some locations along the river corridor, mostly at popular stopping places and near accesses (Figure 4). Elsewhere over most of the river corridor the situation can better be described in the context of alteration rather than damage. Species composition has shifted on the floodplain, generally taking the form of less resistant species being replaced by those better adapted to withstand the impacts of camping and other uses associated with river floating (Sutton, 1976). Although the new equilibrium in species composition appears capable of sustaining present use-levels, long-term studies are needed to verify this hypothesis. A limited amount of site-hardening at selected locations would substantially reduce some of the impacts. Trails leading to points of interest and canoe mooring areas are examples where such techniques might be used judiciously. Direct reductions in

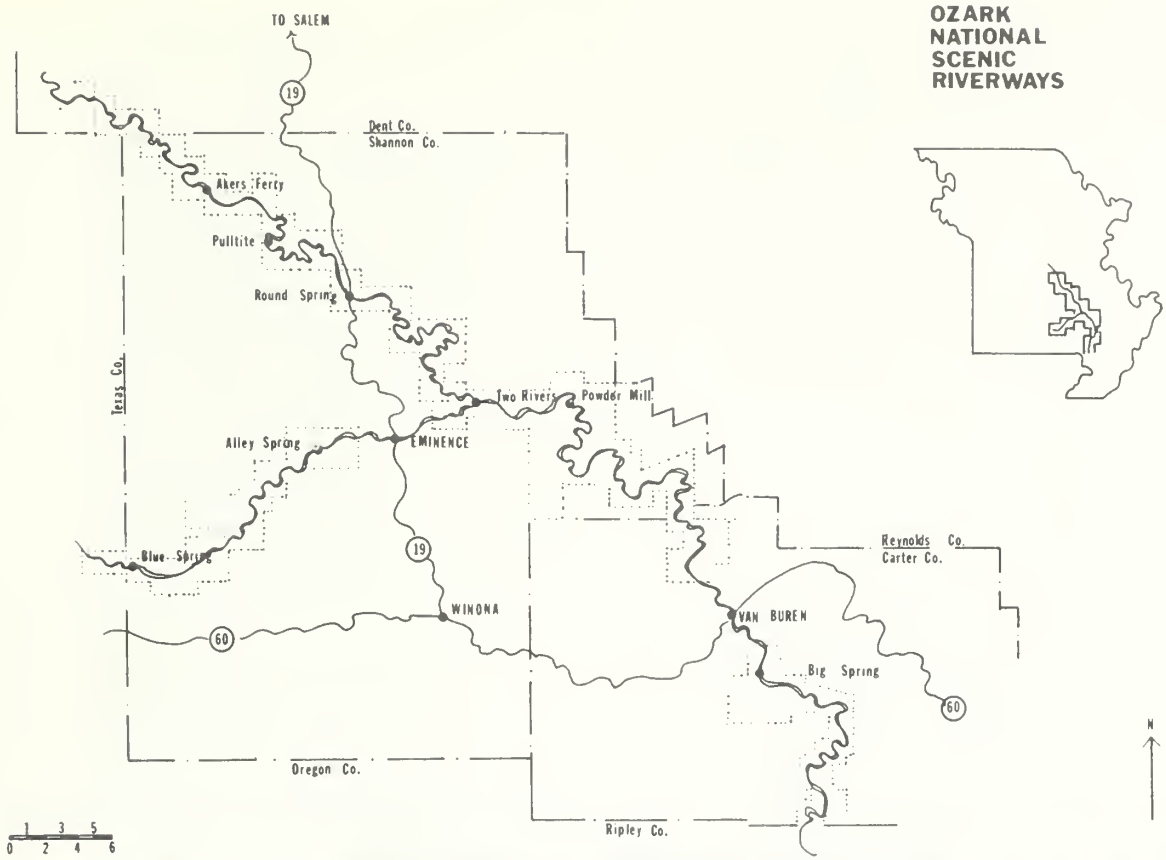



FIGURE 1. Map of Ozark National Scenic Riverways.



FIGURE 2. Saturday morning at Aker's Ferry.



FIGURE 3. Time-lapse cameras were effective for counting canoes.

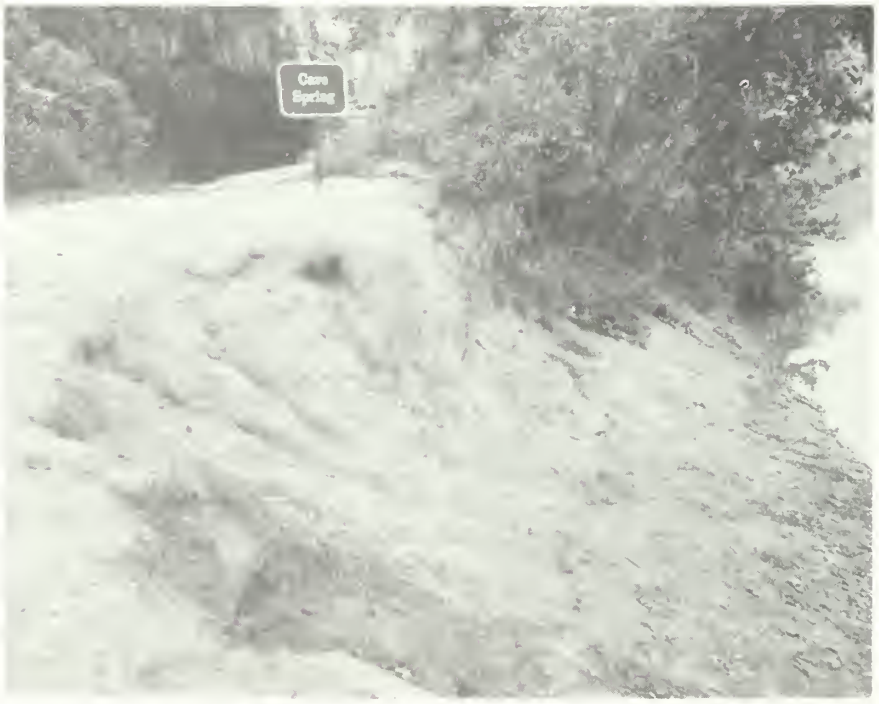



FIGURE 4. Resource damage has occurred at some locations.

floater-use would contribute little toward improvement of these sites unless such reductions were drastic.

Removal or damage inflicted to trees on the floodplain by persons seeking firewood may be a developing problem. This trend should be monitored carefully with a view toward future restriction as necessary to protect the integrity of the floodplain vegetation.

Figure 5 illustrates the 1974 distribution of floater-use at ONSR. It is apparent that a number of options remain for manipulating river-use to accommodate a fairly broad range of management objectives. While no opportunity exists for "wilderness" management of any part of the river corridor, it may be possible to maintain opportunities for a "primitive" experience--a river float with reasonable solitude. Manipulation of traffic through river zoning and/or time separation could be applied with discretion to achieve this result.

Most canoe floaters (48 percent) using the Riverways come from the St. Louis area. The dominant party size among canoeists is from four to nine persons (35 percent of the floaters); at the extremes, only 7 percent comprise groups of two or three people, while 31 percent of the floaters are in the company of 20 or more persons. "Crowding" is perceived as a problem among only a small percentage of canoeists. The majority of floaters indicated the situation they encountered would not prevent them from returning to the area (Habermehl, 1973). Most people learn about the area by word-of-mouth and realize an experience similar to their expectations. Local fishermen have essentially abandoned the upper sections of the river to canoe floaters. They are aware of the increased numbers of canoes downstream during recent years, but seem to be coexisting without serious conflict. Some fishermen have altered their fishing habits to cope with the increased numbers of floaters (Brown, 1976). It appears that a potential exists for conflict between fishermen and canoeists should the latter increase significantly on the lower sections of river.

## CARRYING CAPACITY DECISION-MAKING

An extensive literature has evolved during the past decade dealing with the concept of recreational carrying capacity. Contemporary views on this provocative subject are examined in recent papers by Lime (1975) and Verburg (1975).

Insights from slightly different viewpoints have been offered by Alldredge (1973) and Sudia and Simpson (1973).

A recent paper by Marnell (1976) discusses some of the ambiguities which surround the concept of carrying capacity and attempts to develop a rationale useful to field managers. The central theme of this review is that research cannot by itself generate decisions on recreational carrying capacity. Instead, it is emphasized that data obtained by research should be regarded as a guide for what is essentially an administrative decision-making process. The importance of "management obejctives" and the need for meaningful public involvement are also stressed.

A fallacy which seems to linger is the belief that research is an elixir which will exempt managers from having to make value judgments. This is not the case; indeed, research may raise more questions than it can answer (Lime, 1975). A more plausible approach is for managers to accept the challenge and attendant risks of decision-making and utilize research findings to maximum advantage. An unfortunate reality of the times is that research must be weighed not only in terms of its worth for guiding decisions, but equally for its usefulness in defending management actions. Decisions on recreatonal carrying capacity will in some instances be made by the courts.

In order to comprehend the role of management objectives as they relate to recreational carrying capacity, it may be helpful to review what is embodied by the concept itself. Lime (1975) defines recreational carrying capacity as ... *the amount and character of use an area can sustain over a specified period of time without causing unacceptable changes to the physical environment or to the experience of recreation users.* Several qualifications contained in this definition are noteworthy. Paramount, however, is the implied need for clear and meaningful management objectives, because ultimately these form the basis upon which managers and the public will judge what outputs or "end results" are most appropriate among the available options. Without management objectives as a frame of reference, recreational carrying capacity does not exist and management will either proceed arbitrarily or by default (Marnell, 1976).

Lime (1975) proposes that objectives be set forth in some sort of hierarchical order. Directives contained in legislation and agency mandates establish broad limits within which a certain degree of latitude exists for defining management goals. More specific objectives might be stated in documents such as master plans, recreation management plans, resource management plans, etc. The final step is to identify specific standards, the outputs or "end products" determined most appropriate. For example; how much resource alteration will be tolerated to accommodate certain kinds and intensities of recreational use? To what extent should the principal clientele's enjoyment be compromised? The task of articulating acceptable standards as they relate to these and other considerations may constitute the greatest burden in carrying capacity decision-making.

The approach being pursued at Ozark Riverways follows along these lines. Broad guidelines are contained in basic administrative mandates, (i.e., National Park Service Act, management policies, enabling legislation, Congressional hearings, etc.). More specific objectives appear in a recently prepared Statement for Management, part of the new planning process adopted by the National Park Service. Information obtained through research will be used to guide public review of the issues involved and to give direction to the overall process of policy formulation. Ultimately a River-Use Management Plan will be prepared which, in effect, will dictate a "carrying capacity" for the Riverways and outline the actions required to achieve the desired results.

Some degree of "trial and error" experimentation will be required during Plan implementation and adjustments may be necessary. This is true not only because the possibility exists for mistakes to be made, but also because new information and changing circumstances may alter any decision that is made. Because the Plan for managing river-use at ONSR must remain flexible and responsive to changing conditions, ongoing monitoring

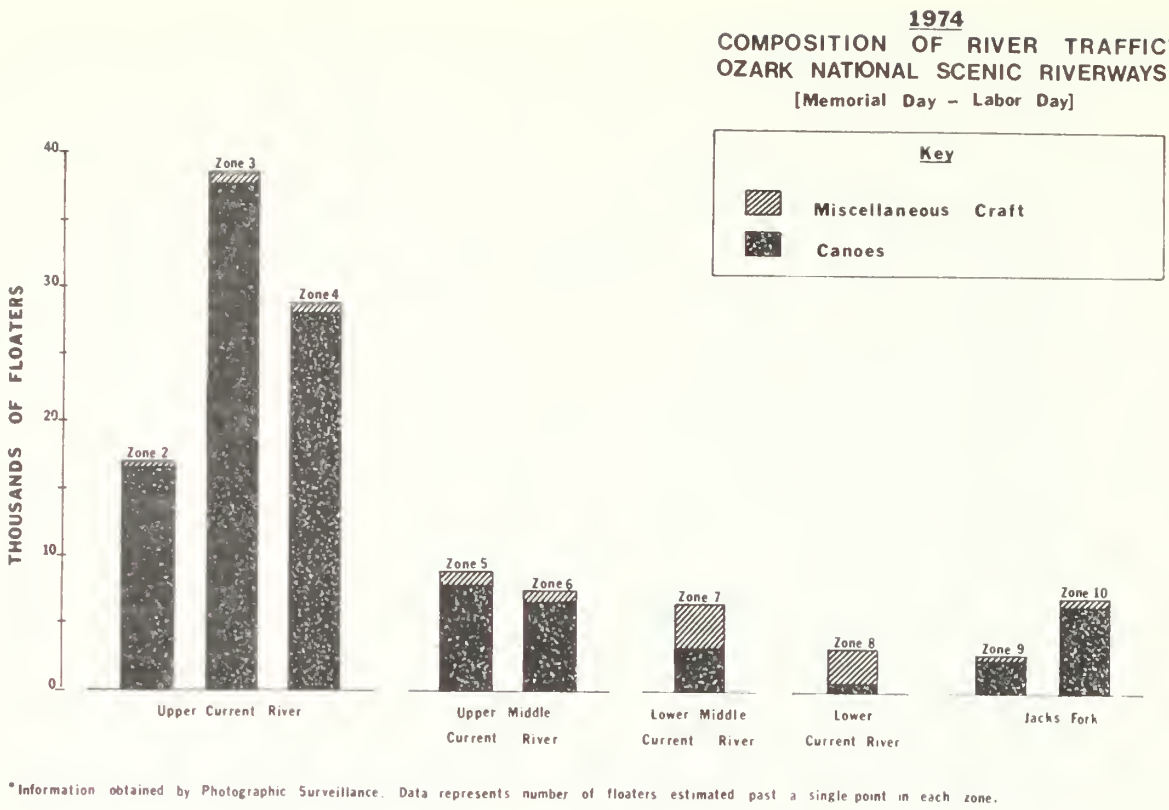



FIGURE 5. Summer float traffic at ONSR during 1974.

programs are planned in most of the disciplines cited earlier to provide a continuing imput of data. This will be useful to ONSR administrators for evaluating and refining future management actions.

LITERATURE CITED

ALEY, THOMAS. 1976. Identification and preliminary evaluation of areas hazardous to the water quality of Alley, Round, and Pulltite Springs, ONSR. Prog. Rep. submitted to NPS, Van Buren, Mo. Sept. 1976. 124 p.

ALLDREDGE, RENDEL B. 1973. Some capacity theory for parks and recreation areas. Trends, Oct-Nov: 20-30.

BARKS, JAMES H. 1977. Water quality in the Ozark National Scenic Riverways. WRI Paper (In prep.), U.S. Geol. Survey, Water Res. Div., Rolla, Mo. 104 p.

BROWN, MARVIN D. 1976. A population of local fishermen and their perceptions of change in a river environment. Unpubl. M.S. Thesis, So. Ill. Univ., Carbondale. 53 p.

CHILMAN, K. C. 1976. Canoeists on the Lower Current River, ONSR. Unpubl. Rep. submitted to NPS, Van Buren, Mo. 15 p.

GISI, DONALD V. 1971. Recreation expectations of first-time visitors to the Ozark National Scenic Riverways. Unpubl. M.S. Thesis, Univ. Mo., Columbia. 53 p.

HABERMEHL, JAMES M. 1973. Determining visitor perceptions of crowding on the Ozark National Scenic Riverways. Unpubl. M.S. Thesis, Univ. Mo., Columbia. 103 p.

LIME, DAVID W. 1975. Some principles of recreational carrying capacity. Paper presented at Southern States Recreation Research Applications Workshop, Sept. 16-18, Asheville, N.C.

MARNELL, LEO F. 1975. Use of time-lapse photography for monitoring river recreation. Paper presented at Workshop for Outdoor Recreation Researchers and Co-operators, March 9-12, Brandon Spring, Land Between the Lakes, Tenn. 10 p.

_____. 1976. Applying recreation carrying capacity concepts. Second Annual John S. Wright Forestry Conference, Proceedings, March 3-5, Purdue Univ., Lafayette, Ind.

SUDIA, TED W. and JAMES M. SIMPSON. 1973. Recreation carrying capacity of the National Parks. Guidelines 3(3):25-40.

SUTTON, STEVEN W. 1976. The impact of floaters on the Ozark National Scenic Riverways. Unpubl. M.S. Thesis, Univ. Mo., Columbia. 152 p.

VERBURG, K. 1975. The carrying capacity of recreation lands: a review. Occasional paper No. 1, Planning Division, Prairie Region Parks, Winnipeg, Manitoba, Canada. 70 p.

WEAVER, GLENN. 1976. Safety evaluation of river-use at Ozark National Scenic Riverways. Report submitted to NPS, Van Buren, MO., Dec. 1975. 48 p.

WEHRUNG, PAT. 1975. Large group float trips at Ozark National Scenic Riverways. Unpubl. M.S. Thesis, So. Ill. Univ., Carbondale. 50 p.

# APPLICATION OF RESEARCH DATA TO CARRYING CAPACITY DETERMINATION

Kenneth C. Chilman and John Burde[1]

The basic issue that we address here, following a series of research papers on riparian biology and human influences on riparian ecosystems, is- Now that we are beginning to gather certain research data, how will these data be used in decisions about limitations of human uses and influences on large wildland areas? The notion of limiting use of large and complex recreational land areas, such as national parks, is frequently discussed as carrying capacity determination (Wagar, 1964; Lime, 1975; Marnell, 1976).

The method which we utilize to address the above question derives from studies in organizational behavior (Whyte, 1969). These studies view organizations as biologists view organisms, and observe and attempt to understand the ways in which organizations adapt to changes in their environments. For several years, we have been working directly with different land managing organizations at the individual management unit level to develop methods for measuring recreational use aspects, and at the same time learn how these measurements are incorporated into carrying capacity decision-making (Chilman and Duffield, 1971; Gisi, 1971; Habermehl, 1973; Wehrung, 1975; Chilman, 1975; Chilman, 1976). An example of the utilization of a series of field research findings for carrying capacity decision-making has been presented in the previous paper (Marnell, 1976).

This paper suggests that researchers in park situations should pay attention to current processes of determining carrying capacity and how these processes are evolving, in order to make utilization of research data more effective. This paper first discusses changes that are occurring in the conceptualization of carrying capacity. Then preobjectives planning is proposed as useful for establishing objectives for carrying capacity determination, and for establishing priorities for further research.

## CHANGING CONCEPTUALIZATION OF CARRYING CAPACITY

As land managers are faced with increasing recreation use and an increasing need to make carrying capacity determinations (and to develop evidence to support their decisions in the face of frequent legal and court case challenges), the physical/biological/social/ecological complexity of wildland recreation areas is becoming more and more apparent.

What are the important factors to consider in carrying capacity determination decisions, and how are they related? Several models have been developed to identify and picture these factors and relationships. One example is shown in Fig. 1 (Line, 1970).

With this model, it was hypothesized that as the elements listed in the chart were identified and measured for individual wildland recreation areas, one or more of the measurements would indicate a 'limit' or 'lowest use level'. This would be the element on which carrying capacity levels would be based for a particular area.

However, in some areas where a series of studies have been conducted (for example, Ozark National Scenic Riverways as discussed in the preceding paper), no 'limiting' element has been readily found. This has led the resident researcher there to propose that "scientific research cannot in itself generate decisions on carrying capacity." Instead, it is emphasized that data obtained by research should be viewed as an input useful for guiding what is essentially an administrative decision-making process. Other fundamental considerations---are 'management objectives' and the need for meaningful public input." (Marnell, 1976).

This suggests the need for a more dynamic model of carrying capacity to incorporate the ideas of 'decision-making process' and 'management objectives'. A model of that type has recently been set forth (Brown et al. 1976) (Fig. 2). This model incorporates the additional notion that changes are continually occurring and must result in continuing evaluations of these complex management situations.

For researchers, one implication of recognizing this shift toward a more dynamic view of carrying capacity is to give attention to direction of changes occurring in phenomena being studied. Instead of just focusing on a baseline measurement at one point in time, research efforts may also be able to indicate direction and speed of change over time. Conscious planning in the research design to obtain repeated monitoring measurements in the future will also be important to assist management decisions.

But another important factor for researchers to recognize is that the managers and other specialists they work with will probably not be trained or knowledgeable about either carrying capacity determination as "process" or about ways to deal with changes in or development of "management objectives".

It has somehow been taken for granted that management objectives are already determined and readily available, when in fact they may exist only in fragmented form. This fragmentation is due to 1) changes in the basic management situation and 2) the nature of the initial, often very general, statements of objectives. It can no longer be assumed that objectives are available and appropriate: conscious planning (with improved data) must develop and refine new objectives.

Researchers interested in carrying capacity have been pointing out the need for attention to management objectives for some time (Wagar, 1964) but only recently has attention been given to objective-setting procedures or strategies. Therefore, we suggest that a procedure is needed which systematically incorporates 1) reexamination of objectives 2) available data and knowledge about the carrying capacity situations 3) inputs from researchers as well as managers and other specialists, and 4) inputs from the

[1]Department of Forestry, Southern Illinois University, Carbondale 62901.

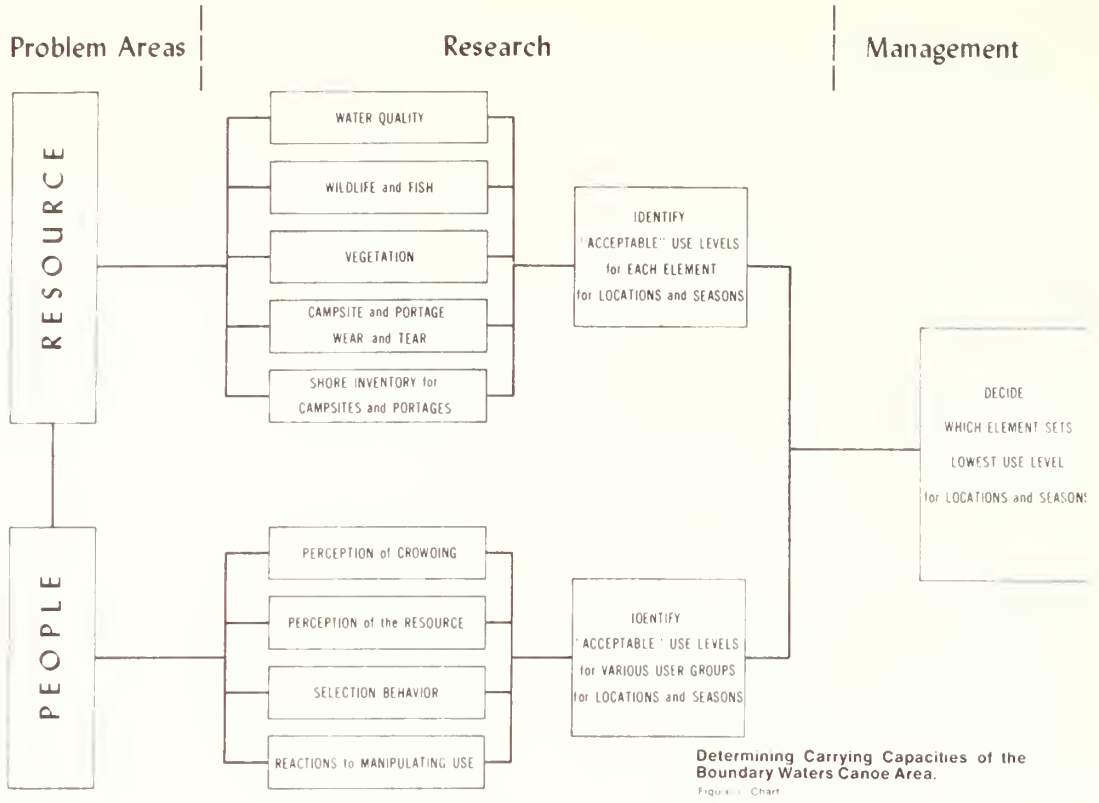



FIGURE 1.

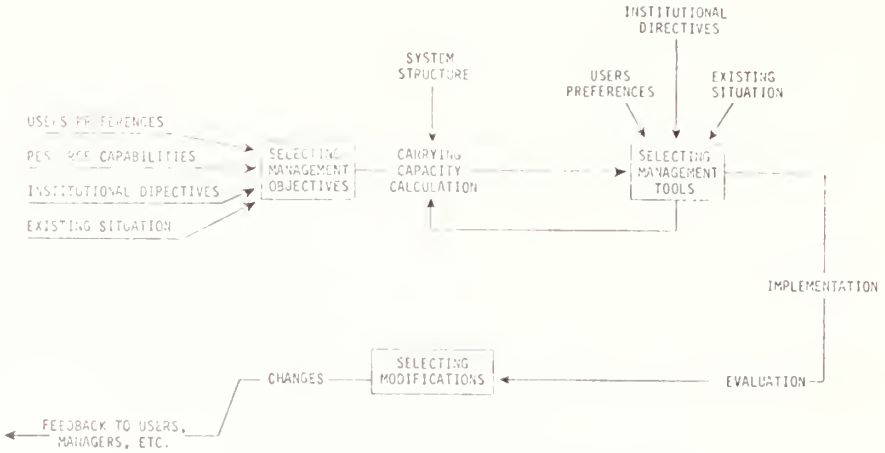



FIGURE 2. Decision points, with their inputs and outputs, in recreational resource management.

user public, on an equitable basis.

## PREOBJECTIVES PLANNING

To get past the assumption that appropriate objectives already exist, and to begin systematic reevaluation of management objectives as a key to carrying capacity determination, we have worked with managers of five different recreation use areas (in three different land managing agencies and in different parts of the United States) in a process which we call "preobjectives planning". This process involves four easy-to-understand phases, integration of existing information, and interaction of researchers and managers during the process.

The four phases, which may overlap to some degree, include: 1) a series of meetings and discussions about the nature of the need for a restatement of objectives, 2) the search for available information and knowledge about the situation past and present, with at least one review meeting to assess whether all available sources have been probed, 3) based on existing knowledge, a statement is made of present direction and of alternatives, and is thoroughly discussed, and 4) selection of desired direction and the writing of a statement of the above for general review. The preobjectives planning situations we have worked with have taken from several months to three years to work through, but they have prepared agency personnel for a more effective role in formal objective-setting procedures of their particular organizations.

The process which we have utilized closely parallels another group process model designed to handle situations where a number of individuals and groups with different ideas and interests need to be brought together so that a common program can emerge (Delbecq and Van de Ven, 1971). Their process has been summarized in five phases:

Phase I: Problem Exploration
- Involvement of client or consumer groups
- Involvement of first-line supervisors

Phase II: Knowledge Exploration
- Involvement of external scientific personnel
- Involvement of internal and external organizational specialists

Phase III: Priority Development
- Involvement of resource controllers
- Involvement of key administrators

Phase IV: Program Development
- Involvement of line administrators
- Involvement of technical specialists

Phase V: Program Evaluation
- Involvement of client or consumer groups
- Involvement of staff and administrative personnel

Delbecq and Van de Ven have elaborated particular activities to occur in sequence in each phase, based on current theories of group decision-making, and have tested their sequence in various situations- from heavily populated areas of Wisconsin to Bureau of Land Management planning situations in Colorado (Reynolds, 1975). Bureau of Land Management staff involved with use of the Delbecq system in Colorado indicate that it works- but it costs. They believe costs may be twice as high as conventional efforts by staff specialists, but that savings are effected "by avoiding false starts, unsupported programs and protracted disputes".

While the preobjectives planning we have done is less formalized than the Delbecq model, the point is that systematic and tested approaches exist to the complex job of objective-setting for large public recreation area situations. Researchers can productively interact in these objectives-setting sequences by interpreting results of existing studies, and by proposing appropriate studies to meet needs for additional knowledge about the park or recreation area in question.

## SOME TENTATIVE CONCLUSIONS

There appears to be a bottleneck involved in current carrying capacity determination efforts. This difficulty appears to be related to needed re-evaluation of management objectives in order to provide an evaluative framework for research measurements of the various phenomena involved in carrying capacity determination for large wildland areas, such as national parks.

While part of the problem of carrying capacity determination is related to the reluctance of most organizations to admit that their objectives may need updating, another part is the lack of knowledge by most managers and researchers about how to proceed with the complex job of objective-setting for large and diverse public recreation areas.

More attention will need to be paid to processes of objectives-setting- such as 'preobjectives planning' and the Delbecq group process model discussed above- in order to make utilization of research efforts on public recreation areas more fruitful for both the researchers and managers involved.

## LITERATURE CITED


BROWN, P. J., DRIVER, B. L., and G. STANKEY. 1976. Human behavioral science and recreation management. Proc. IUFRO Secr., Vienna, Austria: p. 53-63.

CHILMAN, K. C. and B. DUFFIELD. 1971. Carrying capacity determination: Missouri state parks. Report submitted to Misosuri State Park Board, Jefferson City, Mo. 15 p.

CHILMAN, KENNETH C. 1975. Profile: the trail user. Proc. Third National Trails Symposium, National Trails Council, 53 W. Jackson Blvd., Chicago: pp. 19-31.

CHILMAN, KENNETH C. 1976. Reading the visitor's mind. Proc. Conf. on Managing Recreation Resources for Century III, Purdue University: 10 pp.

DELBECQ, A. L., and A. VAN DE VEN. 1971. A group process model for problem identification and program planning. Jour. of Appl. Behav. Sci. 4:466-492.

GISI, DONALD V. 1971. Recreation expectations of first-time visitors to the Ozark National Scenic Riverways. Unpublished M.S. Thesis, University of Missouri-Columbia, 53 p.

HABERMEHL, JAMES M. 1973. Determining visitor perceptions of crowding on the Ozark National Scenic Riverways. Unpublished M.S. Thesis, University of Missouri-Columbia, 103 p.

LIME, DAVID. 1970. Research for determining use capacities of the Boundary Waters Canoe Area. Naturalist 21:9-13.

LIME, DAVID W. 1975. Some principles of carrying capacity. USDA For. Serv., Southeast For. Exp. Sta., Asheville, N.C., General Tech. Report SE-9:122-134.

MARNELL, LEO. 1976. Applying recreation carrying capacity concepts. Proceedings of Second Annual John S. Wright Forestry Conference, Purdue University, Lafayette, Indiana.

MARNELL, LEO. 1976. Ozark River use investigations. Proc. First Conf. on Scientific Research in the National Parks, New Orleans: 10 pp.

REYNOLDS, GEORGE W. 1975. Ask John Q. Public. Our Public Lands 25:4-10.

WAGAR, J. ALAN. 1964. The carrying capacity of wild lands for recreation. For. Sci. Monogr. 7:1-24.

WEHRUNG, PATRICK. 1975. Participation in large group float trips at Ozark National Scenic Riverways. Unpublished M.S. Thesis, Southern Illinois University-Carbondale, 50 p.

WHYTE, WILLIAM F. 1969. Organizational behavior: Theory and application. Homewood, Ill.: Richard D. Irwin, Inc. 268 p.

# ENVIRONMENTAL VARIABLES AND MULTIANNUAL CYCLES IN POPULATION DENSITY OF THE MONTANE VOLE, *MICROTUS MONTANUS*, IN GRAND TETON NATIONAL PARK - A PRELIMINARY REPORT[1]

Aelita J. Pinter[2]

Multiannual cycles in population density of small rodents have been known since antiquity. However, despite the extensive work that has centered around this phenomenon, the search still continues for the causes underlying these fluctuations.

The purpose of the present study was to test the hypothesis that environmental variables and reproductive responses of montane voles, *Microtus montanus*, play a major role in their population dynamics. A number of field and laboratory observations had led to the formulation of this hypothesis.

To start with, preliminary field observations in Grand Teton National Park in 1961, and from 1966 through 1968 (Pinter, unpublished observations) suggested that this particular population of montane voles did, indeed, exhibit the well known multiannual cycles in density. At about the same time laboratory studies began to reveal the remarkable sensitivity of the microtine reproductive system to such environmental variables as diet and photoperiod (Pinter and Negus 1965, Negus and Pinter 1966, Pinter 1968).

If such responsiveness of *M. montanus* to environmental variables existed in the field, it would have enormous adaptive significance for this species for a number of reasons. Under natural conditions for *M. montanus* such factors as temperature, precipitation, cover, and quality and quantity of food vary dramatically and unpredictably on an annual as well as on a multiannual basis. Furthermore, their life expectancy is less than a year. Consequently, any cues these animals could utilize to predict an impending environmental change would, in effect, decrease the intensity of this unpredictability. As a result, the chances of the survival of the species within that environment would be maximized. An example of this might be a seasonally breeding animal that enters gonadal quiescence during a nonbreeding season. If such an animal were to be gonadally competent at the onset of the following breeding season, gonadal recrudescence would obviously have to begin well in advance of the beginning of the actual breeding season. Consequently, the animal should be capable of utilizing some environmental cue that would permit him to initiate gonadal recrudescence at a time when existing conditions are not yet suitable for reproduction.

Since *M. montanus* do not hibernate and are semifossorial, they are rather directly exposed to environmental changes that could be utilized as potential cues. However, the mere presence of a variable is not sufficient. The animal must be capable of physiologically detecting this cue (actually any variable that is detected physiologically can be considered a cue). Furthermore, he must be capable of transducing this information into a biologically appropriate response, thereby adapting to the environmental change.

Laboratory studies had revealed that a long photoperiod and the availability of fresh green plants in the diet stimulated reproductive activity and sexual maturation in *M. montanus*. Conversely, a short photoperiod and infrequent supplementation with dietary greens suppressed reproductive activity and delayed sexual maturation (Pinter and Negus 1965, Negus and Pinter 1966, Pinter 1968). How would voles respond to these variables under natural conditions? The rate of annual photoperiod change always remains the same for a given location. However, the timing of the vegetative growth onset in the spring varies from year to year. Would this significantly affect the onset of breeding in a natural population of *M. montanus*? Would climatic differences from one year to the next, by affecting vegetation characteristics, also affect population parameters in voles? Could the occurrence of a variable (e.g., drought, spring flooding) affect the multiannual cycle more significantly if it appeared during the phase of, say, low, rather than high, population density? These and many more questions had arisen from all preliminary investigations. What had to be done next was to examine the natural populations in the light of laboratory observations.

## MATERIALS AND METHODS

Since the investigation would have to span several years, the northern end of Jackson Hole that lies within Grand Teton National Park was chosen as the study site. Outside of a National Park the study area could be readily destroyed by new construction of roads or buildings - a fate that has befallen many investigators (for example, Whitney 1976).

*Microtus* were collected using Sherman livetraps. Animals were trapped over three study

[1]I wish to express my sincere appreciation to the many students and assistants for their help over the years in various phases of the work. I am particularly indebted to J. Ed Hall, Allen K. McLean and Dr. Janet R. Smith. I also thank Drs. L. Floyd Clarke and Oscar H. Paris, former directors of the Jackson Hole Biological Research Station for their generous help and the provision of totally indispensable facilities at the Station. However, this work could not have been accomplished without the repeated extensions for space and facilities at the Station granted me by the Advisory Committee of the JHBRS at the University of Wyoming. To them I extend my heartfelt thanks for their understanding that some investigations require years for completion. This study is Project No. 173 at the Jackson Hole Biological Research Station. The work was supported in part by a grant from the New York Zoological Society, and in part by the J. Aron Research Fund at the Touro Research Institute, whose support is hereby also gratefully acknowledged.

[2]Department of Biological Sciences, University of New Orleans, New Orleans, Louisiana 70125.

periods each year: a spring study period (approximately within two weeks in late May - early June); a summer study period (approximately mid-July to mid-August), and a fall study period (within the first two weeks in October).

Trapping was carried out in two ways. A permanent grid, covering a half acre (.202 hectares), was established in the summer of 1970, with 121 permanent trapping stations marked with stakes. The grid was trapped during the summer study periods only. These data provided information on the relative population density of *Microtus* from one year to the next, since spacing of the traps within the grid was the same every summer.

Aside from the grid, trapping was also carried out in several other meadows nearby. However, here traps were set as much as possible near sign of recent *Microtus* activity. In other words, they were located in a manner that would maximize the trapping success to provide as many individuals as possible for the evaluation of reproductive status. Consequently, data from these sets could not be used as a reliable indicator of population density.

Animals were classed as juveniles, subadults, or adults, on the basis of weight, total length, and stages in maturation molts. Reproductive status of the males was evaluated on the basis of testicular and epididymidal weight. For females the criteria considered were an open or closed vaginal orifice, and evidence of pregnancy or lactation. Information regarding litter size was derived from embryo counts. An estimated conception date was also determined for each litter. Such estimates, based on known age embryos from the laboratory, have an accuracy of $\pm$ 24 hours. In the absence of visible embryos, estimates of recent litter sizes were based on placental scars.

## RESULTS

Table 1 summarizes the trapping success within the permanent grid. No data are available from this location for the summer of 1969. However, in the summer of 1969 traps had been set nearby utilizing the same spacing that was employed when the permanent grid was established in 1970. Consequently, the summer data for 1969 (Table 2) can be fitted in almost directly with the rest of the data from the grid (Table 1). When this is done, it can be seen that a peak in population density occurred in 1969. The population had declined dramatically by the summer of 1970, as indicated by the very high number of trap nights needed to capture one animal. An increase in population density then ensued through 1973. This was followed by another decline in 1974, and - quite unexpectedly - by a further decline in 1975. The population density rose again in 1976. The density recorded in 1976 was lower than that in 1973; neither the 1973 nor the 1976 peak was as high as that seen in 1969. However, on the basis of presently available data it is as yet impossible to say whether 1976 truly represents a peak (if "peak" is defined as a year having higher populations than the year preceding or following it).

A similar pattern in population density changes was found outside the grid (Table 2). Again, it must be remembered that, with the exception of the summer of 1969, traps outside the grid were generally clumped at sites of recent *Microtus* activity. Therefore, the population density appears to be greater outside the grid (Table 2) than within it (Table 1). However, this is probably a reflection of the difference in trapping methods between the two areas.

Trapping success during the spring study period requires some comment. In the spring meadows in which trapping takes place become severely flooded during meltoff. Large portions of these meadows may remain under several centimeters of water for a number of days. Such flooding must force *Microtus* to retreat temporarily to higher ground. Consequently, spring trapping success under these conditions is not a realistic measure of population density. Rather, it is to a large extent a measure of the success with which one can locate within the habitat the spots to which the voles had retreated. Furthermore, both, the spring and the fall study periods were short (less than two weeks). Consequently, trapping success was sometimes seriously affected by inclement weather, a common occurrence during these seasons in Grand Teton National Park. It also should be noted that no data are available for the fall study periods of 1971, 1972, and 1976, as unexpected circumstances forced the cancellation of these trips.

The reproductive performance of the animals is summarized in Table 3. Sample sizes may frequently be small. However, they do not represent all females trapped during a given period. Rather, only females for whom litter sizes could be determined without a histological evaluation are presented here.

The summer data for reproductively active animals are presented separately for subadult and adult females. At this time of the year the subadult females would be pregnant with only their first or second litter. Adult females would be carrying at least the third or fourth litter. It has been shown in the laboratory that in *M. montanus* litter size increases up to the fifth litter and then declines with each successive litter (Negus and Pinter 1965). Consequently, a lumping of the subadult and adult values might obscure the true reproductive responses of the animals.

Litter size is quite variable on a multiannual basis, and does not seem to be affected by population density. However, as will be shown below, under natural conditions litter size is affected by environmental variables.

It is also noteworthy that during the spring and fall reproduction is limited to adult animals. The absence of subadult breeding during the fall also suggests that the age of a vole may determine its responsiveness to a given environmental variable.

Another variable that could affect the population dynamics of *Microtus* is the onset of spring breeding on a population wide basis. Winter breeding in *M. montanus* in the study areas is apparently quite uncommon, if it occurs at all. This conclusion is based on the observation that all reproductively active females trapped during the spring study period did not show evidence of reproductive activity in the recent past. In other words, females were not lactating; neither did they show placental scars. Consequently, the estimated conception date for embryos of females from the spring study period would also designate the onset of reproductive activity for that female. As will be pointed out shortly, an exception to this was found in the spring of 1969.

Table 4 summarizes the estimated timing for onset of reproduction in *M. montanus* in Grand

TABLE 1. *Microtus montanus* trapped in a half-acre (0.202hectares) grid in Grand Teton National Park, 1970-76 (summers only).

| | (1969)* | 1970 | 1971 | 1972 | 1973 | 1974 | 1975 | 1976 |
|---|---|---|---|---|---|---|---|---|
| Number trapped | (103) | 3 | 10 | 24 | 105 | 62 | 51 | 96 |
| Trap nights per animal | (10) | 818 | 237 | 133 | 12 | 27 | 58 | 16 |

* for explanation of the 1969 column see text.

TABLE 2. *Microtus montanus* trapped in Grand Teton National Park outside the grid, 1969-76.

| | | 1969 | 1970 | 1971 | 1972 | 1973 | 1974 | 1975 | 1976 |
|---|---|---|---|---|---|---|---|---|---|
| SPRING | Number trapped | 56 | 57 | 12 | 5 | 35 | 49 | 37 | 21 |
| | Trap nights per animal | 25 | 16 | 67 | 207 | 29 | 14 | 13 | 36 |
| SUMMER | Number trapped | 103 | 20 | 71 | 148 | 148 | 163 | 103 | 91 |
| | Trap nights per animal | 10 | 212 | 44 | 18 | 9 | 17 | 19 | 17 |
| FALL | Number trapped | 47 | 9 | - | - | 67 | 58 | 26 | - |
| | Trap nights per animal | 13 | 68 | - | - | 13 | 26 | 48 | - |

TABLE 3. Reproductive performance of *Microtus montanus* in Grand Teton National Park, 1969-76.

| | 1969 | 1970 | 1971 | 1972 | 1973 | 1974 | 1975 | 1976 |
|---|---|---|---|---|---|---|---|---|
| SPRING | A_females<br>x= 5.1<br>(3-7)*<br>N=11 | A_females<br>x= 5.3<br>(3-7)<br>N=12 | A_females<br>x= 5.0<br>(5-7)<br>N=5 | A_females<br>x= 5.5<br>(4,7)<br>N=2 | A_females<br>x= 6.2<br>(4-8)<br>N=13 | A_females<br>x= 5.6<br>(4-8)<br>N=18 | A_females<br>x= 5.5<br>(5-7)<br>N=4 | A_females<br>x= 5.3<br>(5-6)<br>N=6 |
| SUMMER | SA_females<br>x= 5.0<br>(4-6)<br>N=4<br><br>A_females<br>x= 6.1<br>(2-10)<br>N=16 | SA_females<br>x= 4.5<br>(4,5)<br>N=2<br><br>A_females<br>x= 6.3<br>(5-7)<br>N=3 | SA_females<br>x= 6.3<br>(5-8)<br>N=4<br><br>A_females<br>x= 5.0<br>(3-7)<br>N=3 | SA_females<br>x= 5.4<br>(4-8)<br>N=12<br><br>A_females<br>x= 6.5<br>(4-9)<br>N=21 | SA_females<br>x= 5.1<br>(4-7)<br>N=23<br><br>A_females<br>x= 5.6<br>(3-8)<br>N=18 | SA_females<br>x= 4.3<br>(3-6)<br>N=12<br><br>A_females<br>x= 5.0<br>(2-8)<br>N=14 | SA_females<br>x= 5.3<br>(3-7)<br>N=23<br><br>A_females<br>x= 6.6<br>(4-9)<br>N=14 | SA_females<br>x= 5.6<br>(4-10)<br>N=8<br><br>A_females<br>x= 5.5<br>(2-9)<br>N=24 |
| FALL | A_females<br>x= 6.2<br>(4-10)<br>N=5 | A_females<br>x= 4.3<br>(3-6)<br>N=3 | | | A_females<br>x= 6.3<br>(4-9)<br>N=3 | | A_females<br>x= 4.0<br>(4)<br>N=1 | |

* range of litter sizes observed

TABLE 4. Estimated onset of spring breeding in *Microtus montanus* in Grand Teton National Park 1969-76.

| 1969 | 1970 | 1971 | 1972 | 1973 | 1974 | 1975 | 1976 |
|---|---|---|---|---|---|---|---|
| April<br>2nd-3rd week | May<br>2nd-3rd week | May<br>2nd-3rd week | May<br>1st week | May<br>1st-2nd week | May<br>1st week | May<br>3rd-4th week | May<br>2nd week |

Teton National Park. It is evident that the onset of spring breeding can be extremely variable from one year to the next. For example, in 1969 reproduction on a population wide basis started in mid-April. Conversely, in 1975 widespread breeding did not begin until the third or fourth week in May. This represents a variability of five to six weeks! Such variability assumes added importance when coupled with a significant phenomenon: field observations indicate that very few, if any, voles born during the first week in July and thereafter will mature in the year of their birth. It now becomes obvious why variations in the onset of spring breeding can have significant repercussions on the population dynamics of *M. montanus*. In the montane vole the gestation period is 21 days. Females can remate in post partum estrus, and several litters can be produced by one female at 21-day intervals (Negus and Pinter 1965). Consequently, if a female started breeding no later than the first week in May, and if she always mated in post partum estrus, she could theoretically produce three litters before the first week in July. This was probably the case in 1972-1974 (Table 4). An extremely early onset of reproductive activity (in 1969) probably even permitted the production of four such litters. Conversely, an inordinate delay in the onset of spring breeding occurred in the spring of 1975. In that year only one, and certainly no more than two litters could be produced by any one female before the first week in July.

The reproductive output by a female before the first week in July has immense significance for a number of reasons. First, the production of three, rather than of two litters, means the addition of more animals by that date. Second, the production of a third litter before early July is not the addition of merely a litter. Laboratory data have revealed that litter size in *M. montanus* increases with each successive litter, up to the fifth litter (Negus and Pinter 1965). Consequently, the addition of a second or of a third litter represents the addition of a litter that is larger than the one immediately preceding it. Third, the production of litters before the first week in July is not an addition of merely numbers of voles. Rather, this represents the addition of *breeders* - these are young that will contribute to the population in the year of their own birth. Fourth, among litters produced before the first week in July there will be a difference in maturation rate. Laboratory studies have indicated that maturation rate in *M. montanus* is most rapid in young born under a long photoperiod and with an abundance of fresh green vegetation in the diet. Conversely, young born and reared under a short photoperiod and with a low level of greens supplementation are significantly older by the time they finally attain sexual maturity (Pinter 1968). A comparable effect could be expected under natural conditions. In other words, the earlier a litter is born in the season, the more rapid would be its maturation rate. A litter born in May would be exposed to a lengthening photoperiod and an abundant supply of vegetatively growing grasses. These young would mature more rapidly than would those born, for instance, in late June - a time of shortening daylength and of a gradual cessation of vegetative growth. The significance of this phenomenon lies in the age at which such young will enter the breeding population. That is, an early onset of spring reproduction would add young that start reproducing at an early age (the reverse, of course, is true if spring breeding gets off to a late start). It is obvious that animals which mature early will make a greater contribution to the population than will those that require a longer time before attaining sexual maturity. Consequently, as outlined above, the timing of spring breeding initiation can have a crucial impact on vole population dynamics.

*Microtus montanus* exhibit remarkable variations in population density (Tables 1 and 2), reproductive success (Table 3), and initiation of spring breeding (Table 4). Their natural environment is also extremely variable. A correlation can now be made for the entire study period between physiological responses and population dynamics of the voles on one hand and some environmental variables on the other.

First, it is important to recognize those environmental factors which not only profoundly affect reproductive responses of voles, but which also vary unpredictably from year to year. Probably the most important among these are the timing of meltoff and the onset of vegetative growth in the spring, and the pattern of precipitation during the summer.

Examples can now be drawn from the data to illustrate how the timing of environmental events might affect not only the duration but also the amplitude of the cycle.

Peak densities of *M. montanus* in 1969 probably resulted from the concurrence of several factors: exceptionally early meltoff, a consequent early vegetative growth, and a very high overwintering population. The significance of the earliest possible initiation of breeding has already been discussed. However, 1969 is an extreme case. Voles born early in the season attain sexual maturity at approximately three weeks of age. Consequently, those young that were conceived in mid-April probably became breeders early in May. This means that as many as two litters produced by one of these young could also become breeders in 1969! The implications of such a situation at the population level are obvious.

Breeding on a population wide basis started early in May in both, 1973 and 1974. However, the failure of these populations to attain the densities seen in 1969 can be explained in terms of the other coincident factors. In 1973 the overwintered population was quite high. However, since breeding in 1973 began about three weeks later than in 1969, any given overwintered female produced one less litter in 1973 than in 1969. Since the population density in 1973 turned out to be lower than that seen in 1969, a further increase was considered a possibility for 1974. Although the overwintering population and the onset of breeding were similar in 1973 and in 1974, a decline occurred in the summer of 1974. This may be linked to a drought in the summer of 1974. The vegetation during most of the summer was short, dry and sparse. This environmental situation was apparently reflected in the reproductive performance. Mean litter sizes were among the lowest (adult females) or even the lowest (subadult females) ever recorded during a summer (Table 3). The impairment of reproductive success was probably the principal cause underlying the decrease in population density in 1974. Consequently, the results obtained from 1973 and 1974 demonstrate that environmental variables (e.g., onset of spring in 1969 vs. 1973) can affect the amplitude of a cycle (e.g., the ultimate densities achieved at the two peaks, 1969 vs. 1973). Furthermore, environmental variables (e.g., drought in 1974) can also affect the length of a cycle (i.e., a peak in 1973

instead of 1973).

A late spring can also have significant repercussions on population dynamics. For example, in the spring of 1975 breeding commenced so late that an actual decline, rather than the anticipated increase, occurred in population density that year. Or, in another case, the recovery from the 1969-1970 crash would have been much more rapid had the onset of breeding not been delayed until late May.

Changes in population density do not always result from the effect of environmental variables acting through the reproductive responses of *M. montanus*. The late winter of 1972 is a case in point. Unseasonably high temperatures in early March caused extensive melting of snow. Since the meadows in the study areas drain extremely slowly, there probably was considerable subnivean flooding. The warm period was followed by a hard freeze. The spring of 1972 was the only instance within the entire study when dead *Microtus* were found, some inside their grass nests. The exact cause of death is unknown. However, winter nests of *M. montanus* are constructed at the snow-soil interface. Consequently, it is likely the animals died from exposure associated with the flooding and the freeze. The extent of mortality during this climatic catastrophe is also not known. Nevertheless, it must have had devastating effects on the population: despite the fact that breeding in 1972 started quite early (Table 4), the rate of increase in population density from 1971 to 1972 was lower than that for any other year showing a rise in population density (Table 1). Evidence that severe winters, especially in terms of wetness and freezing, can seriously affect population densities of small rodents has been summarized by Krebs and Myers (1974).

## DISCUSSION

Doubtless, the fluctuations in population density of *M. montanus* are affected by numerous variables. Furthermore, these probably include not only the extrinsic variables (i.e., the quality of the environment), but also intrinsic variables (i.e., the genetic makeup, or the quality, of the individual). Nevertheless, the data presented here suggest that it is the reproductive success that will, in a large measure, determine the population dynamics of the multiannual cycles of microtines. Or, in other words, the reproductive responses of these rodents are basically a reflection of the environment.

As mentioned earlier, probably two of the most important environmental variables known to affect reproduction and sexual maturation in *M. montanus* are photoperiod and diet (Pinter and Negus 1965, Negus and Pinter 1966, Pinter 1968). The seasonal changes in the reproductive responses of these rodents under natural conditions as observed during the course of the present study can be explained on the basis of such laboratory findings.

Gonadal recrudescence in the spring probably occurs in response to the lengthening photoperiod. Indeed, isolated animals may begin breeding before the appearance of vegetative growth. However, the emphasis here is on the intensity of breeding. In other words, it is not until the appearance of new shoots of herbaceous vegetation that reproduction begins on a population wide basis. For example, reproductive activity was induced in a non-breeding natural population of *M. montanus* by supplementation with sprouted wheat (Negus and Berger 1975). This was a population wide response (100% of the females trapped were pregnant). A nearby unsupplemented population remained reproductively inactive until breeding was initiated by the eventual sprouting of their natural food plants. As yet unidentified substances in vegetatively growing plants have a stimulating effect on reproductive responses - including sexual maturation - in *M. montanus* (Pinter and Negus 1965, Negus and Pinter 1966, Pinter 1968). These plant substances have in the past been given the unfortunate misnomer "plant estrogens". However, it was reported several years ago (Pinter 1968) that these substances stimulate the gonads in intact male *M. montanus*, demonstrating that "plant estrogens" do not remotely act in the manner of classical animal estrogens.

The fact that the appearance of green plants triggers reproduction in natural populations of *M. montanus* explains the variability in the onset of breeding from one year to the next (Table 4). Furthermore, it is again the interaction of photoperiod and nutrition that may explain the failure of young, born after the first week in July, to mature in the year of their birth. Such young are growing up at a time of decreasing daylength. Green plant food is still plentiful. As some of the preferred plants of *M. montanus* reach their fruiting stage and begin to dry, the substances in these plants that exert a stimulating effect on the reproductive system are known to disappear from these plants. There also is evidence that mature grasses contain a compound that inhibits reproduction in *M. montanus* (Berger et al. 1975). However, *M. montanus* may not continue to feed exclusively on their preferred food plants once they begin fruiting and drying. Voles are opportunists when it comes to food selection. In late summer they may feed on maturing plants and still select whatever green vegetation is available, for as long as it remains available. For example, even as late as the fall study period *Microtus* were feeding on newly sprouted herbaceous vegetation. Nevertheless, despite the availability of some green plant food in the fall it is noteworthy that any breeding that may occur at this time is limited to adult animals (although not all of the adults are reproductively active). It would seem, therefore, that once the reproductive system has been activated in early summer it is not readily suppressed by shortening daylength and drying of most herbaceous plants. It is likely that reproduction in adults is maintained for as long as growth of new shoots continues during the fall. In other words, the stimulating effect of these shoots must override any depressing effects of decreasing photoperiod or of inhibitory substances in plants. On the other hand, in young born after early July even the availability of new green shoots in the fall cannot initiate gonadal recrudescence.

An interesting suggestion has been made recently regarding the effects of wildebeest grazing on a plant community. The preposterousness of comparing vole and wildebeest aside, this study may have some implications for *Microtus* populations after all. McNaughton (1976) reports that heavy grazing by migratory wildebeest left a seemingly devastated range. However, after comparisons with an exclosure it became obvious that the removal of the vegetation by the wildebeest had prevented the senescence of the plant community. While plants in the exclosure were flowering, in the grazed areas they were undergoing vegetative growth. Could *Microtus* exert sufficient grazing pressure to prevent senescence of their preferred food plants and also provoke an abundance of vegetative growth? Because such a supply of green plants would presumably permit the continued stimulation of reproduction at a time when senescent plants would

predominate in the food supply. This question cannot be answered on the basis of the present data since the impact of *Microtus* on the vegetation was not investigated. On the basis of casual observations there was only one time during this study when the voles had exerted a grossly visible effect on the vegetation. Following meltoff in the spring of 1970 it became apparent that the meadows had been virtually denuded of vegetation by the large overwintering population. A comparable effect has never been observed in late summer - a time when such a phenomenon would be expected to have significant repercussions on the reproductive performance. However, the cause-and-effect relationship between cropping by *Microtus* and the stimulation of vegetative growth may be a very real occurrence, albeit on a very subtle scale. At any rate, the possibility should not be dismissed. Indeed, it is conceivable that the appearance of the green shoots seen during the fall study period might at least partially be a response to cropping by *Microtus*.

It is not difficult to envision the adaptive significance of the reproductive responses of *M. montanus*. One might view the variables, photoperiod and nutrition (for example, in the spring), as being the coarse and the fine adjustment, respectively, on a microscope. In the spring it is the increase in daylength that initiates gonadal recrudescence, much the same as the coarse adjustment on the microscope might bring a slide into general focus. However, photoperiod is a "constant" variable - at a given geographical point, on any given date, there will always be the same number of hours of light and of darkness. On the other hand, as seen from this study, local climatic conditions vary dramatically and unpredictably from year to year. A reliance solely on photoperiod as a cue for the initiation of reproduction might have disastrous consequences on the outcome of the reproductive effort. Consequently, *M. montanus* have evolved the capability of using a second cue - the onset of vegetative growth in the spring - as the ultimate signal. As a result, reproduction on a population wide basis is triggered by the availability of green plant food (the same as the fine adjustment on a microscope brings the slide into ultimate sharp focus). Young will now be produced as soon as - or, only when - conditions are optimal for their survival. Conversely, the failure of late born young to mature in the year of their birth prevents the production of large numbers of additional young just before winter, when availability of food and of suitable habitat may become a severe limiting factor. By using such environmental cues as photoperiod ("coarse adjustment") and the quality of the diet ("fine adjustment") *M. montanus* have evolved a highly effective mechanism that permits them an exceptionally high degree of adaptation to a changing environment.

This is a preliminary report. Additional data are still being gathered and the collected data are being analyzed in more detail. The extent of the reproductive responses to environmental variables will become more completely apparent when histological studies have been completed. A detailed evaluation of the climatic conditions and of the role of predators in the population dynamics of *M. montanus* is also in progress.

These and other aspects are still under investigation. Nevertheless, it is apparent that environmental variables do act through the reproductive responses of *M. montanus*. In doing so they affect the amplitude as well as the length of multiannual cycles in population density.

## LITERATURE CITED


BERGER, P. J., P. D. GARDNER, E. H. SANDERS and N. C. NEGUS. 1975. A chemical inhibitor of reproduction in *Microtus montanus*. 55th Annual Meeting of the Amer. Soc. Mammalogists, Missoula, Montana (abstract).

KREBS, C. J. and J. H. MYERS. 1974. Population cycles in mammals. Adv. Ecol. Res. 8:267-399.

MCNAUGHTON, S. J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191:92-94.

NEGUS, N. C. and P. J. BERGER. 1975. Experimental triggering of reproduction in a natural population of *Microtus montanus*. 55th Annual Meeting of the Amer. Soc. Mammalogists, Missoula, Montana (abstract).

NEGUS, N. C. and A. J. PINTER. 1965. Litter sizes in *Microtus montanus* in the laboratory. J. Mammal. 46:434-437.

NEGUS, N. C. and A. J. PINTER. 1966. Reproductive responses of *Microtus montanus* to plants and plant extracts in the diet. J. Mammal. 47:596-601.

PINTER, A. J. 1968. Effects of diet and light on growth, maturation and adrenal size of *Microtus montanus*. Amer. J. Physiol. 215: 461-466.

PINTER, A J. and N. C. NEGUS. 1965. Effects of nutrition and photoperiod on reproductive physiology of *Microtus montanus*. Amer. J. Physiol. 208:633-638.

WHITNEY, P. 1976. Population ecology of two sympatric species of subarctic microtine rodents. Ecol. Monog. 46:85-104.

# EFFECTS OF PRESCRIBED BURNING ON SMALL-MAMMAL COMMUNITIES IN LAVA BEDS NATIONAL MONUMENT, CALIFORNIA

R. W. Frenzel, E. E. Starkey and H. C. Black[1]

## INTRODUCTION

Lava Beds National Monument was established in 1925 to preserve and protect the area's extensive volcanic deposits and the location of the Modoc Indian War of 1872-73.

Controlled burning experiments were begun on the Monument in 1972 to determine whether or not this was a feasible means of changing undersirable successional trends, and to cause plant communities to revert to conditions extant in about 1850, before disturbance by white settlers. Current research at Lava Beds is designed to develop a fire-management plan, which would include prescribed burning as a management tool (Martin and Johnson, 1976). Burning may alter the structure of the small-mammal communities, both in abundance and relative species composition.

Because of the significance of the small-mammal communities in the ecology of this area, it is important to know the impact of controlled burning on small-mammal populations and the effects of habitat changes after burning on the small mammal communities. Small mammals are important prey species for various avian and mammalian predators in the area, and changes in the availability of these prey species may effect the predator populations. Small mammals are also potentially important vectors of parasites and disease (Nelson and Smith, 1976). In addition, these rodents may have a significant influence on natural succession after fires, or on any post-fire seeding projects.

## STUDY AREA

Lava Beds National Monument is located in extreme northern California near Tule Lake and contains approximately 18,000 hectares of land. The climate of the area is moderate, although cold weather is possible anytime; snow has been recorded in nearly all months. Winter daily high temperatures average between 5° and 10° C, with lows between 0° and -7° C. Summer highs average 24° - 27° C, with lows 5° - 10° C. Summer precipitation averages less than 3.2 cm per month.

The plant communities of the Monument can be categorized into three physiographic zones: bunchgrass - sagebrush (shrub-steppe), juniper - mountain mahogany, and ponderosa pine - bitterbrush. These zones are separated altitudinally with the sagebruch - bunchgrass lying at the lowest elevations (1220 m), juniper - mountain mahogany at intermediate levels (1370 m), and ponderosa pine - bitterbrush at highest locations (1525 m). The elevation generally increases from north to south and southwest.

Because of the effects of grazing and intensive fire suppression in the Monument since about 1925, mountain mahogany (*Cerocarpus ledifolius*) and antelope bitterbrush (*Purshia tridentata*) have invaded the ponderosa pine (*Pinus ponderosa*) forests in the southern portion of the Monument and have developed dense understory shrub communities. These shrubs together with western juniper (*Juniperus occidentalis*) have increased in the central portion of the Monument. The original bunchgrass and sagebrush (*Artemisia tridentata*) community in the northern portion of the Monument has been invaded by juniper and cheatgrass (*Bromus tectorum*) while sagebrush has increased greatly (Martin and Johnson, 1976).

### *Fleener Sites*

An area of about 120 hectares of sagebrush - bunchgrass called the Fleener site was burned June 23, 1976 to reduce densities of western juniper, antelope bitterbrush and mountain mahogany. Prior to burning, a trapping plot was set up in the area to be burned and a control plot placed adjacent to the burn area in similar vegetation and topography. The control plot was 180 meters from the burn area and the treatment plot 150 meters inside the burn.

### *Cheatgrass Sites*

An area of about 160 hectares of cheatgrass called Hovey Point was burned on June 23, 1976 in an attempt to favor native bunchgrasses and decrease the abundance of cheatgrass, an exotic. A trapping plot was located on the burn 150 meters from the burn's edge. A control plot was located approximately eight kilometers from the burn on an area similar in vegetation and topography.

Concurrent research studying the effects of the fires on vegetation and monitoring burn parameters is presented in these proceedings in a paper by Martin and Johnson (1976).

## METHODS

Mark-recapture trapping plots were set up on the four sampling areas. Each plot consisted of a circle with 40 trapping stations. The stations were placed 7.6 meters apart and marked with metal wire stakes. The diameter of the ring was 97 meters. Two Sherman-type live traps (8 x 8 x 25 cm or 8 x 9 x 23 cm) were placed at each station, one facing east and the other west. Each station was shaded by a small a-frame shelter made of plywood to protect captured animals from extreme heat. A rabbit-sized welded wire live trap (24 x 24 x 80 cm) was placed within 3 meters of every other station. Welded wire traps were baited with apple slices. Sherman-type traps were baited with peanut butter and whole rolled oats.

The Sherman-type traps were prebaited three days before each three day trapping period. Traps were checked and reset once each day, usually in the morning. Specimens caught were all recorded by station number, species, sex, age

[1]Cooperative Park Studies Unit, School of Forestry, Oregon State University, Covallis 97331.

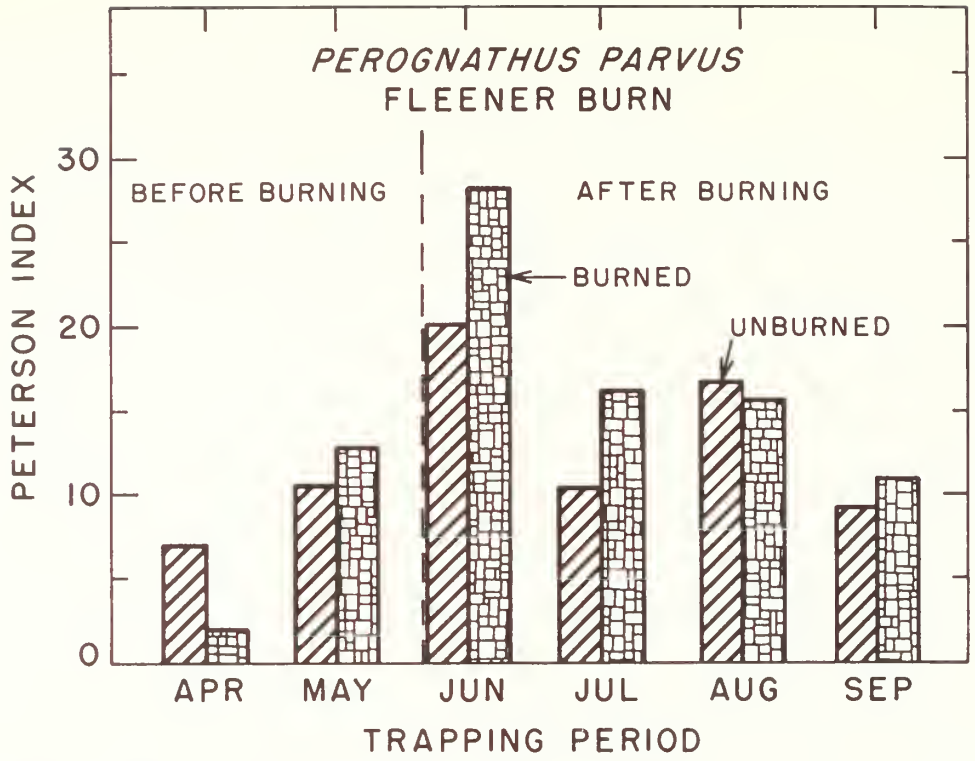



FIGURE 1. Peterson indexes of *Perognathus parvus* populations at Fleener burn and its control.

(by pelage and size) and external signs of reproductive conditions were noted. Animals were released after being ear-tagged with individually numbered trout fingerling tags (Salt Lake Stamp Co., Fingerling #FF). During the last three trapping periods *Peromyscus maniculatus* and *Perognathus parvus* individuals were also given a unique toe-clip because these animals occasionally lost their ear tags.

All four areas were trapped once in April 1976 and again in May before the two treatment areas were burned. They were trapped immediately following the burn in June and at monthly intervals through September 1976, totaling 7200 trap nights. Mark recapture trapping will be repeated on the burned and unburned areas during spring and early summer 1977.

Peterson indexes (Seber, 1973) were used to estimate the numbers of each species on the four areas. First and second days of each trapping period were used as the marking period and the index calculated from the results of the third day. After comparing the calculated estimate for each species to a minimum population estimate based on the total number of different individuals captured in that period, the Peterson indexes for *Microtus montanus* numbers were considered unreliable and the minimum estimates were used as a population indicator.

## RESULTS AND DISCUSSION

A total of eleven different species were captured on the four mark recapture areas during the six monthly trapping periods. Only four species (*Perognathus parvus, Dipodomys heermanni, Peromyscus maniculatus* and *Microtus montanus*) were caught in numbers that allowed population estimates to be calculated. The other seven species captured generally were represented by the capture of isolated individuals which were not recaptured.

Several cottontail rabbits (*Sylvilagus nuttali*) were trapped on the Fleener burn and its control, both before and after the burn date. The number of these animals trapped was too low to draw any conclusions about their populations.

Beldings ground squirrels (*Spermophilus beldingi*) were trapped in small numbers on the Hovey burn site which was near a beldings colony. Few captures were made and were limited primarily to May and June when the squirrels were not hibernating or estivating.

Beechy ground squirrels (*Otospermophilus beecheyi*) were occasionally captured in wire traps at the Fleener sites throughout the study. Because of their size these squirrels are capable of setting off the smaller Sherman style traps without being captured. For this reason Beechey ground squirrels captured in welded wire traps were removed from the area. Because of their low numbers and their range no conclusions were made as to the effect of the fire on their presence. A single capture of a yellow pine chipmunk (*Eutamias amoenus*) occurred at the Fleener burn site prior to burning.

Great Basin pocket mice (*Perognathus parvus*) were trapped in numbers only at the Fleener sites; only one individual was trapped at the Hovey burn site. The Peterson indexes for *Perognathus* on the Fleener sites are shown in Figure 1. The fire seems to have had no apparent effect on *Perognathus* numbers. The indexes for the burn and its control behave in a similar manner, both increasing through June and decreasing through the remainder of the summer.

The other Heteromyid found in the area is the Heermann kangaroo rat (*Dipodomys heermanni*). *Dipodomys* were trapped on both the Fleener and Hovey sites (Figure 2). Trapping at the Fleener

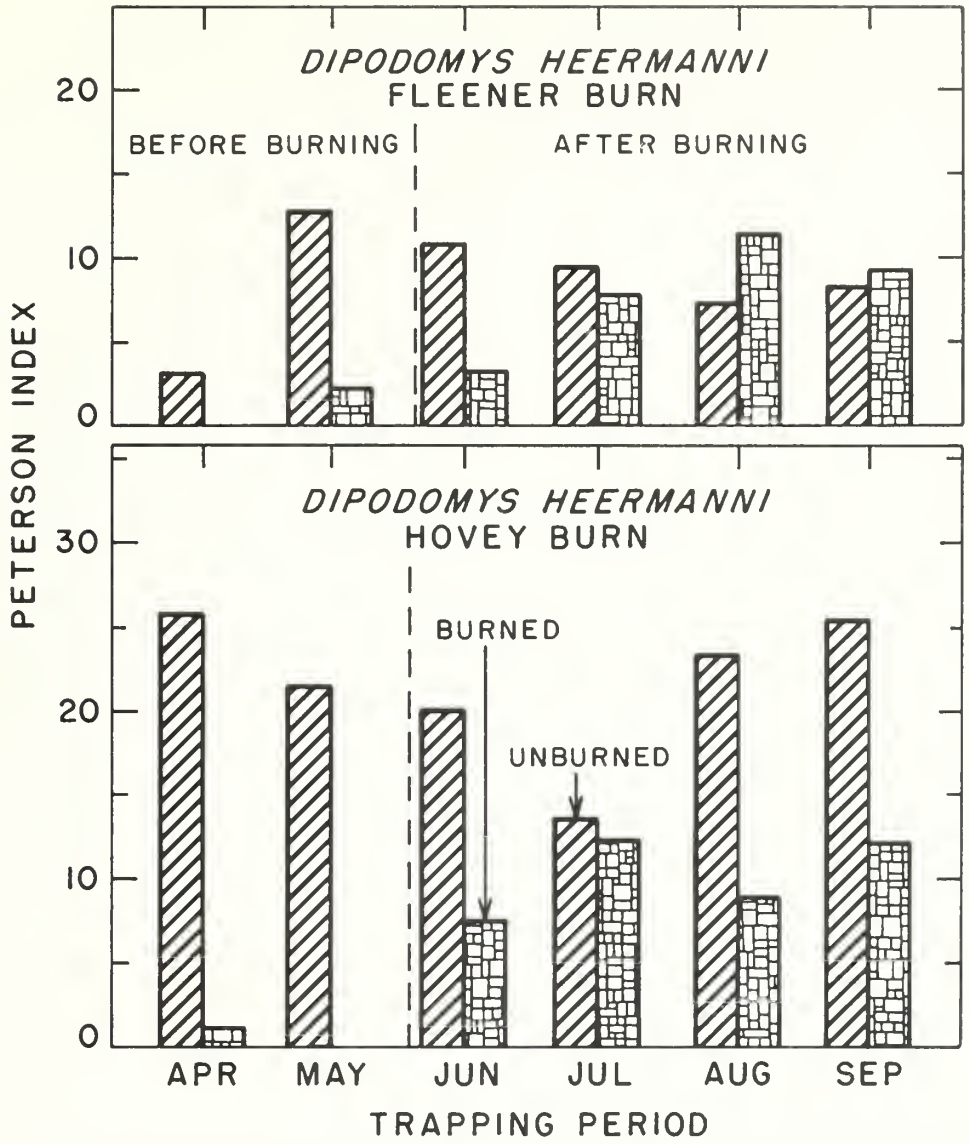



FIGURE 2. Peterson indexes of *Dipodomys heermanni* populations at Fleener burn and Hovey burn and their controls.

control site indicated that the highest number of *Dipodomys* were present in May with approximately 13 animals on the plot. The estimated numbers increased through the summer with the lowest estimate in August of seven animals in the area. The Fleener burn site has only two individual *Dipodomys* trapped before the burn. After the fire the *Dipodomys* showed a general increase in numbers to levels comparable to the control's. Comparison of the curves of the treatment and control population estimates after the burn indicates a significant difference at the .01% level ($F = 21.47$, $F_{.99}(2,4) = 18.0$).[2] However, it is difficult to compare the numbers of the two areas because of their differences prior to the burn. The possibility exists that the *Dipodomys* populations' annual reproductive cycles are out of phase and that the two areas are not supporting different numbers.

Captures of *Dipodomys* on the Hovey burn site prior to the fire were very low, with only one individual being trapped. There was a marked increased in *Dipodomys* captured immediately after the fire with estimates near ten individuals maintained through the summer. The control areas maintained a high number of individuals throughout the field season with estimates around twenty with a low estimate of approximately 13 in July. A comparison of the estimates on the treatment and control areas after the burn does not reveal a significant difference ($F = .44$, $F_{.95}(2,4) = 6.94$).

It appears that *Dipodomys* populations increased in the burned sites. However the difference in preburn populations, between control and treatment areas at Hovey and Fleener sites make it difficult to draw any conclusions about the effects of these fires on *Dipodomys*. The hypothesis that this species of *Dipodomys* may favor burned sites and move into these areas following a fire would be supported by studies showing certain *Dipodomys* species favor disturbed sites (Beatley, 1976). However, replication of our study and more intensive research would be necessary to provide any definite conclusions.

[2] Curvilinear regression, full (F) and reduced (R) models.

$$F = \frac{SSE(R)-SSE(F)}{df(R)-df(F)} \div \frac{SSE(F)}{df(f)},$$

where SSE = sum of squares residual (Draper and Smith 1966).

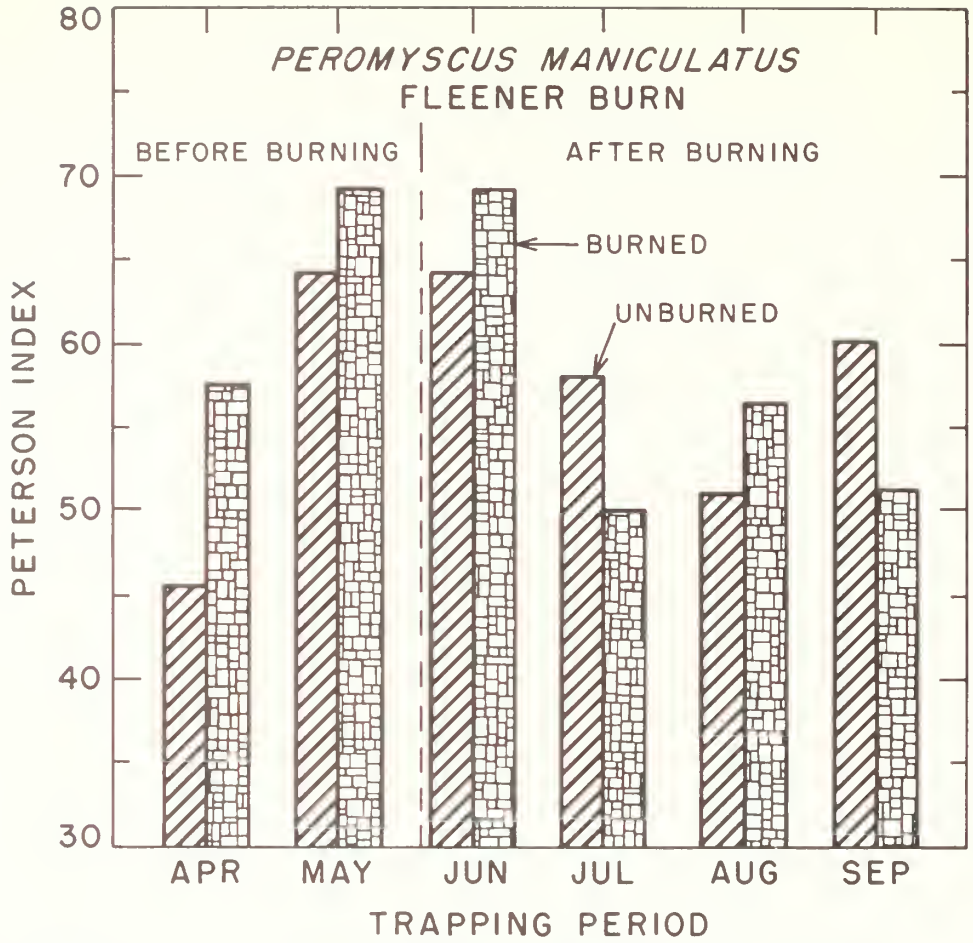



FIGURE 3. Peterson indexes of *Peromyscus maniculatus* populations at Fleener burn and its control.

The Cricetids were represented by four species: the western harvest mouse (*Reithrodontomys megalotis*), the canyon mouse (*Peromyscus crinitus*), the deer mouse (*Peromyscus maniculatus*), and the bushy tailed wood rat (*Neotoma cinerea*). Only one *Reithrodontomys* was trapped and this occurred at the Hovey control site. *P. crinitus* captures were limited to two individuals trapped on the Fleener burn site.

*P. maniculatus* was the most abundant rodent captured on the Fleener sites. Peterson indexes indicate numbers as high as 69 on a plot (Figure 3). The monthly estimates on the two Fleener sites indicate that the populations of the areas were similar before the fire and continued to follow the same general pattern throughout the summer. The fire had no apparent immediate effect on the *P. maniculatus* population.

As an indication of how many animals were lost in the fire, or left the area as a result of the burn, the proportion of animals tagged in April and recovered in May when no burn occurred was compared to the proportion of animals tagged in May and recovered in June, after the fires. These proportions compared to the same calculations on the control showed that recovery of tagged animals was independent of whether or not the area was burned ($x^2 = .00038$, $x^2_{.95(1)} = 3.84$).

Estimates of the numbers of *P. maniculatus* on the Hovey burn and control sites are shown in Figure 4. Both areas had definite decreases in the estimated populations through the summer. Numbers on the control area dropped markedly from a high in April of over 40 to a low of 8 in June. The two areas appeared to have similar population

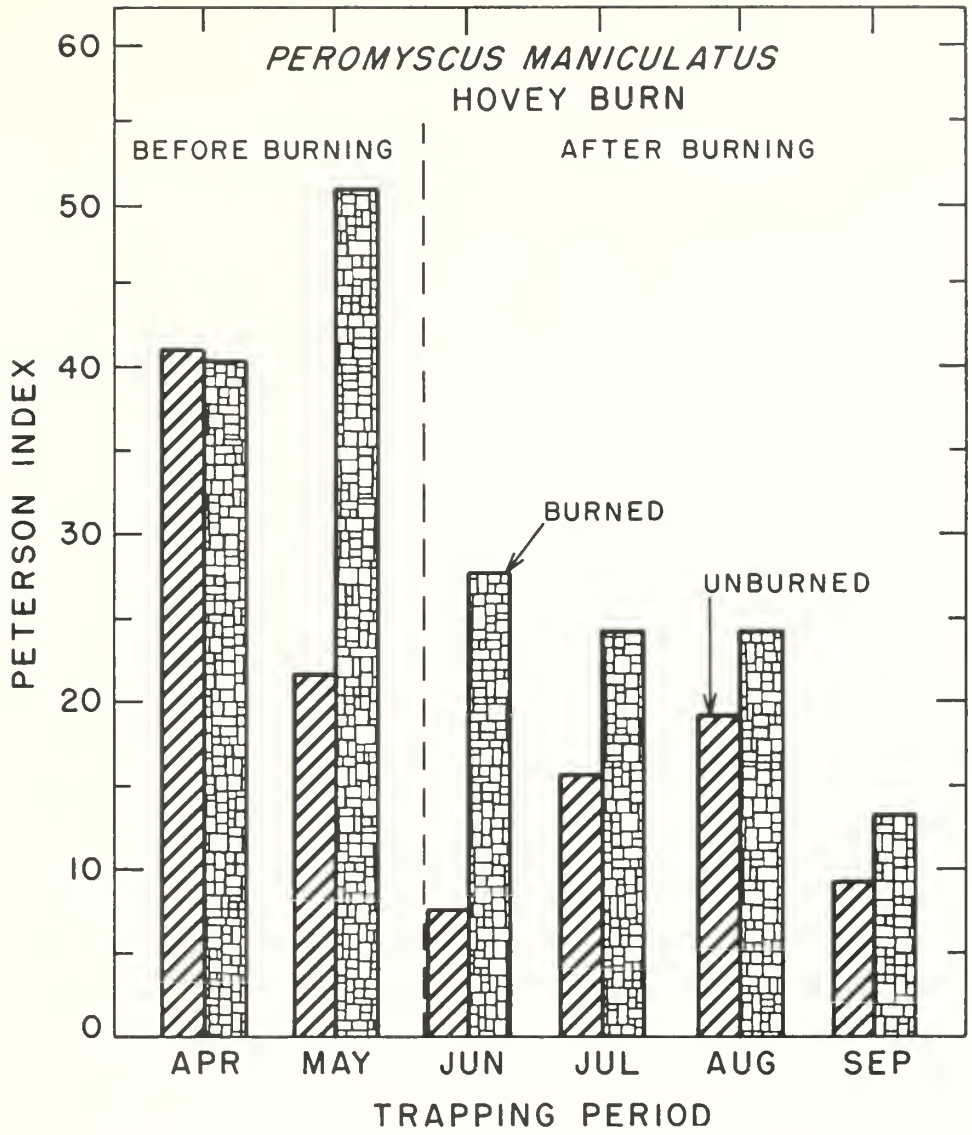



FIGURE 4. Peterson indexes of *Peromyscus maniculatus* populations at Hovey burn and its control.

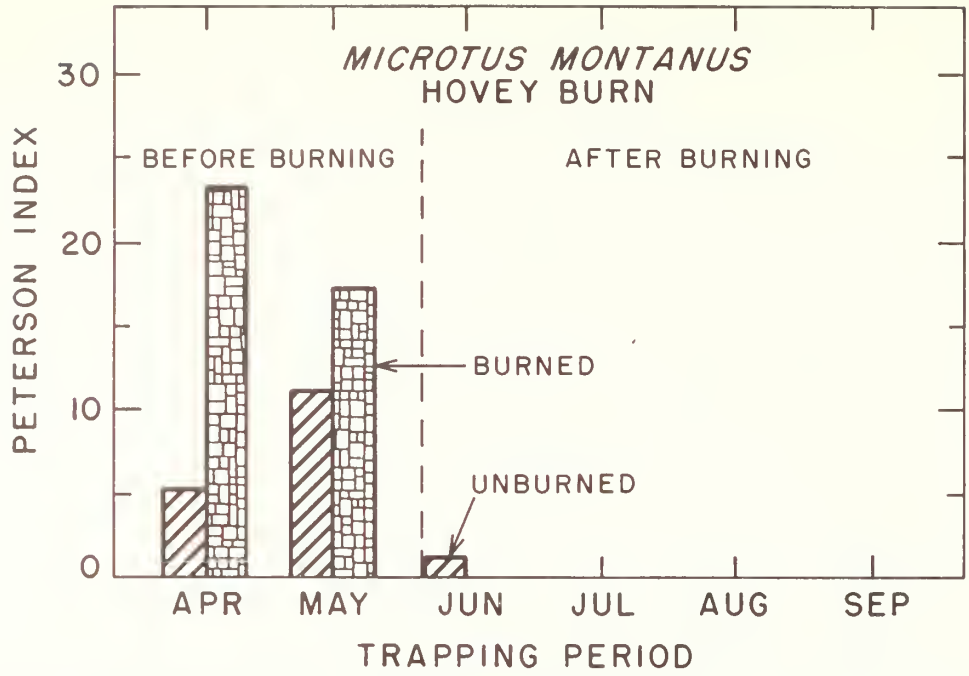



FIGURE 5. Total different *Microtus montanus* captured during each period at Hovey burn and its control.

levels during the last three trapping periods. Comparison of the curves of the population estimates following the burn does not reveal a significant difference at the .05% level ($F = 5.44$, $F_{.95}(2,4) = 6.94$), despite the marked differences in their population estimates for June.

Hovey burn percent recovery of tagged *P. maniculatus* between the two dates before burning and the period after the burn compared with the control showed that recovery of *P. maniculatus* was independent of burning ($x^2 = .058$, $x^2_{.95}(1) = 3.84$). This indicates that few deer mice were lost on the area due to the immediate effects of the fire.

An individual bushytailed wood rat (*Neotoma cinerea*) was trapped on the Fleener burn following the fire. No others were captured on the other areas.

*Microtus montanus* were trapped only on the Hovey sites (Figure 5). *Microtus* were trapped regularly on the two sites in April and May. In June no *Microtus* was caught on the burned site and only one individual was trapped on the control. No *Microtus* was trapped or observed through the summer. Judging from the extensive tunnels and pathways in the cheatgrass the *Microtus* populations in the area had been quite high. Either the *Microtus* crashed, emigrated to other areas or became untrappable by our method. No conclusions can be made regarding the effect of the burn on this species.

In general, it appears that the burns have had no immediate effect on the major small mammal species. The possible exception would be *Dipodomys*. Our data indicate that *Dipodomys* may move into burned areas; however, we do not have a proper control to support this.

LITERATURE CITED

BEATLY, JANICE C. 1976. Environments of kangaroo rats (*Dipodomys*) and effects of environmental change on populations in southern Nevada. J. of Mammology 57(1):67-93.

DRAPER, N. R. and H. SMITH. 1966. Applied Regression analysis. John Wiley and Sons, Inc. New York.

MARTIN, R. E. and A. F. JOHNSON. 1976. Fire ecology and management of Lava Beds National Monument. Proceedings of the First Conference on Scientific Research in the National Parks. Nov. 9-12, 1976. New Orleans (in press).

NELSON, B. C. and C. R. SMITH. 1976. Ecological effects of a plague epizootic on the activities of rodents inhabiting caves at Lava Beds National Monument, California. J. Med. Ent. 13(1):51-61.

SEBER, G. A. F. 1973. The Estimation of Animal Abundance and Related Parameters. Hafner Press, New York.

# POPULATION ORGANIZATION AND REGULATORY MECHANISMS OF PINE MARTENS IN GRAND TETON NATIONAL PARK, WYOMING

Tim W. Clark[1] and Tom M. Campbell[2]

Pine martens (*Martes americana*) range from 1-3 pounds, are weasel-like and inhabit northern coniferous forests. Historic overexploitation as a fur resource eliminated or reduced their populations and ranges and their present status is largely unknown. Many basic questions concerning population organizational systems and regulatory mechanisms characterizing unexploited martens remain unanswered. Grand Teton National Park (GTNP) offered an area protected for over twenty-five years and abundant martens. In addition it can serve as a "control" for other areas. *Progress* based on the first fourteen months of a long-term field study aimed at determining the role which animal behavior and environmental factors play in regulating marten populations and social organization will be given here.

## GTNP STUDY (CONTROL AREA)

The GTNP study area (7000 feet) is located in the southern part of the Park on a large bench at the foot of the Tetons. It is 2.5 miles X 1.5 miles (3.75 sq. mi.). The area was burned in 1879 and today the forest is a relatively equal mixture of lodgepole pine, subalpine fir and Engleman spruce.

In addition, a second ecologically similar study area on nearby Teton National Forest (TNF) was studied in the summers and falls of 1975 and 1976. This area was partially logged (400 ac. out of 1600 ac.) in five selective cuts and one clear cut. Pine marten population behavior and ecology were contrasted between this experimentally altered area and the GTNP control site.

Population structure and dynamics are being determined by live trapping (totaling nearly 3000 trap-days). To date, twenty martens, eleven residents (present for at least ninety days), three temporary residents (present seven to ninety days), and six transients (present less than seven days) have been marked. All were adults and showed a sex ratio of 1 M : 1.3 F. Two resident females showed evidence of producing a litter.

Nine specific hypotheses have been formulated on marten organizational systems and regulating mechanisms and are being tested. Circumstances preclude even a brief glance at all nine here. But several will be mentioned with data testing each. These nine hypotheses range from ecological (e.g., food densities) to behavioral (e.g., territorial behavior) factors.

First, the relationship of marten densities and distributions is being investigated in relation to rodent prey densities. Prey densities and distributions were sampled with a large live trap grid and a series of lines. Tentative conclusions indicate that certainly food is not limiting in the summer. The eight feet of snow cover on the study area has thwarted efforts to monitor winter rodent densities. However, it may be that limited access routes to get at the rodents, below the deep snow cover, are more restrictive on marten winter densities than the actual density of rodents.

Second, any prey selectivity by martens is being checked by analyzing scats collected throughout the year. Contents of scats will be compared with feeding trials and with relative densities of the prey rodents from the live trapping studies. Shrews, red-backed voles, red squirrels, deer mice, grouse, and chipmunks have been identified so far. Data analysis is incomplete at this time and quantitative conclusions will be forth coming.

Thirdly, a differential marten use of the more complex structure of the vegetation or heterogenous areas (e.g., ecotones) vs. the simpler, more homogenous areas (e.g., monospecies stands of lodgepole pine) was tested. By comparing marten capture rates in these two types of areas based on 930 trap-days over eight months it showed that martens did not, to a significant degree, utilize the more structurally complex areas of the study area. No comparative prey densities are available for the two areas.

Fourthly, working on the assumption that food might be limiting in winter we snow tracked martens to see how often and the ecological setting in which prey were captured. Fourteen such sites were found over twenty days of tracking in February and March. One site was on the surface where a ruffled grouse was taken. The other thirteen were in association with large ($\bar{x}$ dbh = 15") dead, fallen trees protruding up out of the snow. Martens would follow these trees down below the snow's surface to extensive galleries formed by snow covered vegetation and fallen trees near ground level. These downed "entry" trees seem critical to marten survival in the winter by providing access to the rodent prey active under the snow.

Additionally, space use by males and females was investigated from the trapping data. Only the 1975 (Apr., May, July, Aug.) data are given here. Home range sizes for males (N=2) average 600 acres, over twice as large as females (N=3) ($\bar{x}$ = 223ac). There were marked trends of exclusive use of specific areas by individual males when capture sites were plotted on a map. This suggests that males tend to be territorial with each other. Females greatly overlapped areas occupied by other females. This suggests a spatial tolerance among females. Also males and females tend to overlap each other, again suggesting tolerance.

Lastly, population increases and decreases were determined from capture data. Thirteen new marten appeared in the study area, eight males and

[1]Department of Biology, Idaho State University, Pocatello 83209.

[2]Box 2705 Jackson, Wyoming 83001.

five females. Six of the eight (75%) new males showed up from August to November (Fall) and three of the five (60%) new females appeared during this period. Eleven animals disappeared from the study area, five males and six females. Three of the five males (60%) disappeared in the same four months of Fall as did two of the six females (33%). During the summer (June and July) of both 1975 and 1976 no new marten was captured and no residents disappeared -- this is the only time of the year when the population was stable. This coincides with parturition and early growth and development of young. Overall, the marten population was clearly fluid with animals coming and going throughout most of the year. However, from this information, our other data (in preparation) and the literature, a tentative model of marten population organization in relation to some ecological correlates can be constructed. By examining the adaptive significance of these systems in relation to situations in which martens evolved and in light of existing evolutionary theory, we may gain insight into the evolution.

The verbal model follows. Marten populations seem to be organized around adult male territories in the summer and less rigidly defended territories or home ranges in the winter. The male summer territory is of a "classic" type. Ecologically, adult males can afford the cost to hold areas when available prey biomass is greatest -- early spring to mid-fall. This is the period when young are born, grow, and mature, and when breeding and dispersal occur. This territory is maintained against all other adult males. By tolerating adult females and young (especially their own), adult males maximize the possibilities for reproductive encounters each year and provide an area of reduced competitive pressure for the growth and development of their offspring. It may be that territories are rigidly maintained up to the early part of the breeding period, ensuring that most females will be successfully impregnated early in the season by males controlling territories in which the females live. As territorial boundaries begin to disintegrate, males move into other areas and into contact with other females. At this time, increasing aggression causes dispersal of young and spacing of the population in a situation optimally favorable to successful overwintering. Territorial collapse occurs when the prey biomass drops sharply and the cost to rigidly defend a large area is too great.

The entire system briefly outlined above may be "food sensitive" with different organizational systems occurring at different parts of the annual cycle in response to the levels of available resources. The predictions of this model are being tested in the nine hypotheses mentioned above. With quantified long-term population dynamics investigations and later with the aid of predator-prey models and bioenergetics studies, we hope to understand the way martens are organized in space and time.

## TNF STUDY (EXPERIMENTAL AREA)

The Grand Teton National Park marten study has added value aside from the basic ecological and behavioral information being gleened from it. The Park data are serving as a control for a comparable study area on Teton National Forest (TNF). The Teton National Forest site, about fifteen miles away, is being experimentally altered by logging operations.

The experimental study area located in Teton National Forest is 1600 acres, of this one-quarter was recently harvested in the form of one clearcut and five selective cuts. The clearcut eliminated 100 percent of the trees within the twenty-four acre block while the selective cuts removed approximately sixty percent of all trees in the remaining 376 acres of timber harvest.

Methods similar to those used in the Grand Teton National Park control study area to determine marten population organization were employed in the experimental forest study area. Comparative information on study areas, efforts, population dynamics and structure are given in Table 1. Seventeen martens were captured and of these, 9 were residents, one was a temporary resident, five were transients and two were young of the year. The sex ratio was 1.4 M : 1 F. Two resident females showed evidence of producing a litter.

Of the 1987 trap-days recorded, 1416 were from control lines with a capture rate of 6.7 martens per 100 trap-days while 571 trap-days recorded in harvest blocks following timber harvest produced only one capture for a capture rate of 0.2 martens per 100 trap-days. This would indicate that martens did not utilize harvest blocks, at least within one year after harvest.

Monthly capture rates on marten control lines during the two summers of trapping varied from 5.9 to 7.1 captures per 100 trap-days. These capture rates coincide with those of the Grand Teton National Park control study area and indicate that the marten population in the experimental study area was also stable during the months of June and July. The two transients and the two young of the year were all captured between August and October which also follows the patterns of marten movements found in the Grand Teton National Park control study area during the same time.

As shown in Table 1, capture rates in undisturbed areas differ significantly ($x^2=6.1$, ldf; d=0.2) from those in disturbed (harvested) areas. This indicates that martens are not utilizing logged blocks within one year after harvest. Capture rates also differ between the control study area (GTNP) and the experimental site (TNF). Mean capture rates on the GTNP site were high because of repeated captures of two individual martens (i.e., 37 for one, 67 for the other). It was not uncommon to capture these two trap-prone martens 7 to 9 days of each 10 day trapping session. No martens on the TNF study showed this trap response.

By continuous monitoring of the rodent prey base of martens, it was determined that the small mammals were affected by timber harvest in at least three ways. First, rodent captures increased significantly, immediately following harvest operations while species composition remained unchanged. We conclude that this was due to the disturbance factor involved with skidding the cut timber, creating a lack of food for the rodents and, in turn, increasing their susceptibility to capture. Secondly, the clear cut resulted in the change of rodent species composition over the next several months from large numbers of red-backed voles before harvest to that of predominantly white-footed deer mice six months after harvest. This was due to the opening up of the forest canopy, thusly changing the site from a mesic to a more xeric situation. Thirdly, species composition in the selective cuts remained essentially the same but there did occur a small but significant decline in species densities resulting from destruction of habitat.

TABLE 1. Comparison of marten population structure and dynamics between Grand Teton National Park (GTNP and control area) and Teton National Forest (TNF) (experimental area).

| Parameters | GTNP Site (Control) | TNF Site (experimental) | |
|---|---|---|---|
| Study area size (acres | 2440 ac | 1600 ac | |
| Trapping Period | Aug. '75 - Aug. '76 | Sept.- Oct. 1975, June-Sept. 1976 | |
| | | Undisturbed | Disturbed |
| Trapping Effort (trap-days) | 3224 | 1416 | 571 |
| Total Captures | 291 | 95 | 1 |
| $\bar{x}$ No. Captures/martens | 13.2 | 5.8 | 0 |
| Captures/100 TD | 9.0 | 6.7 | 0.2 |
| Population Structure | | | |
| Total martens | 22 | 17 | |
| Males | 12 | 10 | |
| Females | 10 | 7 | |
| Ratio | 1.2 M : 1 F | 1.4 M : 1 F | |
| Resident (♂, ♀) | 11 (8, 3) | 9 (6, 3) | |
| Temporary Resident ( " ) | 3 (0, 3) | 1 (1, 0) | |
| Transient ( " ) | 6 (3, 3) | 5 (4, 1) | |
| Young ( " ) | 1 (1, 0) | 2 (0, 2) | |
| Home Range Size | | | |
| ♂ | 600 ac | 600 ac | |
| ♀ | 223 ac | 200 ac | |

Spatial distribution and space use of martens were also investigated in the experimental study area. Results derived from trap data show that home range sizes for both males and females are comparable to those found in the control study area, averaging 600 acres for males (N=3) and 200 acres for females (N=1). Males showed territorial use of specific areas, but were tolerant of overlapping females' range.

Because of timber harvests, home range shifts may have occurred. Harvest blocks were found to occur in, or on the boundaries of, the defined home ranges of three males and three females. Approximately twenty percent of one males' home range was affected by two harvest blocks and another had eight percent affected by one harvest block. These two male home ranges border each other east and west and if any resulting range shift occurred, it did so in a north or south direction and was therefore undetected as it was off the study area. No change in trap utilization or home range boundaries was observed as a result of the logging operations. Because female home ranges are so small and traps were placed so far apart, no conclusions can be formed concerning female home range shifts. But if females are tolerant of other females and tolerated by males as the data indicates, range shifts caused by timber harvest may be insignificant.

Radio telemetry equipment was used in the experimental study area to gain insight on daily activity periods, refining home range descriptions more accurately and also establishing ecological characteristics of marten resting sites. From 330 hourly observations we found that martens were most active during the evening and night and tended to rest from late morning to late afternoon. Few movements were recorded during adverse weather conditions (e.g., rain and snow). Martens tend to select large, dead, rotten Engelmann spruce and subalpine fir trees (dbh 14-24 inches) most frequently for resting sites but also used dwarf-mistletoe bundles in subalpine fir trees and slash/piles caused by timber harvest for resting.

In conclusion the Grand Teton National Park marten study site offers an undisturbed situation where marten behavioral ecology could be studied. Also such an area served as a control for a nearby experimental area in Teton National Forest where logging operations altered marten habitat.

# MAMMALS OF GUADALUPE MOUNTAINS NATIONAL PARK[1]

John E. Cornely, Hugh H. Genoways and Robert J. Baker[2]

Guadalupe Mountains National Park is a relatively new national park authorized by an act of Congress on 15 October 1966 and established on 30 September 1972. The park includes 76,468.6 areas of Culberson and Hudspeth Counties of Trans-Pecos Texas. The Guadalupe Mountains form a rugged V-shaped range extending from Southeastern New Mexico south into Texas and abruptly terminating in the spectacular cliff faces of 8,078 foot El Capitan. North of El Capitan several peaks rise over 8,000 feet including Guadalupe Peak (8,751 ft.), the highest point in Texas. A major geological feature of the park is the uplifted Capitan reef of Permian age. This 4,000 foot section of marine limestones is the world's largest known fossil reef (Mathews, 1973).

This paper is based upon a more extensive report to be published in a book, "Biological Investigations in the Guadalupe Mountains National Park" currently in press (Genoways, *et al*, 1977). Anyone interested in additional information concerning mammals or other aspects of the flora and fauna in the Guadalupe Mountains is referred to that work.

Vernon Bailey of the U.S. Biological Survey conducted the first mammal survey of the Guadalupe Mountains in August 1901 (Bailey, 1905). He reported 17 species of mammals inhabiting the Guadalupe Mountains and listed two species of possible occurrence. In 1938, 1939, and 1940, William B. Davis conducted field work in the Guadalupe Mountains and reported the presence of 35 species of mammals (Davis, 1940; Davis and Robertson, 1944). La Val (1973) studied the distribution and ecology of 13 species of bats in McKittrick Canyon in 1968 and 1970.

This paper is based on our field work from late May, 1973 through August, 1975. The objectives of our study were to survey the mammals occurring in Guadalupe Mountains National Park and to correlate their distributions with major plant associations. Such an inventory is preliminary to the development of any sound management program.

Zoogeographically, the Guadalupe Mountains are an island inhabited by animals of Rocky Mountain affinities surrounded by Chihuahuan desert. Elevations within the park range from 3,650 feet to 8,751 feet. The lower elevations are characterized by floral and faunal elements of the Chihuahuan desert. The higher elevations contain montane elements. The complex interactions of many factors including the wide variation of elevations, a variety of soil types, and the rugged dissected topography of the mountains, have resulted in a unique and diverse community of plants and animals. The mammals of Guadalupe Mountains National Park are a unique mixture of desert, grassland, riparian woodland, montane, and widespread species.

## DISCUSSION

During historical times, 65 species of mammals have occurred in the area now occupied by Guadalupe Mountains National Park. Included are 13 species of bats, three leporids, 29 rodents, 14 carnivores, and six artiodactyls. Another nine species possibly occur or have occurred in the park.

### *Extirpated Species*

Nine of the 65 species known from the park have been extirpated from the area. Most, if not all, of these species have disappeared as the direct or indirect result of human activity.

*Cynomys ludovicianus*.--In 1901, prairie dogs were abundant in Dog Canyon, which derived its name from the numerous colonies in the area (Bailey, 1905). Davis (1940) reported scattered colonies along the eastern edge of the mountains. Presently, there are no prairie dogs within the park, although a few colonies persist on private land to the east. Prairie dogs were removed by poisoning because they were believed to compete with livestock for food.

*Perognathus hispidus paradoxus*.--One specimen of this grassland species was obtained in 1901 by Vernon Bailey (Bailey, 1905). The hispid pocket mouse has been eliminated from the area apparently by alteration of grassland habitat by overgrazing or environmental changes or both.

*Canis lupus monstrabilis*.--The gray wolf was removed from the park area by predator control activities. One specimen was preserved from the Guadalupe Mountains (Bailey, 1905). According to Bailey, the gray wolf was a troublesome killer of livestock in the area.

*Ursus arctos*.--The grizzly bear has been removed from much of its former geographic range. This species probably occurred in the Guadalupe Mountains at one time, but was eliminated by a

[1]We most gratefully acknowledge the field assistance of Dallas E. Wilhelm and Margaret A. O'Connell. Without their assistance, this project would not have been completed. James W. Cottrell and Peter V. August also assisted in field work. David K. Northington and Tony L. Burgess helped with vegetation descriptions. Our work in the park was greatly facilitated by the following park personnel: Donald A. Dayton; John Chapman; Gary M. Ahlstrand; Philip Van Cleave; and Roger Reisch. We acknowledge the Department of Biological Sciences and The Museum of Texas Tech University for supporting most of the laboratory phases of this study. Field portions of this work were supported by a contract with the National Park Service (CX 7000 4 0145), administered by Mr. Roland H. Wauer, Chief Scientist, Southwest Region, NPS. We would like to thank Dr. David J. Schmidly, Texas Cooperative Wildlife Collection, Texas A&M University, and Dr. Don E. Wilson, National Bird and Mammal Laboratory, National Museum of Natural History, for allowing us to examine specimens in their care.

[2]The Museum and Department of Biological Sciences, Texas Tech University, Lubbock.

combination of habitat alterations and predator control.

*Cervus elaphus merriami*.--Merriam's elk once inhabited the Guadalupe Mountains, but is now extinct (Murie, 1951). The primary factor driving this species to extinction was probably hunting pressure, however, increasing aridity of the region and competition with livestock may have contributed to their demise. The Merriam's elk was probably gone from the Guadalupe Mountains prior to 1900 and was extinct by 1906 (Curry-Lindahl, 1972).

*Odocoileus virginianus texanus*.--White-tailed deer were never abundant in the park area and have not been reported in the area for many years. This species was probably removed by hunting.

*Antilocapra americana americana*.--Although pronghorn were probably never abundant in the park area, Bailey (1905) reported seeing them along edges of the Guadalupe Mountains. They were apparently eliminated by habitat alteration and hunting.

*Bison bison bison*.--The bison which once grazed around the periphery of the Guadalupe Mountains were removed by hunting and habitat alteration by the middle of the nineteenth century.

*Ovis canadensis mexicana*.--In 1901, mountain sheep were relatively common in the Guadalupe Mountains (Bailey, 1905). In 1940, Davis estimated that no more than 25 bighorns remained. Sporadic reports of bighorn sitings in the Guadalupe Mountains were received until 1959 (Gross, 1960). Mountain sheep no longer occur in the Guadalupe Mountains. A combination of hunting, disease introduced by domestic sheep, and competition with domestic livestock resulted in their extirpation from the park.

### *Species Rare in the Park*

Five species are rare in their distribution in Guadalupe Mountains National Park. Four of these species are confined to the montane regions of the park. The montane areas consist of relict coniferous forest, including some deciduous elements, and grassy meadows. Due to protection from fire, much of the forested area is dense and contains a large amount of dead fall timber. Encroachment of the montane habitat by desert species of plants and animals could ensue with a continued trend toward aridity. If such conditions ever occur, the montane element of the mammalian fauna will undoubtedly be eliminated.

*Sylvilagus floridanus robustus*.--This large subspecies of cottontail is confined to dense coniferous forest stands in The Bowl and is the rarest mammal in the park. The taxon is confined to the Chisos, Chinati, Davis, and Guadalupe Mountains of Texas. These populations are evidently completely isolated; therefore, if the population in the Guadalupe Mountains is lost, no natural repopulation would be expected.

*Eutamias canipes canipes*.--Gray-footed chipmunks are found in wooded areas at intermediate to higher elevations in the park. This subspecies is known only from the Guadalupe Mountains; therefore, its existence must be protected. Chipmunks are relatively common in the park at the present time, but their populations should be periodically monitored.

*Ammospermophilus intepres*.--The Texas antelope ground squirrel occurs in the park at intermediate elevations in grassland and desert areas. This species has a relatively restricted geographic range in northern Mexico, Texas, and New Mexico. These squirrels are not common in the park.

*Thomomys bottae guadalupensis*.--The Guadalupe Mountains pocket gopher is endemic to the Guadalupe Mountains. It is primarily distributed in montane meadows and slopes. Although these pocket gophers are not common, we believe that they are in no present danger in the park.

*Microtus mexicanus guadalupensis*.--The Guadalupe Mountains vole is found in isolated pockets of montane meadow in the park. This subspecies is restricted to the Guadalupe Mountains of Texas and the Manzano, Capitan, and Sacramento Mountains in New Mexico. Because the vole habitat is limited in the park and is very attractive to park visitors, the status of this mammal and its habitat will need periodic monitoring.

### *Mammalian Faunal Relationships Within the Park*

Within the park, we recognize four mammalian distributional zones based upon major vegetation types (Gehlback, 1967, undated; Warnock, undated) and the distribution of some indicator species of mammals. For a species to be a good indicator, it should be relatively abundant and its distribution should be restricted, or nearly so, to the zone for which it is an indicator. The four zones and their indicator species of mammals are: desert--*Dipodomys merriami, D. spectabilis, Spermophilus spilosoma, Onychomys torridus*, and *Neotoma micropus*; grassland--*Sigmodon hispidus*, and *Reithrodontomys megalotis*; riparian woodlands--*Procyon lotor*; montane--*Sylvilagus floridanus, Peromyscus boylii, Neotoma mexicana*, and *Microtus mexicanus*.

The grassland habitat was found to contain the most mammalian species (41) and the montane the least (27). The desert habitat and the riparian woodland habitat each contained 31 species. The mammalian fauna of Guadalupe Mountains National Park is predominantly Southwestern in affinities with Chihuahuan Desert forms being the chief component.

The elimination of nine species of mammals from the park area in historic times and the presence of five additional species relatively rare in the park emphasize the need for sound resource management decisions in Guadalupe Mountains National Park. This survey must be considered a starting point not an end in itself. With this in mind, we have submitted the following recommendations to the National Park Service for future research and development in the park.

1. An inventory of the larger mammals in the park should be undertaken. A project is currently in progress to gather information on the resident elk herd, but similar work is needed on mule deer, bear, coyote, bobcat, mountain lion, and fox. These mammals play important roles in the ecosystem and it is imperative that more information be gathered about them.

2. A program of periodic censusing of mammals should be established to identify population trends. During these censuses, special efforts must be made to monitor the status of the species that are rare in the park. Careful monitoring of these mammals may prevent their loss from the park.

3. The following areas are considered to be

the most biologically significant from the standpoint of mammals in the park and as such should be protected: Upper Dog Canyon; The Bowl; Nipple Hill area; Lewis Well area; McKittrick Canyon; and every spring and waterhole in the park.

4. A special effort should be made to determine if the following mammals occur within the park boundaries: *Notiosorex crawfordi; Myotis evotis; Euderma maculatum; Lasiurus borealis; Spermophilus mexicanus; Tamiasciurus hudsonicus; Onychomys leucogaster; Vulpes macrotis;* and *Dicotyles tajacu.*

5. High priority should be given to repairing or rebuilding the boundary fences on the south and west sides of the park. During our survey, a large number of cattle have been observed within the park boundaries and the number seems to have increased from 1973 to 1975. This area of the park recovers very slowly from grazing even in total absence of livestock; therefore, it is imperative that the fences be repaired and the cattle removed.

6. Most of the species rare in Guadalupe Mountains National Park probably occur in Carlsbad Caverns National Park as well. We strongly recommend that a mammal survey be conducted in Carlsbad Caverns National Park. A management program consistent in both parks could then be developed, increasing the chances of preserving rare species.

CHECKLIST OF RECENT MAMMALS OF GUADULUPE MOUNTAINS NATIONAL PARK

| Species | Status | Habitat |
|---|---|---|
| *Myotis velifer* | common | widespread |
| *M. thysanodes* | " | " |
| *M. volans* | uncommon | montane |
| *M. californicus* | common | " |
| *M. leibii* | " | widespread |
| *Lasionycteris noctivagans* | uncommon | montane |
| *Pipistrellus hesperus* | common | widespread |
| *Eptesicus fuscus* | " | " |
| *Lasiurus cinereus* | " | montane |
| *Plecotus townsendii* | " | " |
| *Antrozous pallidus* | " | widespread |
| *Tadarida brasiliensis* | " | " |
| *T. macrotis* | uncommon | riparian woodland |
| *Sylvilgus floridanus* | rare | montane |
| *S. audubonii* | common | desert |
| *Lepus californicus* | " | " |
| *Eutamias canipes* | " | montane |
| *Ammospermophilus interpres* | uncommon | desert |
| *Spermophilus spilosoma* | " | " |
| *S. variegatus* | common | riparian woodland |
| *Cynomys ludovicianus* | extirpated | grassland |
| *Thomomys bottae* | uncommon | montane |
| *Pappogeomys castanops* | " | desert |
| *Perognathus flavus* | " | " |
| *Perognathus hispidus* | expirpated | grassland |
| *P. penicillatus* | common | desert |
| *P. intermedius* | uncommon | " |
| *Dipodomys ordii* | " | " |
| *D. spectabilis* | " | " |
| *D. merriami* | common | " |
| *Reithrodontomys megalotis* | " | grassland |
| *Peromyscus eremicus* | uncommon | desert |
| *P. maniculatus* | common | widespread |
| *P. leucopus* | uncommon | desert |
| *P. boylii* | common | montane |
| *P. pectoralis* | uncommon | grassland |
| *P. truei* | " | montane |
| *P. difficilis* | " | " |
| *Onychomys torridus* | common | desert |
| *Sigmodon hispidus* | " | grassland |
| *Neotoma micropus* | " | desert |
| *N. albigula* | " | widespread |
| *N. mexicana* | " | montane |
| *Microtus mexicanus* | uncommon | " |
| *Erthizon dorsatum* | common | widespread |
| *Canis latrans* | " | " |
| *C. lupus* | extirpated | " |

| Species | Status | Habitat |
|---|---|---|
| *Urocyon* | common | widespread |
| *Ursus americanus* | uncommon | montane |
| *U. arctos* | extirpated | " |
| *Bassariscus astutus* | uncommon | widespread |
| *Procyon lotor* | common | riparian woodland |
| *Mustela frenata* | uncommon | widespread |
| *Taxidea taxus* | " | desert |
| *Spilogale gracilis* | " | " |
| *Mephitus methitus* | common | widespread |
| *Conepatus mesoleucus* | " | " |
| *Felis concolor* | uncommon | " |
| *F. rufus* | " | " |
| *Cervus elaphus merriami* | extinct | " |
| *C. e. nelsoni* | common | " |
| *Odocoileus hemionus* | " | " |
| *O. virginianus* | extirpated | " |
| *Antilocapra americana* | " | grassland |
| *Bison bison* | " | " |
| *Ovis canadensis* | " | montane |

LITERATURE CITED


BAILEY, V. 1905. Biological survey of Texas. N. Amer. Fauna, 25:1-222.

CURRY-LINDAHL, K. 1972. Let them live. William Morrow and Co., New York, xix+394 pp.

DAVIS, W. B. 1940. Mammals of the Guadalupe Mountains of western Texas. Occas. Paps. Mus. Zool., Louisiana St. Univ., 7:69-84.

DAVIS, W. B., and J. L. ROBERTSON, JR. 1944. The mammals of culberson County, Texas. J. Mamm., 25:254-273.

GEHLBACH, F. R. 1967. Vegetation of the Gaudalupe escarpment, New Mexico-Texas. Ecology, 48:404-419.

_____. Undated. Description and development of the living landscape of Guadalupe Mountains National Park, Texas. Rept. National Park Service, U.S. Dept. Interior, Santa Fe, New Mexico.

GENOWAYS, H. H., R. J. BAKER, and J. E. CORNELY. 1977. Mammals of the Guadalupe Mountains National Park, Texas *In:* H. H. Genoways and R. J. Baker (eds.), Biological Investigations in Guadalupe Mountains National Park, Texas. National Park Service. In Press.

GROSS, J. E. 1960. History, present, and future status of the desert bighorn sheep (Ovis canadensis mexicana) in the Guadalupe Mountains of southeastern New Mexico and northwestern Texas. Trans. Desert Bighorn Council, 4:66-71.

LA VAL, R. K. 1973. Occurrence, ecological distribution, and relative abundance of bats in McKittrick Canyon, Culberson Co., Texas. Southwest. Nat., 17:357-364.

MATHEWS, W. H. 1973. A guide to the National Parks. Nat. History Press, Garden City, N.Y., xx+529 pp.

MURIE, O. J. 1951. The elk of North America. Stackpole Co., Harrisburg, pa., 376 pp.

WARNOCK, B. H. Undated. Plant communities of the Guadalupe Mountains in Texas and nearby carlsbad Caverns National Park, Carlsbad, New Mexico.

# RHYOLITE RADIONUCLIDE UPTAKE BY SELECTED PLANT SPECIES AND POCKET GOPHERS IN YELLOWSTONE NATIONAL PARK[1]

Kenneth L. Diem and Garth S. Kennington[2]

The unique geologic character of Yellowstone National Park has shaped and influenced the biota of that area in ways that are all too often little appreciated and more frequently poorly understood. From 1961 through 1965, we undertook a comparative study of the influence of five different rock substrates on the physioecology of the northern pocket gopher *Thomomys talpoides* (Diem and Kennington 1963). Beginning in 1963, we monitored bony animal tissues for the presence of radionuclides. This report summarizes those radionuclide findings and their relation to current analyses of ground water from comparable rock substrates.

With the exception of the Moran area, the study areas for this investigation are located in the south portion of Yellowstone National Park and the north portion of the Teton Wilderness at elevations between 2,438-3,048 m. The Huckleberry Ridge area lies east and south of the South Entrance to Yellowstone Park at an elevation of 2,804 m. It is adjacent to the Teton Forest Huckleberry Ridge Game Exclosure on a bearing 81° west of south, 76 mm from the fiducial center of aerial photograph DZT 6 - 65. The soils of this area are derived from Early Cretaceous freshwater sediments of the Cloverly and Morrison undivided formations. The parent rock material consists of massive sparkly sandstone and olive-green, gray and buff thin bedded sandstone.

The Big Game Ridge area is due east of Huckleberry Ridge at an elevation of 2,926 m. It is adjacent to the west side of the Teton Forest Big Game Ridge Game Exclosure on a bearing of 62° east of north, 55 mm from the fiducial center of the aerial photograph EHJ - 1AA - 20. Soils of this area are derived from the Late Cretaceous freshwater sediments of the Harebell formation. The parent rock strata consist of very thick sandstones, conglomerates, claystones and shales.

The Two Ocean Plateau area lies within Yellowstone National Park, 2.4 km north of Mariposa Lake at an elevation of 2,804 m. It can be located on a bearing of 52° east of north, 44 mm from the fiducial center of aerial photograph EHJ - 1AA - 138. Soils of this area are derived from the Wiggins formation which is an early Oligocene pyroclastic composed of reddish-brown to gray andesitic conglomerate interbedded with white tuff and claystones (Love 1956).

The Pitchstone Plateau area lies within Yellowstone Park, north and west of the Park's South Entrance and 0.8 km south of Phantom Spring at an elevation of 2,621 m. It can be located on a bearing of 22° east of south, 50 mm from the fiducial center of aerial photograph VV AS M32 AMS 5565. The soils of this area are very immature, being derived from a Quaternary rhyolite thought to be only 70,000 years old. The parent rock formation consists mostly of rhyolitic glass or pitchstone having a dull resinous luster and contains 30-50% phenocrysts of quartz and sanidine (Christiansen and Blank 1972).

The Moran study area lies within Grand Teton National Park adjacent to the northeast corner of the University of Wyoming Research Station at an elevation of 2,073 m. It can be located on a bearing of 54° west of north, 46 mm from the fiducial center of aerial photograph 20 VV16PS-M: 189 - 311RW. The soils of this area have developed from alluvial and glacial material which extends to depths exceeding 61 m.

The three highest study areas are sub-alpine grassland-forb associations bounded by the fir-spruce-whitebark pine community. The Pitchstone area is a dry sub-alpine meadow surrounded by a lodgepole pine community. The Moran area is part of a big sagebrush-grassland community.

Except for the northern pocket gopher, small mammal populations on the study areas were very low. Elk use of the study areas on a relative basis, ranked from high to low utilization, was as follows: Big Game Ridge, Huckleberry Ridge, Two Ocean Plateau, Pitchstone Plateau and Moran. Deer were occasional grazers on all areas but their numbers were very low.

## METHODS AND PROCEDURES

Northern pocket gophers were trapped with 14 cm Macabee gopher burrow traps. Traps were checked hourly and captured specimens were immediately preserved in a dry ice freezing chest until placed in laboratory freezer facilities.

An index to pocket gopher densities was determined for each study area from soil mound counts made in late August and early September. The belt transect census procedure described by Howard (1961) was used. Census transects were located in all variations of the habitat immediately adjacent to and considered as representative of each study site. Lengths of the transects varied from 732 m - 2,743 m depending on variability of the habitat and pocket gopher densities.

Longitudinal sections of dissected incisors and femurs of the pocket gophers were cut for autoradiograph exposure. These bony tissues were exposed on 125 mm x 175 mm sheets of Kodak no screen X-ray film for a period of 6 weeks.

[1]We are particularly indebted to Dr. J. D. Love, U. S. Geological Survey, University of Wyoming, for his invaluable encouragement and geologic advice and assistance. Robert Casebeer, formerly with Teton National Forest and Robert Bendt, formerly with Grand Teton National Park provided valuable assistance with many field problems and logistics. For their technical assistance, we wish to express our appreciation to former University of Wyoming Professors Ronald Parker and Hudson Eldridge. Financial support for this study was received from the U.S. National Park Service, the New York Zoological Society, the Olympic Natural History Association, and the University of Wyoming through the Jackson Hole Biological Research Station and the Department of Zoology and Physiology.

[2]Department of Zoology and Physiology, University of Wyoming, Laramie.

Selected plants were collected and preserved as dried, pressed specimens. Some of these pressed specimens which were major food plants of the gophers were also placed on X-ray film for autoradiographic monitoring. They were exposed for a period of 8 months.

## RESULTS AND DISCUSSION

Figures 1 and 2 characterize the autoradiographs of the incisors and femurs of 152 pocket gophers living on five different rock substrates. Identical autoradiograph results were obtained when replicates of those incisors and femurs were exposed for a separate 6-week period. An important aspect common to Figures 1 and 2 is the relative degree of radioactivity in the bones of the immature Pitchstone specimens. Even more interesting is the degree of activity in the Pitchstone immature female in Figure 2, captured on August 27, 1962. This individual weighed 55% less than the average of 31 immature females collected. This weight suggests she was no more than 2 months old at the time of capture. The Pitchstone immature male in Figure 1 was average in weight, based on 22 immature specimens. Enlarged testes and embryos in adult specimens captured in early August provided evidence of prolonged breeding seasons.

A source of the concentrated radionuclides appears to be the food plants. Figures 3 and 4 characterize the degree of radioactivity concentration detected in autoradiographs of gopher food plants, i.e., *Lupinus, Erigeron, Achillea* and *Agoseris*. Note particularly the radionuclide concentrations in the root stock and flower heads.

The influence of these radionuclide concentrations, if any, on the pocket gopher population was not readily apparent. The sample sizes for variables of sex, age and area were too small to make any valid comparisons of differences of whole body weights or organ weights. Gross examinations of dissected animals revealed no anatomical abnormalities in the Pitchstone specimens.

Gopher population densities on the study areas in 1962, '63 and '65 are presented in Table 1. A clear relationship of population density to radionuclide influences is not as stark as the average of 49 gophers/ha on Pitchstone and 237/ha on the other four areas imply. The Pitchstone substrate environment is very undeveloped with a very thin impoverished soil which is very drought prone. Alone, these conditions could inhibit any forage production needed to support a population density such as occurred on the other four areas. Consequently, while the radionuclides may be suppressing the size of the pocket gopher population, other factors also could play an equal or greater role in limiting the gopher population size.

Efforts to identify the specific radionuclides with a variety of alpha and beta analysis techniques, i.e., low background beta counting systems, X-ray fluorescence, X-ray microprobes and neutron activation were unsuccessful. Several of the techniques did suggest that the radionuclides were decay products of uranium. At this point, it was decided to set our data aside with the hope that some future development would overcome this dilemma.

In May 1974, we learned of artesian wells with 1,894 l/min flows of 33 C water originating in or near rhyolite formations. These wells are northwest of Buhl, Idaho, on the south side of the Snake River in a rhyolite formation described by Young and Mitchell (1973) as a member of the Idaho Group volcanics of Pliocene and Pleistocene age. In view of the similarity between the Yellowstone and the Idaho rhyolite formations, we obtained a water sample for nuclide analysis. Results of the analysis conducted by the E.P.A. radiological laboratory in Las Vegas (Lammering, J.W., *pers. comm.*) are presented in Table 2. Patterson (1952) has stated that natural radioacitivity in continental rocks is normally expected to be due to uranium, thorium and their decay products. Consequently, the presence of Ra 226 in groudwater is not an unusual phenomenon. The 88 Ci/l radioactivity level for Ra 226 is high but is not the highest level recorded in groundwaters of the U.S.

What is most significant about the Idaho Group rhyolite water sample is the circumstantial identification of the nuclides associated with Pitchstone rhyolite formation. Uranium and thorium produce a number of radioactive decay products. The alpha, beta and gamma emitting nuclides, i.e., Uranium 238, Thorium 232, and Ra 226 are hazardous. While Uranium 238 is not taken up by plants, its decay products of Ra 226, Lead 210 and Plutonium 238 are. If the nuclides of Table 2 are present on the Pitchstone rhyolites, that would explain the marked concentration of radioactive material in the gopher food plants and the subsequent rapid uptake of those nuclides by the very immature individuals of the gopher population. The very nature of growth and development of the bony tissue in an immature gopher would naturally tend to concentrate those bone seeking radionuclides in their skeleton.

If the radionuclides of Table 2 are a common constituent of rhyolite lava flows, their distribution in the Northern Rocky Mountains could be extensive. Christiansen and Blank (1972) estimate that rhyolite flows ranging in age from 2 million years to 70,000 years cover 6500 $km^2$ in Yellowstone National Park and the surrounding states. These flows support human populations which are widely separated but frequently have rather dense concentrations of seasonal and residential segments.

## CONCLUSIONS

The variety of evidence of elevated levels of natural radioactivity associated with young rhyolite rocks indicates there is a need for intensive radiological studies and analyses of the rhyolite environments.

Most important for park management considerations are: (a) identification of specific radionuclides and determination of their radioactivity levels; and (b) determination of the distribution and concentration of those radionuclides within the physical and biological components of the ecosystems associated with rhyolite substrates. Special attention should be given to those public, domestic and recreational use waters which originate in or flow through rhyolite formations, particularly since the Environmental Protection Agency's Interim Primary Drinking Water Regulations limit combined Ra 228 levels to 5 pCi/l (U.S. Environmental Protection Agency 1975).

Also, the rhyolite flows provide the opportunity for important basic research investigations which will increase our understanding of the influences of strong alpha and beta emitter

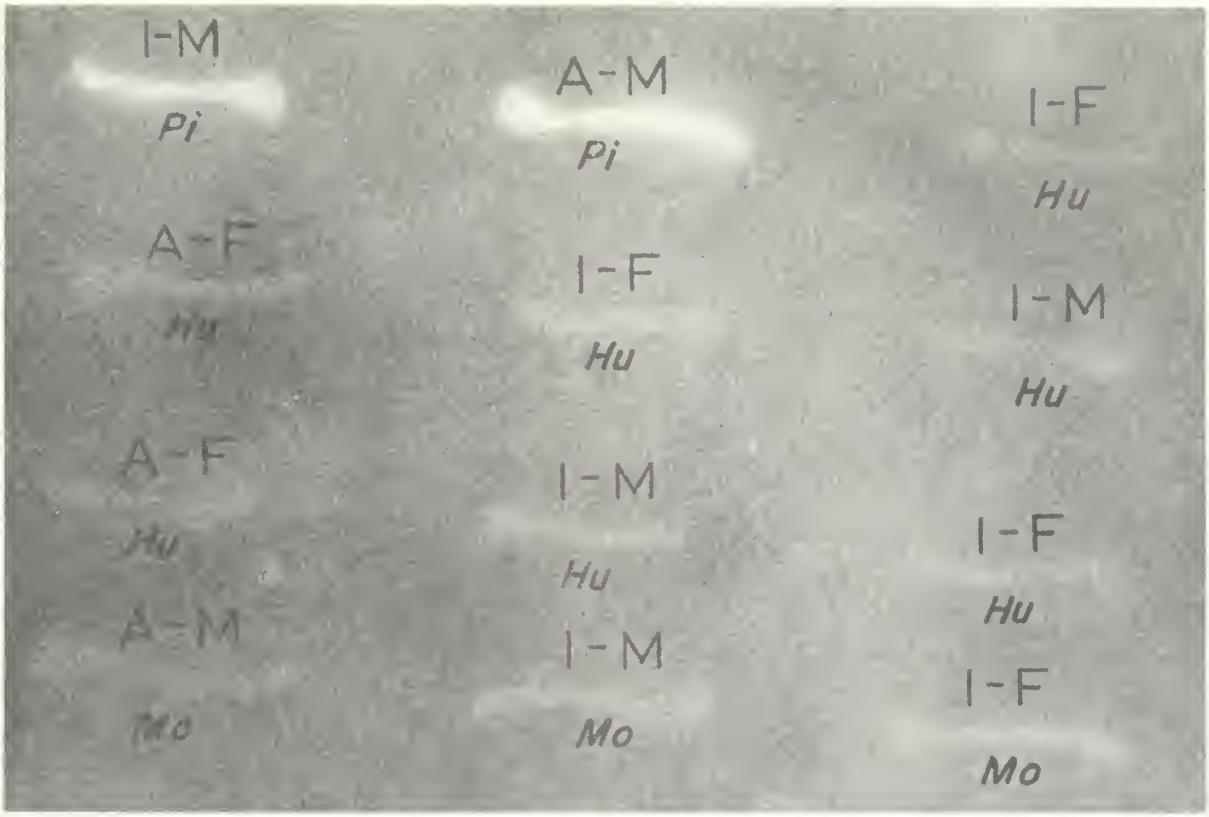



FIGURE 1. Autoradiograph of northern pocket gopher (*Thomomys talpoides*) femur--6 weeks exposure. Age and sex of individual are given above and the study site abbreviation is given below each femur.

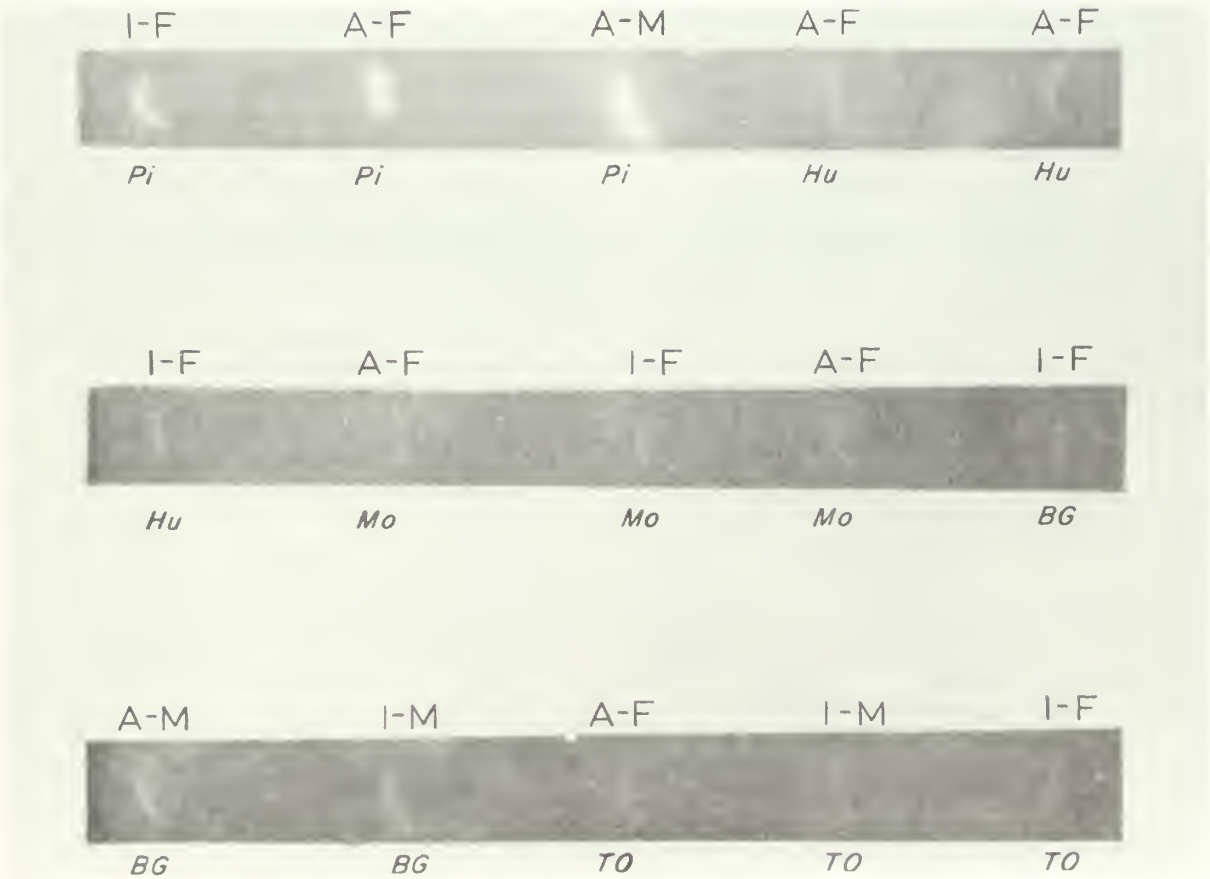



FIGURE 2. Autoradiograph of northern pocket gopher (*Thomomys talpoides*) incisors--6 weeks exposure. Age and sex of individual are given above and the study site abbreviation is given below each incisor.



FIGURE 3. Autoradiograph of mountain dandelion (*Agoseris glauca*) from Pitchstone Plateau--8 months exposure.



FIGURE 4. Autoradiograph of yarrow (*Achillea millefolium*) from Pitchstone Plateau--8 months exposure.

TABLE 1. North pocket gopher, *Thomoys talpoides*, population densities in soils of five geological locations, 1962-65.

| Area and (Formation) | Gophers per Hectare 1962 27 Aug.-2 Sept. | 1963 22 Aug.-30 Aug. | 1965 21 Aug.-27 Aug. |
|---|---|---|---|
| Huckleberry Ridge (Cloverly-Morrison) | 368 | 210 | 212 |
| Big Game Ridge (Harebell) | 252 | 250 | 227 |
| Two Ocean Plateau (Wiggins) | 257 | 237 | 74 |
| Pitchstone Plateau (Rhyolite) | 50 | 54 | 42 |
| Moran (Glacial-Alluvial) | 324 | 294 | --- |

TABLE 2. Natural activity levels of radionuclides contained in artesian well water associated with Idaho Group rhyolite substrate, Buhl, Idaho.

| Radionuclide | Activity Level |
|---|---|
| Radium - 226 | 88 pCi/l |
| Uranium - 234 | < 0.06 pCi/l |
| - 235 | < 0.03 pCi/l |
| - 238 | < 0.05 pCi/l |
| Thorium - 230 | < 0.02 pCi/l |
| - 232 | < 0.1 pCi/l |

radionuclides on living systems. Ideally, it would be desirable to use a predator of pocket gophers as a study species for concentration of the radionuclides. Unfortunately, predators of the pocket gopher are neither abundant enough to justify or make practical their collection and/or they are not confined in their seasonal movements solely to the rhyolite areas. Consequently, the pocket gopher remains as the best available species. Comparative histological studies of tissues from the respiratory tract, digestive tract, circulatory system and skeleton of gophers on rhyolite flows and adjacent non-volcanic substrates would be valuable to determine the absence or presence and nature of short term exposure somatic damage. Simultaneously, comparative genetic studies of chromosome numbers, configurations and the nature and degree of chromosomal structural aberrations should be conducted. The numerous pocket gopher generations produced under these radioactive conditions in the absence of many man caused environmental pollutants make their populations ideal for the foregoing studies.

Lastly, beyond the Park's boundaries, geothermal power developers may need to be concerned about natural radiation problems where thermal waters are closely associated with rhyolite substrates.

LITERATURE CITED

CHRISTIANSEN, R. L. and H. R. BLANK, JR. 1972. Volcanic stratigraphy of the Quaternary rhyolite plateau in Yellowstone National Park. U.S. Geo. Survey Prof. Paper 729 - b. 20 p.

DIEM, K. L. and G. S. KENNINGTON. 1972. Some aspects of substrate influence on the physioecology of dependent plant and animal populations. Mimeo. Completion Report to U. S. Natl. Park Ser. 32 p.

HOWARD, W. E. 1961. A pocket gopher population crash. J. Mamm. 24:258-260.

LOVE, J. D. 1956. Cretaceous and Tertiary stratigraphy of the Jackson Hole area, Northwestern Wyoming. Jackson Hole field conference guidebook. Wyo. Geol. Assoc., Casper.

PETTERSSON, H. 1952. Radium and the deep sea. Amer. Sc. 245-255.

YOUNG, H. W. and J. C. MITCHELL. 1973. Geothermal investigations in Idaho - Part I, geochemistry and geologic setting of selected thermal waters. Idaho Dept. of Water Admin., Boise. Water Info. Bull. No. 30.

U.S. ENVIRONMENTAL PROTECTION AGENCY. 1975. Interim primary drinking water regulations (40 CFR Part 141). Notice of proposed maximum contaminant levels for radioactivity. Federal Register, August 14.

# RABBITS AND OTHER MAMMALS OF SAN JUAN ISLAND NATIONAL HISTORICAL PARK

A. R. Weisbrod, W. F. Stevens, and G. E. Nordquist[1]

The presence of non-native animal species in national parks has long been of concern to the National Park Service, because such parks are to represent a "natural" situation found prior to the advent of European contact. Similarly, historical park areas are administered to present an accurate depiction of a significant historical period or event. Thus, the occurrence of the European rabbit, *Oryctolagus cuniculus*, in San Juan Island National Historical Park was cause for a study supported by the National Park Service to determine the feasibility of regulating or otherwise managing these exotic introduced beasts.

San Juan Island is the second largest island in the San Juan Archipelago which is located in northern Puget Sound, Washington, about 130 kilometers north of Seattle (Figure 1). The Archipelago consists of over 450 shoals, reefs, rocks, and islands of which 172 are named. Three islands, Orcas, San Juan, and Lopez account for over 80 percent of the total land area in the Archipelago. The islands form a structural arc across the northern end of the Puget Lowlands. They emerge from the sea as low lying northwest to southeast ridges connecting the Cascade Mountains to the east with the Vancouver Island Ridges to the west (Danner, 1957; McKee, 1972). These ridges in the Islands' "Turtleneck Ranges" include sedimentary and volcanic rock of paleozoic and mesozoic origins. Pre-Devonian crystalline rocks, sandstones, and shales from the lower Tertiary are also found in the group (Easterbrook, 1969).

The San Juans lay directly in the path of the great Pleistocene cordilleran glaciers that formed in the western British Columbia mountains and flowed south out of the Georgia Depression into the Puget Lowlands. At its greatest extent, about 15,000 BP, 1700-1800 meters of ice covered the islands. Most of the landscape was smoothed and shaped by this event. Consequently, much of the topographic character of the Island is a result of the recent glacial deposits (McKee, 1972). At no time since the Pleistocene glaciations have the islands been connected directly either to the mainland or Vancouver Island.

San Juan Island resides in the rain shadow of both the Olympic Peninsula and the Vancouver Island ridges. It contains some of the driest locations in western Washington (two year mean of 482 mm at American Camp Unit) with a range of 482 mm at the American Camp Unit to 737 mm at the northern end of the Island. Mean winter temperature is 5°C and mean summer temperature is 14°C. Snow is rare and usually melts within a day. Winds are frequent, often gusting to 40 kilometers/hour; occasional storms will blow a steady 130-150 kilometers per hour.

The Island vegetation is typical of the other islands in the Archipelago. The Island is roughly divided into 40 percent forest--composed of Douglas fir (*Pseudotsuga menziesii*) with grand fir (*Abies grandis*) with Pacific madrone (*Arbutus menziesii*) on drier sites. Twenty percent of the island is prairie-meadow vegetation characterized by several fescue grasses, sedges, thistle, and bracken fern. A single species of cactus (*Opuntia fragilis*) may be found on open dry ground. The remainder of the Island is agricultural or residential.

San Juan Island National Historical Park is composed of two units totaling slightly over 709 hectares. The Park was established in 1968 to commemorate the famous "Pig War" that took place during the mid-nineteenth century between Great Britain and the United States in which the boundary between the United States and Canada was settled. The 500 hectare American Camp Unit is located at the dry southern end of the Island where prairie dominates the landscape and the forest stands are found on the wetter north-facing slopes. The English (= British) Camp Unit is located on the Island's wet northern shore and totals slightly more than 200 hectares. It is largely forest except for the maintained openings which comprise the historical scene, and a few natural meadows on the southwest slopes of Mount Young.

The Park's major resource management problem is the presence of the introduced European rabbit, *Oryctolagus cuniculus*. The same species is a major pest mammal in Australia, New Zealand, England, and on several islands off the California coast (Zeuner, 1963). The presence of the rabbit in large numbers alters vegetation patterns, disrupts archeological sites, invites poaching thus endangering visitors (Stevens, 1975).

The study was conducted over a two year period from 1972 to 1974. Two categories of methods were employed: 1) Those methods which were recurring and regular, i.e. the censuses, collections, etc. and 2) those methods used only once. The populations were censused daily, during intensive study periods, and as many as 10 censuses were taken on some days. We used "line of sight" techniques to obtain "above ground" estimates of the rabbit densities. Four census lines were established from which the daily counts were made. The counts were made at all hours of the day and night (randomly selected), and at all seasons of the year.

There were 150 specimens collected, standard measurements were recorded, and the animals were autopsied. Reproductive tracts of females were saved. Representative specimens have been deposited in the Washington State Museum at the University of Washington.

Vegetation and habitats were described using standard techniques proposed by Daubenmire (1968). A total of seven rabbit proof exclosures were established ranging from 9 square meters to 560 square meters. Comparable control exclosures were established, each of which had openings allowing for rabbit access.

Weather data were recorded every day

[1]National Park Service Cooperative Park Studies Unit, College of Forest Resources, University of Washington, Seattle 98195.

investigators were afield. Approximately 250 rabbits were live-trapped and tagged for individual recognition. Each individual was weighed, measured, and sexed. Marking permitted rabbit identification with telescope up to 800 meters under good conditions. Over 1000 captures and recaptures were recorded during the 19 months of live-trapping. Electric activity recorders were used to record nocturnal rabbit activity patterns.

## RESULTS

The rabbits found on San Juan Island range from 39-48 cm long. Weights are generally around 1.75 kilograms. Pregnant does are more, most other rabbits are less. Pelage polymorphism is present in the population but at low frequencies where the rabbits are subject to natural predation. Such polymorphism is more common where the rabbits are protected by human activities, e.g. around the town of Friday Harbor.

The rabbits are found throughout the Island in winter densities ranging from means of less than three animals observed per hectare, to regions where mean winter densities are about 45 animals per hectare, during several censuses in late summer. The rabbits occupy the open lands (natural or manmade) in greater abundance than forests. The latter typically contains the fewest number of rabbits. No part of either the Park or the Island is without rabbits.

Considerable variation in activity was observed. Rabbits tend to exhibit a bimodal daily cycle with peaks about sunrise and sunset, when animals are most frequently encountered above ground. Considerable variation occurs in above ground activity as a result of weather, visual presence of predators, and habitat in which the rabbits are living. Forest rabbits tend to be nocturnal, shrubland rabbits are diurnal, while the prairie rabbits are extremely variable in their activity patterns.

The rabbit's breeding season on the Island begins in mid-March and extends into June. The annual average of three litters, with a mean of 7.27 kittens per litter, seems to be produced synchronously. Each group of litters first emerges from the warrens within a few days of each other during the breeding season. Kittens achieve about 70 percent of their adult body weight in the subsequent six to eight weeks following their first emergence (Figure 2). The fecundity rate here reported is the highest for the species while the number of litters produced is the lowest. Kitten survival is also low and a mean ratio of one adult to 2.62 young was recorded at the end of the breeding seasons (Mykytowycz and Fullager, 1973).

The European rabbit is the only leporid that can be regarded as a colonial beast with a highly developed social structure. Rabbits live in warrens, a complex subterranean burrow system containing passageways, enlarged chambers, several openings, and which are under constant excavation by the rabbits. Several warrens were live-trapped to obtain all the individuals in the warren. We found a mean of 8 adults to 60 young prior to post-breeding dispersal. By the following spring, about eight rabbits could be found in each warren.

The locations of 372 warrens in a 48 hectare field were mapped. These warrens had a mean entrance number of 9.35 entrances and the range of entrance was between one and 56. Ninety percent of the warrens had less than 30 entrances. There are 7.71 warrens per hectare on the American Camp prairies (Figure 3). The average warren will cover about 770 square meters of surface and contain over 100 meters of burrow system below ground.

The major cause of rabbit mortality is probably weather. However, there are a variety of predators, both avian and mammalian that prey upon the rabbits. There are 13 species of raptors reported preying upon the rabbits of 21 raptors known from the Island. Great horned owls are probably the most efficient avian predators. Bald eagles concentrate in considerable numbers during the winter and feed extensively on rabbit by scavenging their prey from other raptors. Four resident mammalian predators are known to prey upon the rabbits. Feral and farm dogs and cats also take rabbits opportunistically. Raccoons may seasonally take young but rely mostly on scavenging. A small population of *Mustela putorius* is also present on the Island and probably fares almost exclusively on the rabbits.

Additional work was undertaken to investigate the presence and distribution of other mammal species on the Island. There were 38 locations trapped in 1974 for a total of 2,525 "trapnights" that resulted in the collection of 128 non-rabbit specimens.

Nineteen mammal species may be found on San Juan Island, of which 14 species probably occur within the present boundaries of the Park (Table 1). An unexpected result was the capture of *Mustela putoris*, the European polecat, or ferret. Apparently, a small population of polecats has become established on the Island. Polecats or ferrets are frequently used to hunt rabbits. Some individuals have escaped from the owner-hunters, and they are now apparently living and perhaps breeding among the rabbits. Ferrets were observed in the Park and elsewhere on the Island, by the investigator, Park staff, and Island residents. Three ferret specimens have now been taken.

The most common non-rabbit mammal is the mouse, *Peromyscus maniculatus*. This mouse was collected at 65 percent or 23 of the trap sites. *Sorex vagrans* was taken at six sites. *Rattus rattus* and *Microtus towsendii* were taken at three and two sites respectively. The latter seems to have increased its population during 1976.

The shrews were obtained from non-forested areas only. The rats were found only along the beaches dwelling apparently among the driftwood thrown up by storm tides. The *Microtus* were found solely in grassy meadows surrounded by dense forests on the northern end of the Island. All other small mammal species were taken at a single site only. Road-killed and other specimens of the larger carnivores were obtained throughout the study, e.g. an otter (*Lutra canadensis*) was obtained from a crab pot placed in park waters.

Thirteen trapping sites were located within the boundaries of the Park of which five yielded no specimens and the remaining eight sites produced specimens. It seems likely there is a relationship between the presence of rabbits in high densities and the occurrence of other mammal species. Table 2 shows that at high densities

TABLE 1. Mammals of San Juan Island, modified from Nordquist, 1975.

| | NAME | REFERENCE |
|---|---|---|
| * | Sorex vagrans | |
| * | Myotis lucifugus | Dalquest (1940a) |
| * | Myotis yumanensis | Dalquest (1940a) |
| * | Myotis californicus | Dalquest (1940a) |
| * | Lasionycteris noctivagans | Dalquest (1940a) |
| * | Eptesicus fuscus | Dalquest (1940a) |
| * | Oryctolagus cuniculus | Stevens (1975) |
| * | Peromyscus mainculatus | |
| | Microtus townsendii | |
| | Ondatra zibethica | |
| | Rattus norvegicus | Taylor and Shaw, 1929 |
| * | Rattus rattus | |
| | Mus musculus | Taylor and Shaw, 1929 |
| | Canis familiaris | |
| * | Felis domesticus | |
| * | Procyon lotor | |
| | Mustela vison | Schoen, 1972 |
| * | Mustela putorius | |
| * | Lutra canadensis | |
| * | Odocoileus hemionus | |

* Present in San Juan Island National Historical Park.

TABLE 2. Trapping results from 13 sites in San Juan Island National Historical Park.

| Trap Site | Location | Number Mammals Captured | Number of Species | * Catch/Unit Effort | Number of Rabbits/hectare |
|---|---|---|---|---|---|
| 74-A | British Camp | 3 | 1 | 5.76 | <3 |
| 74-B | British Camp | 0 | 0 | -- | <3 |
| 74-9 | American Camp | 8 | 1 | 27.11 | <3 |
| 74-22 | American Camp | 1 | 1 | 3.33 | <3 |
| 74-25 | British Camp | 2 | 1 | 7.84 | <3 |
| 74-26 | British Camp | 5 | 2 | 5.74 | <3 |
| 74-C | American Camp | 0 | 0 | -- | 15± |
| 74-1 | American Camp | 4 | 3 | 4.59 | 15± |
| 74-15 | American Camp | 15 | 1 | 17.64 | 15± |
| 74-20 | American Camp | 5 | 2 | 11.49 | 15± |
| 73-A | American Camp | 0 | 0 | -- | 45± |
| 74-23 | American Camp | 0 | 0 | -- | 45± |
| 74-30 | American Camp | 0 | 0 | -- | 45± |

* See Nelson and Clark, 1973

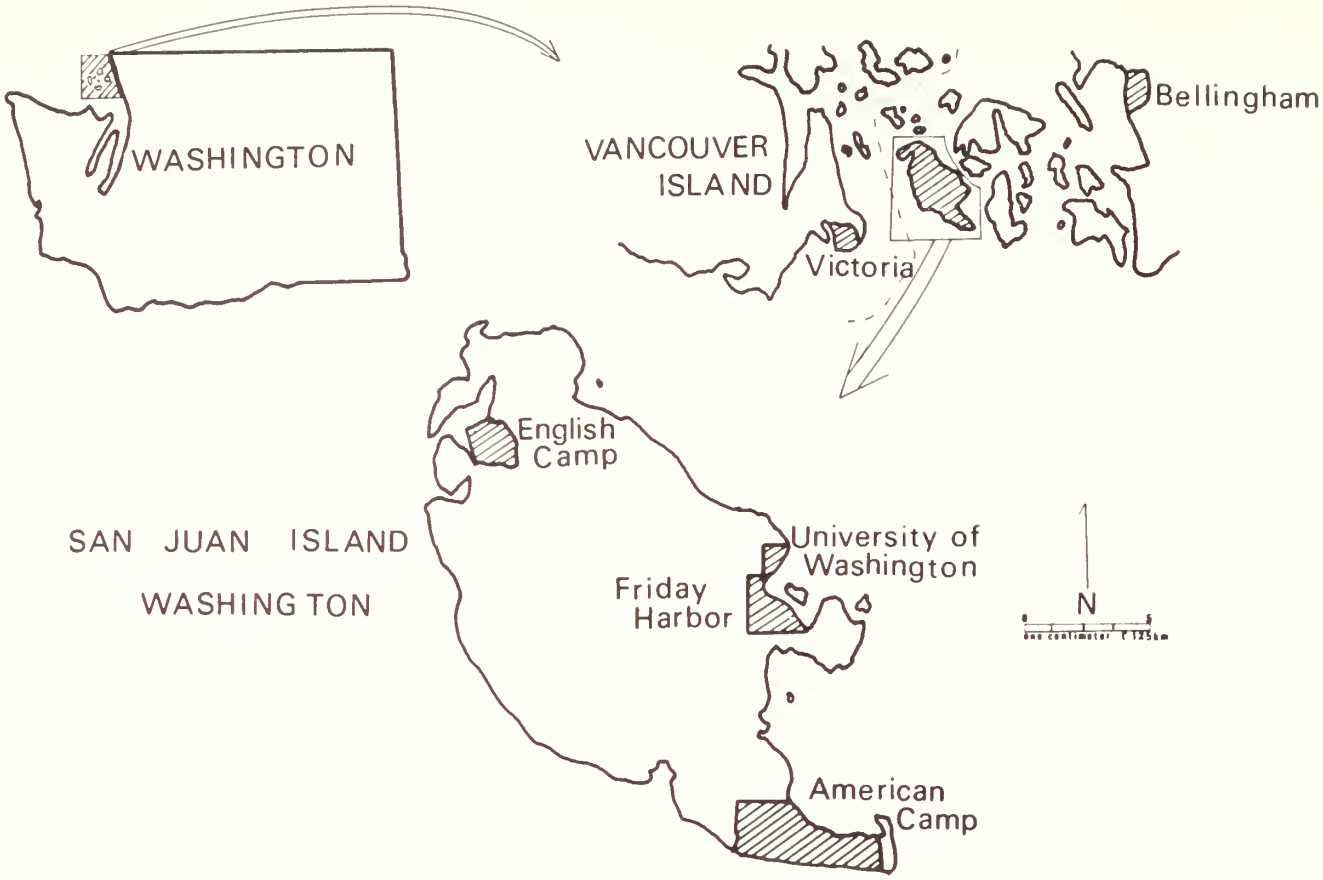



FIGURE 1. Map of San JuanIsland shoiwng its location (48° 30' N. 123° 4' W) and the position of the two units of San Juan Island National Hisotircal Park in relation to the town of Friday Harbor and the University of Washington's Friday Harbor Marine Laboratories.

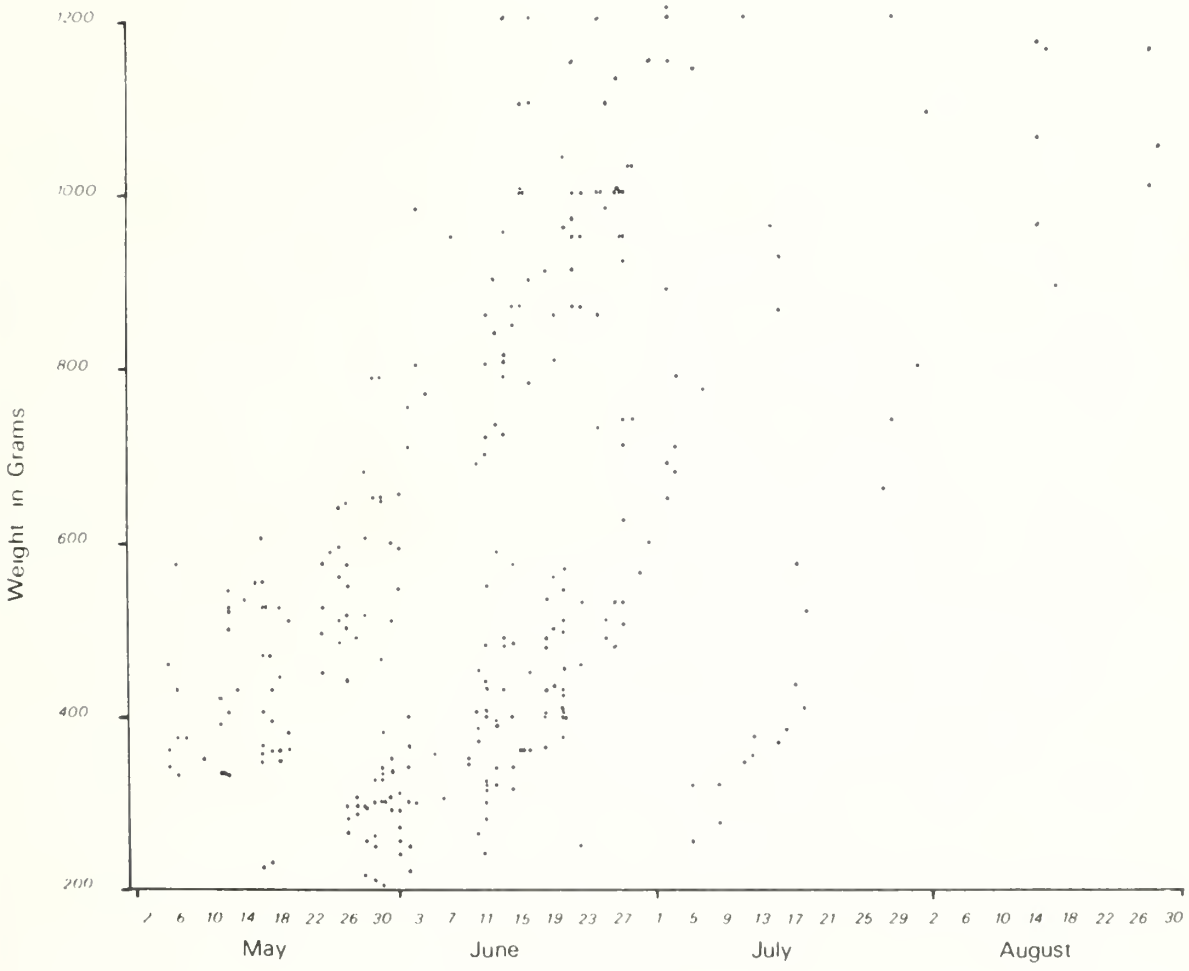



FIGURE 2. A live weight scattergram of marked and recaptured American Camp kittens from the 1973 and 1974 breeding seasons. Breeding synchrony is suggested by distinct litter groupings. Reduced recover for third litter resulted from lowered trapability in July and August.

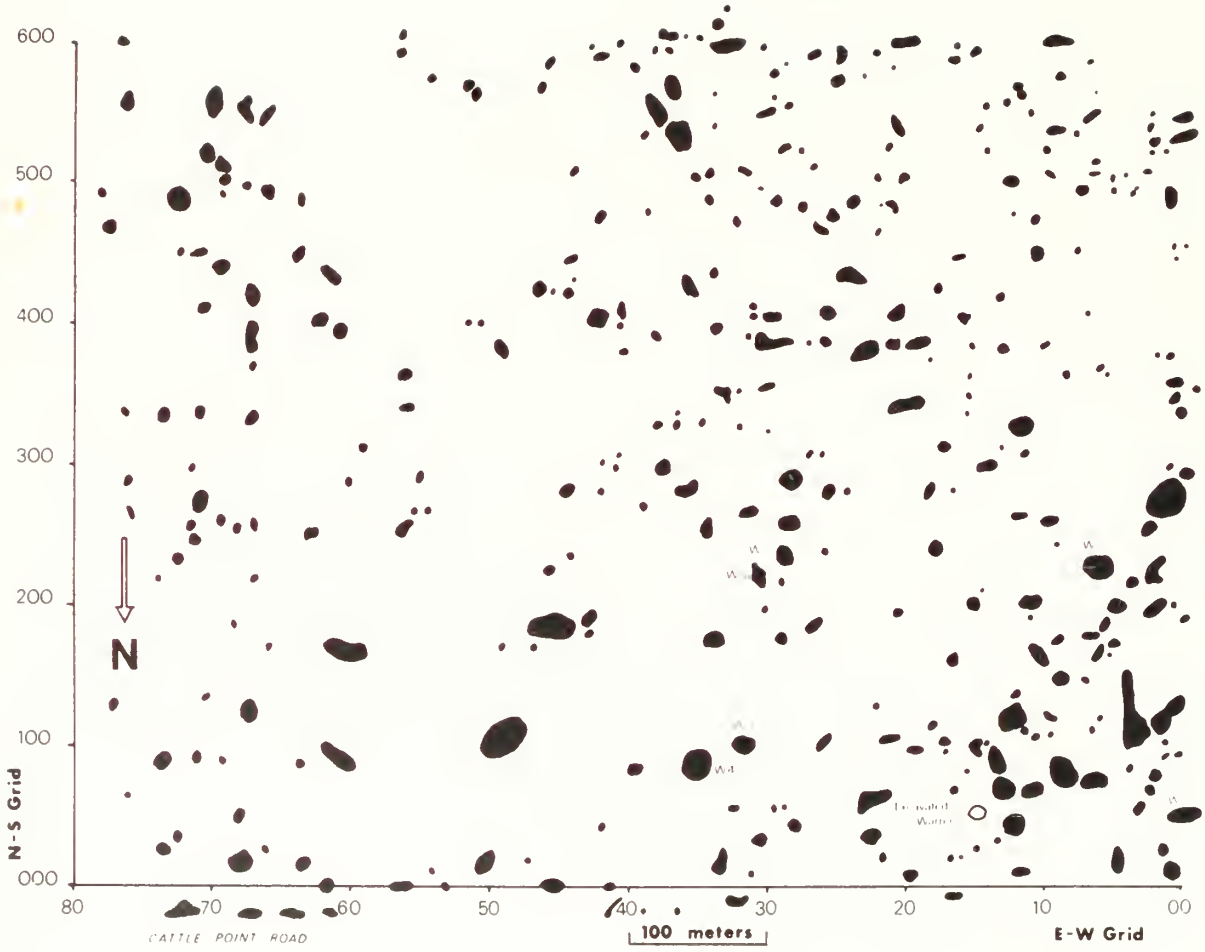



FIGURE 3. A schematic map showing the warren distribution within a 48 hectare gridded study area of the American Camp Unit's prairie. "W" indicates location of a warren subjected to intensive study.

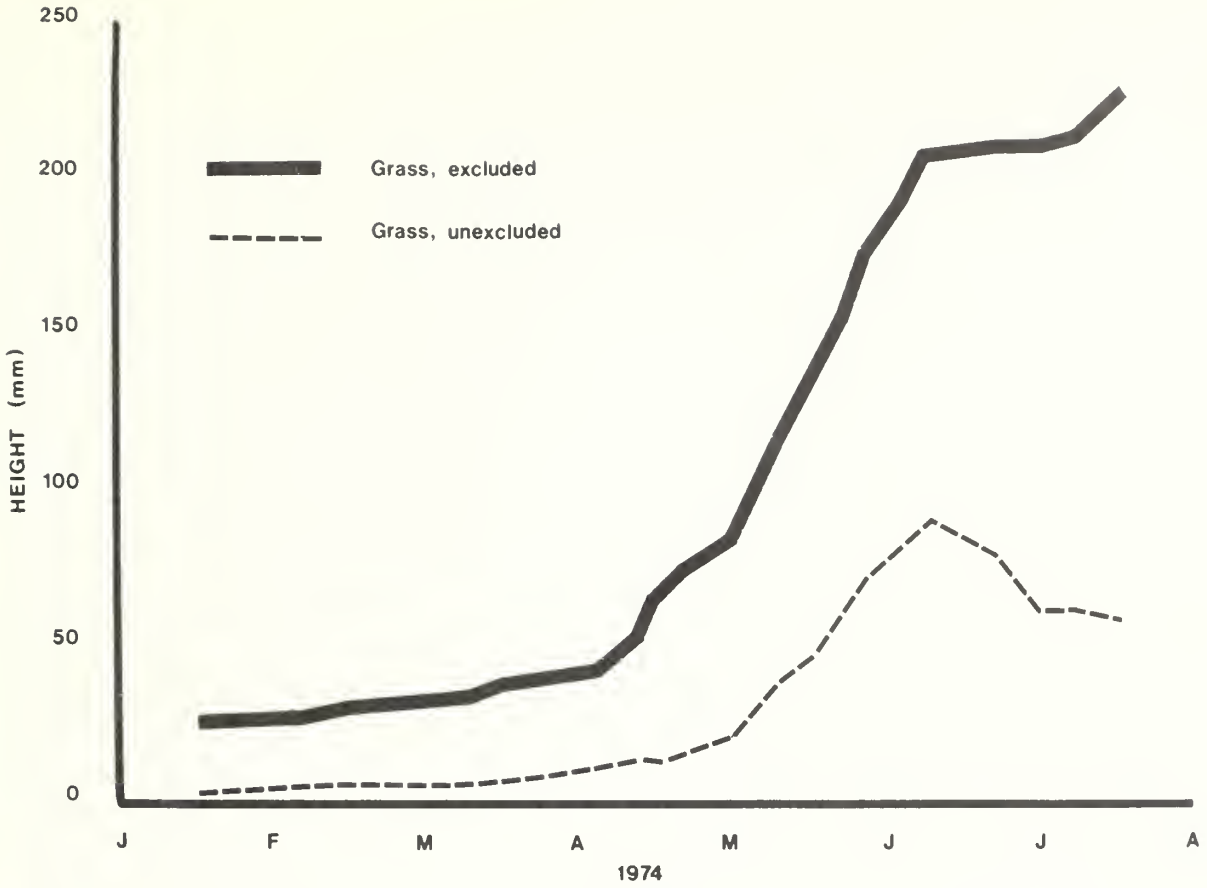



FIGURE 4. A comparison of grass growth during 1974 between seven study exclosures and adjacent control areas of identical size into which rabbits had free access.

(45 rabbits per hectare) no other mammal was obtained, while at lower densities (3-15 rabbits per hectare) several species could be found. Similarly, our pellet-transect censuses to estimate the black-tailed deer population densities show that deer are 10 times more abundant in low density British Camp than in the high density areas of American Camp. There are about 0.44 deer per hectare in British Camp and 0.04 deer per hectare in the American Camp Unit. The apparent effect of rabbit densities on other organisms is further supported by data from the exclosures (Figure 4). These data show that in a high rabbit density area the grasses within exclosures achieved about four times the growth of those grasses outside the exclosure and which were subject to rabbit grazing.

It appears likely that the introduced European rabbit is an important environmental factor affecting not only the Park's historical and archeological sites, but they are probably the dominant vertebrate animals on the Island, apart from man. We have recommended to the Park managers that eradication of rabbits from the Park is unlikely, but that control measures, such as plowing warrens followed by erecting rabbit proof fences in the vicinity of those archeological sites and historic structures subject to rabbit damage, are feasible to protect specific areas. We have further recommended continued work to investigate the details of rabbit social behavior and their environmental physiology in hopes of elucidating some of the questions we have briefly presented here and that perhaps will offer future clues to better regulation of this exotic species in a fascinating park area.

## LITERATURE CITED


DAHLQUEST, W. W. 1940. Bats in the San Juan Islands, Washington. Murrelet. 21(1):4-5.

DANNER, W. T. 1957. Stratigraphic reconnaissance in the northwestern Cascade Mountains and San Juan Islands of Washington State. Ph.D. Thesis. University of Washington. 562 pp.

DAUBENMIRE, R. 1968. Plant communities: A textbook of synecology. Harper and Row, N.Y. 300 pp.

EASTERBROOK, D. J. 1969. Pleistocene chronology of the Puget Lowlands and San Juan Islands, Washington. Geol. Soc. Amer. Bull., 80(11): 2273-2286.

MCKEE, B. 1972. Cascadia: The geologic evolution of the Pacific Northwest. McGraw-Hill, Inc., N. Y. 394 pp.

MYKYTOWYCZ, R. and P. J. FULLAGER. 1973. Effect of social environment on reproduction in the rabbit. J. Reprod. Fert., suppl. 19:503-522.

NELSON, L., JR. and F. W. CLARK. 1973. Correction for sprung traps in catch/effort calculations of trapping results. J. Mamm., 54(1): 295-298.

NORDQUIST, G. E. 1975. The distribution of mammals on San Juan Island, Washington. Honors thesis. Univ. of Wash. 55 pp.

SCHOEN, J. W. 1972. Mammals of the San Juan Archipelago: Distribution and colonization of native land mammals and insularity in three populations of *Peromyscus maniculatus*. M. S. Thesis. Univ. Puget Sound. 119 pp.

STEVENS, W. F. 1975. The biology of the European rabbit, *Oryctolagus cuniculus*, on San Juan Island, Washington. M.S. Thesis, Univ. Wash. 151 pp.

TAYLOR, W. P. and W. T. SHAW. 1929. Provisional list of the land mammals of the State of Washington. Occ. papers Conner Museum Wash. State Univ. 2: 32 pp.

ZEUNER, F. E. 1963. A history of domesticated animals. Hutchinson, London.

# DISTRIBUTION AND RICHNESS OF MAMMAL SPECIES IN MOUNT RAINIER NATIONAL PARK

A. R. Weisbrod and J. A. Dragavon[1]

There has been recent interest by the National Park Service in determining the major biotic, geologic, and other environmental resources found in national parks. Consequently, the Service instituted a series of studies designed to provide the Service with basic information about the numbers of plants and animal species, and their distributions within the parks. It is hoped the Service will continue studies of the various kinds of biotic associations and ecological communities in order to provide the information enabling the Service to better protect and manage these reserved public lands.

We undertook a study of the mammals of Mount Rainier National Park as a portion of this developing program. Mt. Rainier National Park is located on the western edge of the south central Cascade Mountains of Washington State (Figure 1). This 98,000 hectare park was established in 1899, and is one of the oldest parks in the Pacific Northwest. It is dominated by the presence of a dormant Pleistocene strato-volcano - Mount Rainier - that rises from sea level (outside park boundaries) to over 4,000 meters in elevation (McKee, 1972). The Park boundary begins about 600 meters elevation.

## METHODS

We trapped the Park opportunistically during the field season of 1974, and we trapped systematically during the summers of 1975 and 1976 by dividing the Park into four quadrants, roughly approximating the Park's major river drainages. Sites were selected on the map at specified elevations -- 3500 feet (1067m); 4500 feet (1372m); 5500 feet (1677m). Each site was sampled with two parallel traplines, which were separated by a 20m interval. Standard traplines were used, consisting of 20 stations located at 10 meter intervals. Each station used two museum specials and one rat trap (Manville, 1950). Expedient trapping techniques were employed to capture those mammals not normally susceptible to snap traps (e.g., carnivores). A total of 53 sites were trapped. The results of 1974 and 1975 that are here reported since we are still processing much of the 1976 work.

Each of three elevations within a quadrant was trapped simultaneously. In addition, a fourth trapline was established outside of the Park for comparison to Park results. Each of the quadrants was visited three times at 16-day intervals throughout the summer. Quadrants were rotated every four days there by completing a circuit around the Park every 16 days. Data taken at each location provided elevation, azimuth (orientation of the line on the contour), slope, aspect, soil temperatures, air temperatures, and habitat measures.

[1]National Park Service Cooperative Park Studies Unit, College of Forest Resources, University of Washington, Seattle 98195.

The habitat was sampled according to techniques employed by Moir and Franklin (1976) who are conducting a vegetation study of the resources survey program. Following their techniques, we obtained measures of stand composition, canopy cover, shrub composition and cover, and ground composition and cover. These measures are here presented as four percent cover classes. (0-25%, 25-50%, 50-75%, 75-100%.) The data at 3500 feet represent actual percentages. After completing the 3500 foot survey, it was noted that the habitat data tended to arrange itself into observed "natural" classes of vegetation. It was decided to use the four cover categories above as a reasonable substitute to single percentage estimates.

The design permits comparison of differences between elevations, between quadrants, and within quadrants. A total of slightly more than 900 specimens was obtained during the 1974-1975 field seasons. An additional 400 specimens were procured during the summer of 1976. Standard mammal measurements were taken on all specimens. All prepared specimens have been deposited in the Washington State Museum at the University of Washington, Seattle.

## RESULTS

Habitats varied considerably along the same contours. East side habitats were distinctly different from west side habitats at the same elevations while north and south side showed similar variation. In general, the east side of the mountain is drier than the west side, and contains a number of plant species more typical of interior mountain forests, while the west side of the Park is surprisingly like the Olympic rain forests much farther to the west. (For a more complete review of the mountain's vegetation, see Franklin and Dyrness, 1973, and Moir and Franklin, 1976.)

In general, the relationship between mammal occurrence and the geography, aspect, and slope data does not provide definitive information, although some interesting tendencies do appear. For example, while 87 percent of the species taken at 3500 feet (1067m) were obtained on the north side of the mountain, most of these species preferred south-facing slopes. At the same time, most species seemed to prefer steeper slopes. However, since there are more steep than non-steep slopes, no strong conclusions can be drawn. Additionally, the tendency toward steeper slopes can largely be explained by the greater frequency of *Peromyscus maniculatus* captures on these slopes. One-third of all specimens taken on sites with steep slopes were *P. maniculatus*. *P. maniculatus* is a relatively adept climber, at least when compared with the local microtines. Similar non-specific tendencies occur with these parameters at 4500 feet (1372m) and 5500 feet (1677m) contours.

Canopy cover alone does not show a strong relationship to diversity. At lower elevations (3500 feet and 4500 feet), the heavier the canopy cover, the more species and individuals that are accounted for in the data. At 4500 feet, the

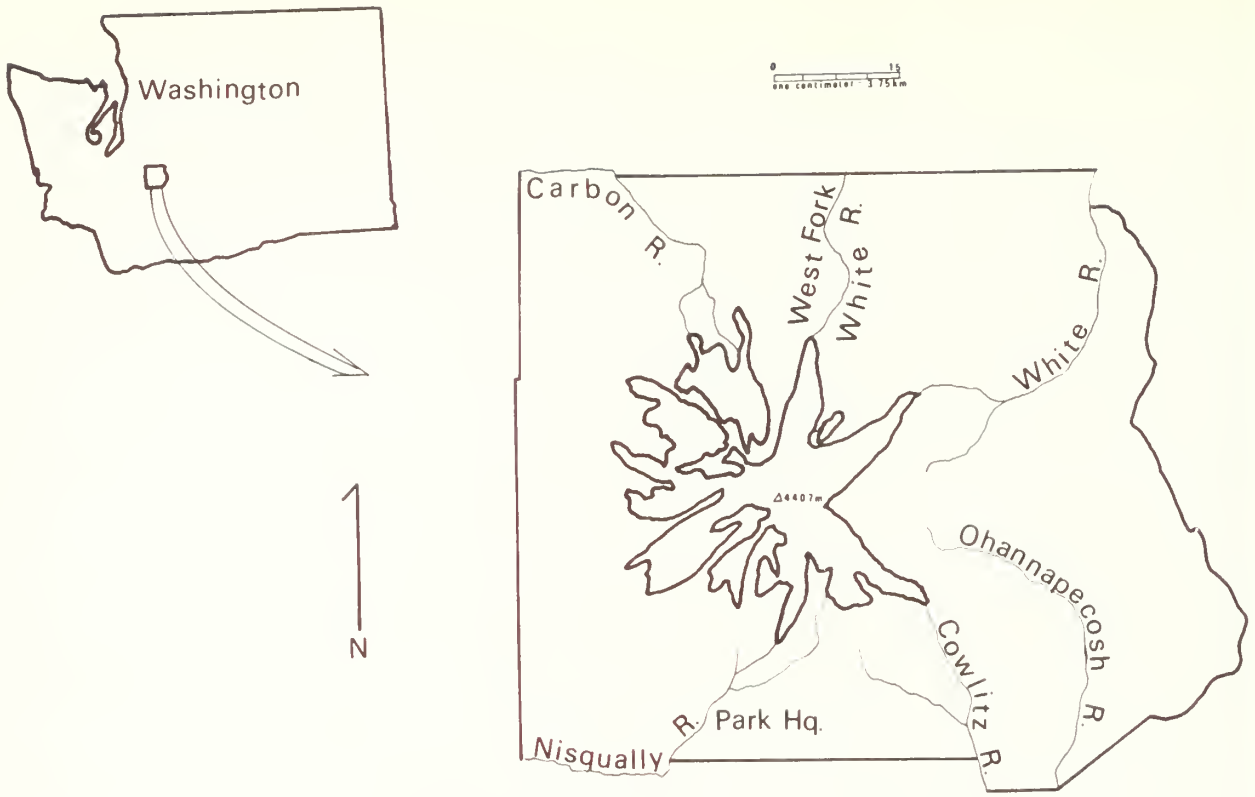
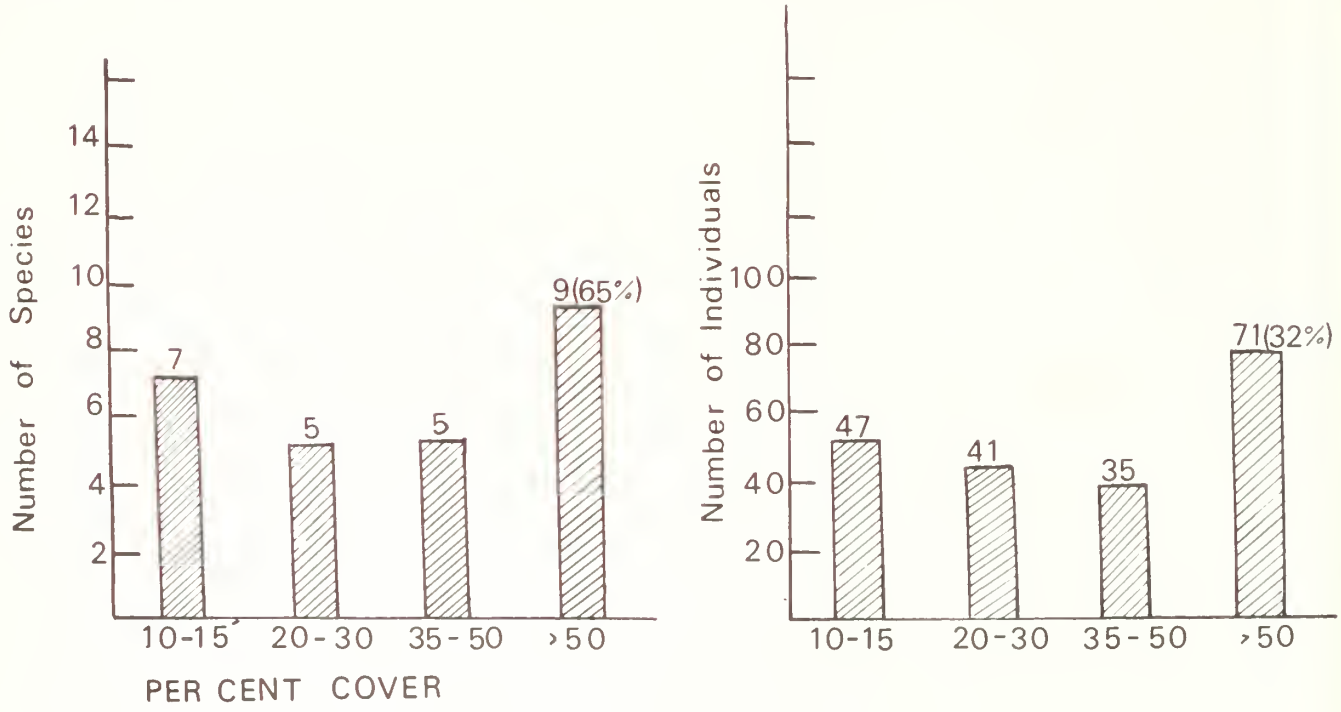



FIGURE 1. A map of Mount Rainier National Park showing its location and major river drainages within the Park's boundaries.




SHRUB

FIGURE 2. Distribution of mammals by shrub cover classes at 3500 feet elevation. These categories are percent cover. The number on each bar is the total number of species/individuals taken in that category The percentage in parenthesis is the percent of total captured.

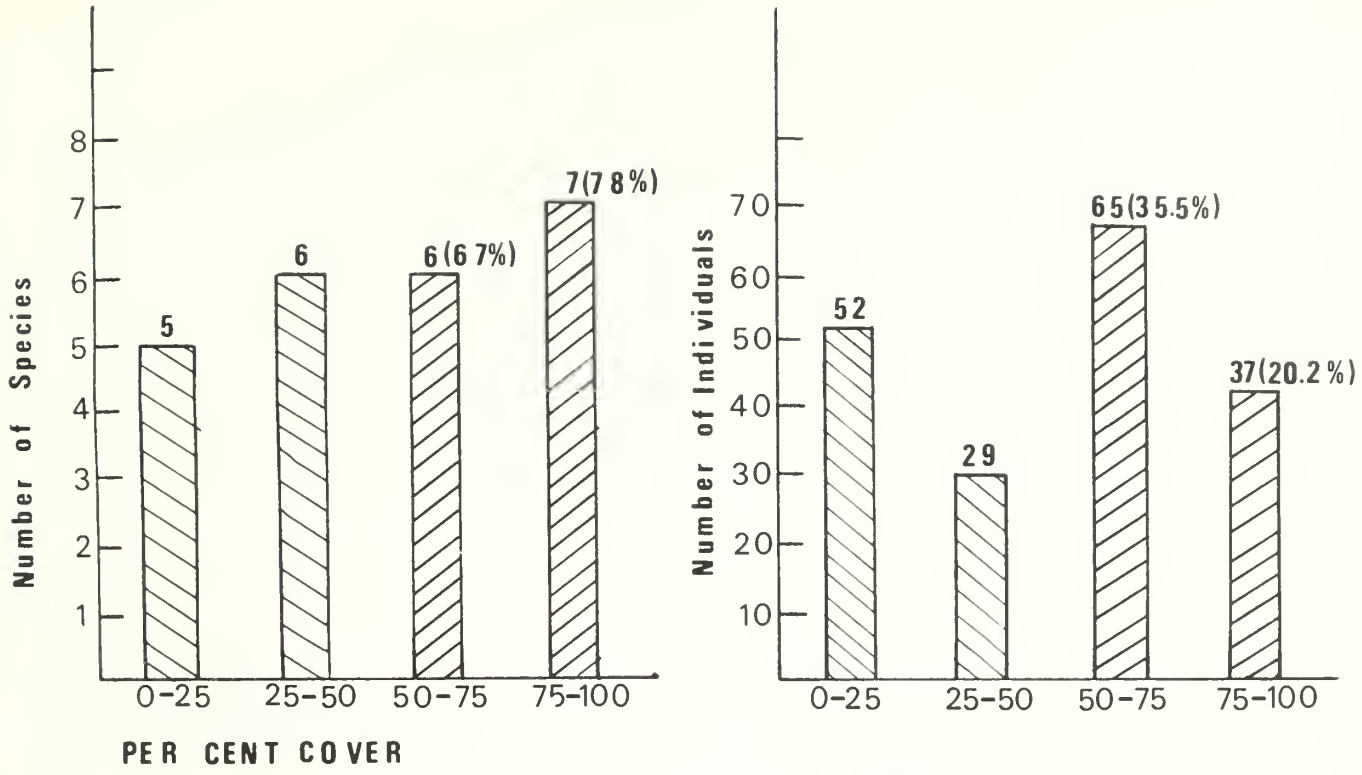



FIGURE 3. Distribution of mammals by shrub cover classes at 4500 feet elevation. These categories are percent cover. The number on each bar is the total number of species/inidividuals taken in that category. The percentage in parentheses is the percent of total captured.

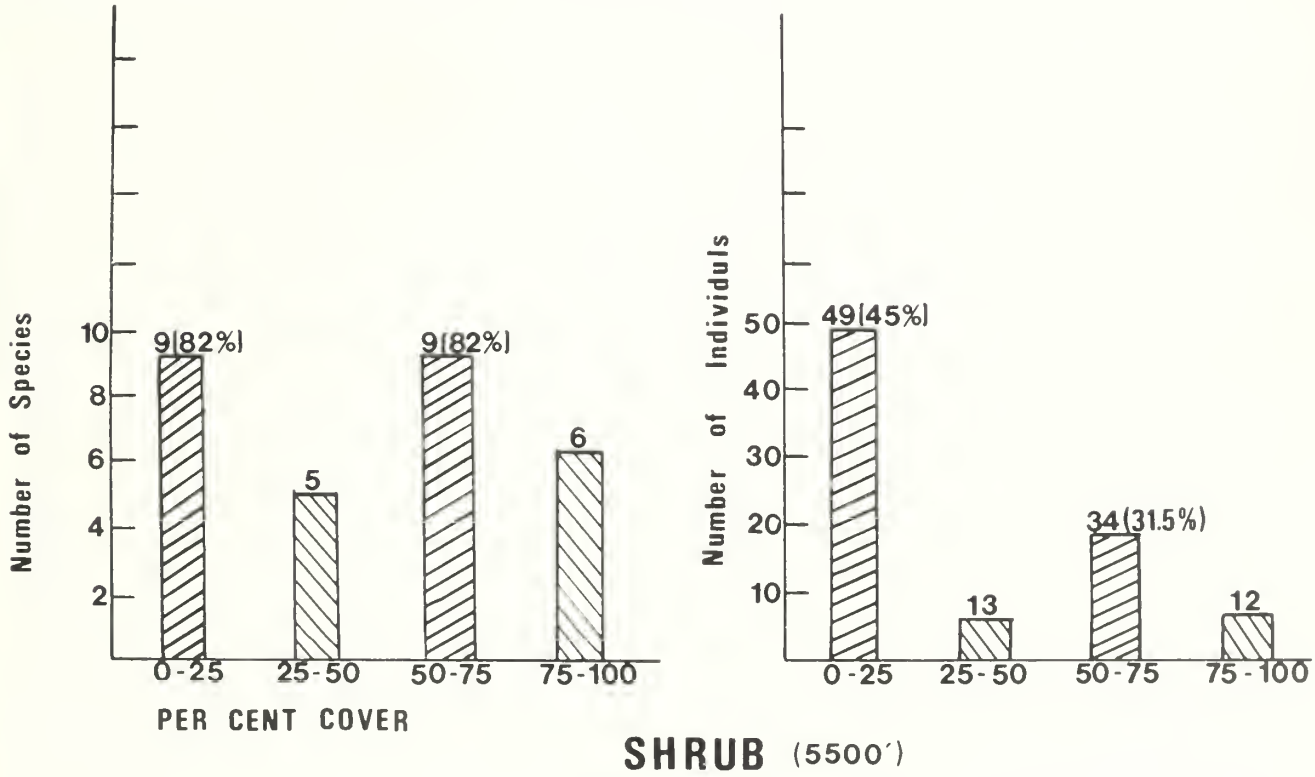



FIGURE 4. Distribution of mammals by shrub cover classes at 5500 feet elevation. These categories are percent cover. The number on each bar is the total number of species/individuals taken in that category. The percentage in parenthesis is the percent of total captured.

50-75 percent cover category shows that a small effort (8 percent) returned a disproportionate (67 percent) of the total species captured and 24 percent of the individuals. However, one line bordered a marsh (Frog Heaven). The trap sites adjacent to this marsh accounted for nearly 65 percent of captures at this contour. Adjusting the data for this factor brings the category roughly into line with the rest of the 4500 foot data. The percent of total traplines per cover category (i.e. effort) may be used as a comparative statistic since all traplines had the same number of traps operating for the same number of trapnights. At 5500 feet, the canopy data show nearly a one-to-one ratio of effort results. The 0-25 percent category accounted for about 80 percent of the effort and returned about 80 percent of the mammal data.

Ground cover data are similar to those of Canopy Cover since there is no uniformity of results among the elevations examined. Dense ground cover (at 3500 feet) tended to have more species and numbers of individuals than less dense ground cover. There seems to be a real distinction between the over 50 percent and the under 50 percent categories of ground cover. *P. maniculatus* were taken about as often in both situations. However, the ground squirrel, *Spermophilous lateralis*, and jumping mice, *Zapus trinotatus*, were captured in more open areas while the microtines were caught more frequently in the densely covered areas. Trapping effort at 4500 feet in the 75-100 percent cover category produced poor results. The most likely explanation lies in the fact that these sites were depauperate in shrubs. The significance of shrub cover is discussed below.

One quarter of all 3500 foot contour trapping sites had shrub cover densities exceeding 50 percent; however, these sites accounted for nearly one-third of the total number of captures and 65 percent of the total species obtained at this elevation (Figure 2). Similarly, at 4500 feet, the greatest return in captures occurred in shrub cover categories exceeding 50 percent. On the other hand, the fewest captures occurred in low cover density sites regardless of the ground cover. These are the same traplines showing few captures for the varying ground cover densities mentioned for this elevation (Figure 3). Unfortunately, the relationship seems less strong at 5500 feet. The shrub cover of 0-25 percent produced 45 percent of captures with 35 percent of trapping effort. This largely results from the high *Eutamias amoenus* capture rate in that cover class. Shrub covers of 50-75 percent returned about 32 percent of all captures, but with only 20 percent of the total trapping effort (Figure 4).

Typically, the high yield traplines in the shrub cover categories are the same trapline for which canopy cover classes and ground cover classes display the highest returns for each of those parameters. The converse is not true. That is, not all of the high yield trap sites in a given canopy class are the same traplines showing high results for given ground cover groupings nor are "high yield" trap sites for a ground cover division the same as the high yield canopy sites. However, the sites in high yield shrub density classes are the same as the high yield sites in both the canopy class and ground cover classes. Thus, shrub density classes seem to be a more reliable indicator of mammal species occurrence at this stage in our analysis.

We are still evaluating much of this data and will continue to do so for some time. One of our goals is to determine if a particular species or genus or group of plant species can account for a large proportion of the variation in the mammal data. Techniques of gradient analysis seem to be most useful for accomplishing this goal, and we are currently applying these techniques to the data (Whittaker, 1973; Poole, 1973). We hope by applying such techniques it will be possible to relate the mammal data to regular variation in physical and vegetative structure in such a way as to provide useful information for park management which increasingly must consider the entire ecosystem prior to making intelligent land use decisions.

## LITERATURE CITED


FRANKLIN, J. F. and W. T. DYRNESS. 1973. Natural Vegetation of Oregon and Washington, USDA Forest Service General Technical Report PNW-8, 417 pp.

MANVILLE, R. H. 1950. A Comparison of Trapping Methods, Journal of Mammalogy 31(4), pp. 337-383.

MCKEE, B. 1972. Cascadia, the Geologic Evolution of the Pacific Northwest, McGraw-Hill, Inc. 394 pp.

MOIR, W. and J. F. FRANKLIN. 1976. First Year Report to NPS on Studies of Forest Ecosystems at MORA; USNPS Mimeo Report. 36 pp.

POOLE, W. 1972. An Introduction to Quantitative Ecology. McGraw-Hill, Inc. 394 pp.

# MAN-CAUSED MORTALITIES OF COYOTES RADIO-MARKED IN GRAND TETON NATIONAL PARK[1]

Walter M. Tzilkowski[2] and Frederick F. Knowlton[3]

The purpose of this study was to document and describe coyote (*Canis latrans*) mortality in Grand Teton National Park, an environment assumed to be minimally influenced by man.

## STUDY AREA

The study area is 25,600 hectares of the valley floor of Grand Teton National Park. This area includes 2,400 hectares of private inholdings. The valley floor is a flat, glacial outwash plain. Glaciated ridges, terraces bordering the Snake River, potholes formed from melting glacial ice blocks, alluvial fans, and braided stream bottoms contribute to the topography (Love and Reed 1968).

The climate is characterized by long, cold winters and short, cool summers. The area receives a mean annual snowfall of 327 cm. and is generally snow covered from November to April. There is an increasing gradient of accumulated snow from the southeast to the northwest. Maximum accumulated snow depths at Moose, near the center of the study area, range from 84 to 178 cm (Dirks 1974).

## METHODS

Coyotes were captured within the park during the periods 14 May 1974 to 6 June 1974, 6 September 1974 to 19 September 1974, and 4 September 1975 to 24 September 1975. Steel traps equipped with tranquilizer tabs (Balser 1965) were used to capture the coyotes. Each tranquilizer tab contained 500 mg of Transvet.[4] Young of the year were referred to as pups; all others were classed as adults.

Each coyote was collared with a multiple-use transmitter (Kolz et al. 1973). The transmitter facilitated relocation and provided mortality detection. Individual coyote transmitters were identifiable through combinations of operating frequencies and pulse rates. Upon detection of a mortality signal, a search was made for the coyote. Three coyote mortalities were recovered directly from human cooperators. Field necropsies were generally adequate to determine the immediate cause of death. The time, location, and cause of death were recorded at the time of recovery.

## RESULTS

Fifty-two coyotes (26 males and 26 females) four months of age or older, were collared with mortality style transmitters (Table 1).

Recovered dead were 19 coyotes (37 percent). Ten males (38 percent) and nine females (35 percent) were recovered. Six pups, one male and five females (46 percent) and 13 adults, nine males and four females (33 percent) were recovered (Table 2). Within the park boundary nine mortalities (47 percent) were found. Thirty-three percent of the within-park mortalities were recovered on private inholdings (Table 3).

Man was responsible for 17 mortalities (90 percent): 13 were gunshot, one was trapped, one was clubbed, and two were roadkills (Table 4).

Seven of the man-caused mortalities (42 percent) were recovered within the park perimeter. Five of these coyotes were shot, two of which were on non-federal inholdings, and two coyotes were roadkills.

Samples from the falls of 1974 and 1975 were compared with respect to frequency and time of mortality. Five transmitters, two in 1974 and three in 1975, failed early in the field season. These were not included in the comparison. All known mortalities occurred between October and May. Ten of the 1974 coyotes (53 percent) while only one of the 1975 coyotes (eight percent) were recovered (Table 5).

## DISCUSSION

The extent, cause, and timing of mortality have been documented for several other coyote populations manipulated by man to varying degrees.

Murie (1940) and Krefting (1969) reported causes of coyote mortality in Yellowstone and Isle Royale National Parks respectively. Murie (1940) tentatively attributed all known coyote deaths (27 during the period 1936 to 1939) in Yellowstone to natural causes: starvation and disease. Krefting (1969) noted the decline of the coyote population on Isle Royale coincided with the introduction of the timber wolf. He speculated: "A reduced food supply and direct killing by wolves are the factors that probably contributed most to the coyote's disappearance. A combination of these and other factors plus the

[1]Research funded by the U.S. Fish and Wildlife Service, Contract No. 14-16-0008-1120, through the Massachusetts Cooperative Wildlife Research Unit. Wendell E. Dodge and James J. Kennelly provided administrative support and expertise in many aspects of the project. The National Park Service cooperated with and supported the study in many ways. We appreciate the efforts of Lloyd Loope, biologist, who initiated the Park Service's involvement. Also, we express our appreciation to Gary Everhardt, Director of the National Park Service, former Grand Teton National Park superintendent, and Superintendent Robert Kerr for project approval and support. We wish to express our deepest appreciation to biologists William Barmore and Peter Hayden, and resource management specialist Robert Wood, who provided facilities, materials, and advice. Their contributions to the project were significant. Jim Barmore and Kelly Rubrecht, research assistants, performed highly conscientious and creditable tasks. Wells Stephenson, project trapper, was responsible for capture of the coyotes. This brief mention does not indicate the extent of his contribution to the project.

[2]P.O. Box 207, Moose, Wyoming 83012.

[3]U.S. Fish and Wildlife Service, Unit of Predator Studies, Utah State University, Logan 84322.

[4]Reference to trade names does not imply endorsement of commercial products by the federal government.

TABLE 1. Numbers of coyotes readio-marked by sex, relative age at time of marking, and period of capture.

| Sex/Age | Period of Capture: Spring 1974 | Fall 1974 | Fall 1975 | Total |
|---|---|---|---|---|
| Male | | | | |
| pup | - | 2 | 3 | 5 |
| adult | 9 | 8 | 4 | 21 |
| Female | | | | |
| pup | - | 5 | 5 | 10 |
| adult | 7 | 6 | 3 | 16 |
| Total | 16 | 21 | 15 | 52 |

TABLE 2. Numbers of coyotes by sex, relative age at time of radio-marking, and fate.

| Sex/Age | Fate of Coyotes: Known dead | Not known dead | Total |
|---|---|---|---|
| Male | | | |
| pup | 1 | 4 | 5 |
| adult | 9 | 12 | 21 |
| Female | | | |
| pup | 5 | 5 | 10 |
| adult | 4 | 12 | 16 |
| Total | 19 | 33 | 52 |

TABLE 3. Numbers of coyote mortalities by sex, relative age at time of radio-marking, and location of recovery.

| Sex/Age | Location of Recovery: In park | In-holding | Out of park | Total |
|---|---|---|---|---|
| Male | | | | |
| pup | - | - | 1 | 1 |
| adult | 4 | - | 5 | 9 |
| Female | | | | |
| pup | - | 1 | 4 | 5 |
| adult | 2 | 2 | - | 4 |
| Total | 6 | 3 | 10 | 19 |

TABLE 4. Numbers of coyotes by sex, relative age at time of radio-marking, and cause of death.

| Sex/Age | Cause of Death: Man: Rifle | Trap | Club | Vehicle | Starvation | ? | Total |
|---|---|---|---|---|---|---|---|
| Male | | | | | | | |
| pup | 1 | - | - | - | - | - | 1 |
| adult | 7 | 1 | - | 1 | - | - | 9 |
| Female | | | | | | | |
| pup | 3 | - | 1 | - | 1 | - | 5 |
| adult | 2 | - | - | 1 | - | 1 | 4 |
| Total | 13 | 1 | 1 | 2 | 1 | 1 | 19 |

TABLE 5. Numbers of coyote mortalities by month, year of death, and period of original marking.

| | Month | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | S | O | N | D | J | F | M | A | M | J | Total | |
| Fall 1974 coyotes | 0 | 1 | 1 | 1 | 2 | 3 | 1 | 1 | 0 | 0 | 10 | 1974-1975 |
| Fall 1975 coyotes | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1975-1976 |

fact that it was an island situation probably was necessary to cause extinction." (Krefting 1969:30). In Yellowstone and Isle Royale National Parks, man was not directly responsible for any of the coyote mortalities noted.

Clark (1972), Hawthorne (1971) and Knudsen (1976) described coyote mortality patterns among populations that were exploited by man. The basis of most coyote mortality studies has been the recovery of marked coyotes. Hawthorne (1971) recovered 23 ear-tagged coyotes (23 percent) in northeastern California during the period 1966 to 1969. Light to moderate coyote exploitation practices were assumed in effect. Clark (1972) recovered 51 ear-tagged coyotes (30 percent) in the Curlew Valley astride the Utah-Idaho border during the period 1966 to 1970. Knudsen (1976) used radio-transmitters as a marking technique in the Curlew Valley. In 1972, 48 radio-marked coyotes (52 percent) were recovered compared to 19 radio-marked coyotes (58 percent) in 1973. Moderate to intense coyote exploitation practices were in effect in the Curlew Valley. Man was directly responsible for 96, 98, and 98 percent of the marked coyote mortalities recovered by Hawthorne (1971), Clark (1972), and Knudsen (1976), respectively.

The proportion of man-caused mortalities recovered from this study in Grand Teton National Park, 90 percent, is comparable to exploited populations. Man-caused mortalities recovered within the park, 42 percent(includes two killed on private inholdings) were comparable to man-caused mortalities recovered outside the park, 58 percent. Murie (1940:29)stated, "In modern times it is necessary to add the trapper to the list of controls of coyote populations, even in the case of a national park." During the period 1974 to 1976, both within and outside of the park, man was the principal mortality agent on coyotes radio-marked within Grand Teton National Park.

## LITERATURE CITED


BALSER, D. S. 1965. Tranquilizer tabs for capturing wild carnovors. J. Wildl. Manage. 29(3):438-442.

CLARK, F. W. 1972. Influence of jackrabbit density on coyote population change. J. Wildl. Manage. 36(2):343-356.

DIRKS, R. A. 1974. Climatological studies of Yellowstone and Grant Teton National Parks. Unpub. Rept. Dept. of Atmospheric Resources. Univ. of Wyoming, 37 pp.

HAWTHORNE, V. M. 1971. Coyote movements in Sagehen Creek Basin, northeastern California. Calif. Fish and Game 57(3):154-161.

KNUDSEN, J. J. 1976. Demographic analysis of a Utah-Idaho coyote population. M.S. Thesis. Utah State Univ. Logan. 195 pp.

KOLZ, A. L., G. W. CORNER and R. E. JOHNSON. 1973. A multiple-use wildlife transmitter. U.S. Fish and Wildlife Serv. Rept. Wildlife No. 163:II + 11 pp.

KREFTING, L. W. 1969. The rise and fall of the coyote on Isle Royale. Naturalist 20(4):24-31.

LOVE, J. D. and J. C. REED, JR. 1968. The creation of the Teton landscape. Grand Teton Natural History Assoc. 120 pp.

MURIE, A. 1940. Ecology of the coyote in Yellowstone. Fauna of the Natl. Parks of the U.S., Fauna Ser. 4. 206 pp.

# HUMAN DISTURBANCE AT WOLF DENS - A MANAGEMENT PROBLEM[1]

Richard C. Chapman[2]

## INTRODUCTION

The Mount McKinley National Park management staff closed areas near active wolf dens in 1973 following several reported cases by concerned individuals of human disturbance at active wolf dens. In 1974 the National Park Service (NPS) in Alaska initiated this study of the effects of human disturbance on wolves (*Canis lupus*).

In most cases the mere presence of humans has been sufficient to disturb wolves at dens and rendezvous sites. Upon detecting the presence of humans near pups, adult wolves may react by fleeing, barking, howling, temporarily abandoning pups at the homesite, moving pups from the homesite, watching the intruder intently, or by showing no alarm at all. These reactions occur singly and in various combinations. The response is extremely variable and depends on a number of factors. The most important factors seem to be the number and social position of wolves at the homesite, their previous history of contact with humans, and the severity of the disturbance. It should be noted that pup mortality has not been reported to occur as a result of human disturbance. For more detailed discussions of human disturbance see Stephenson (1974) and Chapman (in prep.).

The NPS is concerned about two aspects of this problem. First, repeated disturbance of wolves in Mount McKinley National Park may result in wolves abandoning their primary den sites for more remote areas, thus possibly reducing visitor opportunities to see wolves. Second, there may be significant changes in ecological processes if wolves are excluded from portions of the Park. Such long term effects of human disturbance are poorly understood. Current precautionary measures are subjectively based. Present NPS policy is to protect denning areas with temporary closed areas approximately 85 $km^2$ in size.

This study sought to accurately establish the size and duration of closed areas necessary to protect wolves from human disturbance. Practical considerations dictate that closed areas not pinpoint homesites, and that they be manageable. The present study was designed to define realistic criteria for such closed areas rather than to test the hypothesis that wolf populations and the ecosystem will function normally without protection.

[1]Many people have contributed to the success of this study. I thank Rick Sinnott, Catherine Curby, Raymond Wiggs, Harold "Chip" Downing, and Elissa Mannheimer, my field assistants; James Curatolo, Robert Ritchie and David Reseneau of Renewable Resources Consulting Services, Ltd.; Robert Stephenson of the Alaska Department of Fish and Game; bush pilot Walt Audi; and Gary Brown and Steven Buskirk of the Mount McKinley National Park staff. Drs. Frederick Dean and Peter Lent provided direction throughout the study. I also wish to thank Dr. Frederick Dean, Catherine Curby, Robert Stephenson, and James Curatolo for critically reviewing early drafts of this manuscript. The National Park Service funded this project in its entirety, and the Fish and Wildlife Service permitted us to work in the Arctic National Wildlife Range.

[2]Cooperative Park Studies Unit, University of Alaska, Fairbanks 99701.

## METHODS

The general plan of this study was to experimentally disturb wolves at homesites to permit an accurate assessment of the circumstances surrounding each case of human disturbance. Initially, denning wolves were observed for periods of several days in a manner that did not disturb them. Following this we allowed wolves to detect human presence at various distances and documented their response to disturbance.

NPS policy does not permit intentional disturbance of active wolf dens and this restriction was not waived for this study. During 1974 a den on the East Fork of the Toklat River in Mount McKinley National Park was observed for 335 hrs between 22 June and 26 July at a distance of 0.8 km.

In 1975 studies were undertaken in northeastern Alaska on the north slope of the Brooks Range. A den in the Echooka River valley was observed for 187 hrs between 29 June and 8 July. The wolves there were disturbed on 30 June by placing our observation tent approximately 0.4 km from the den.

In 1976 two dens on the north slope of the Brooks Range were observed. A den in the Kongakut River valley was observed for 113 hrs during three 4-day periods between 4 June and 29 July; it was disturbed by hiking to the den proper on 26, 27, and 28 July. A den and subsequent rendezvous sites in the Hulahula River valley were observed for 1,196 hrs between 5 June and 2 August. Wolves were observed from a small, navy blue tent placed on a knoll approximately 1.2 km from the den. Two base camps were located 1.4 km, and a third 3.4 km, from the den. These wolves were disturbed in several ways. First, approximately 90 percent of our activity was within 1.6 km of the den. Second, between 14 and 26 June a small tent, usually unoccupied, was placed at diminishing distances of approximately 2.0, 1.6, 1.2, and 1.0 km from the den; it was left at each location for 2, 2, 2, and 6 days, respectively. Lastly, on several occasions I was detected by wolves when I approached within 0.2 km to photograph them.

In addition to the field work a thorough literature review was undertaken. Sixty-one cases of human disturbance at wolf homesites were found. Eight cases of human disturbance were obtained via personal communications.

A more detailed discussion of the methods used is presented by Chapman (in prep.).

## DURATION OF THE CLOSED AREA

### *Pre-whelping Activities and Whelping Dates*

Wolves visit and prepare one to several den sites within their home range as much as 4-5 weeks

prior to whelping (Young and Goldman 1944; Jordan et al. 1967; Haber 1968; Clark 1971; Stephenson and Johnson 1973). As parturition nears, the pregnant female probably remains in the vicinity of a selected den (Young and Goldman 1944, Mech 1970).

In Mount McKinley National Park pups are usually whelped during the first 2 weeks of May (Murie 1944, Haber 1968, Buskirk pers. comm.).

In the arctic most pups are whelped between mid-May and early June (Kuyt 1962; Kelsall 1968; Clark 1971; Lentfer and Sanders 1973; Stephenson 1974). Pups first ventured outside the Hulahula den on 8 June which indicates a birth date between 18 and 25 May. Physical development of pups at Kongakut and Echooka dens was similar to those at the Hulahula den, which suggests similar birth dates.

At more southerly latitudes whelping is reported to occur during late April to early May in southeast Alaska (Garceau 1960), early to mid-April in Wood Buffalo National Park (Soper 1942), early to mid-May in Algonquin Privincial Park (Rutter and Pimlott 1968), mid-April to mid-May in Jasper National Park (Carbyn 1974), and mid- to late April in Isle Royale National Park and in Minnesota (Van Ballenberghe and Mech 1975).

In general, most whelping occurs during a 2-3 week period in any given area (Rausch 1967, Van Ballenberghe and Mech 1975).

### *Whelping Den Abandonment*

Whelping dens are used by wolves for varying lengths of time. In Mount McKinley National Park most recorded dates for the movement of pups to a second den or a rendezvous site are between early June and early July, when pups are 4-8 weeks old (Murie 1944, Haber 1968, present study). In 1976, however, a den was used until approximately 24 August.

Arctic wolves usually leave whelping dens in July, but moves have been reported to occur in early June and in August (Kuyt 1962; Stephenson and Johnson 1972; Stephenson 1974). On Baffin Island the abandonment of whelping dens occurred between early July and early August, when pups were 4-9 weeks old (Clark 1971). In the present study at least one pup remained at the Kongakut den on 29 July when observations were terminated. Pups were moved from the Hulahula whelping den on 23 June, but three were returned on 25 June and a fourth 8 hrs later on 26 June. The whelping den area was abandoned for the season on 14 July.

In southern Canada and in Minnesota it is probably rare for pups to remain at whelping dens beyond 1 July. In Jasper National Park pups were moved between late May and mid-June, when pups were 3-6 weeks old (Carbyn 1974). One den in Algonquin Provincial Park, however, was vacated on 8 July (Voigt 1973).

In some cases, wolves may take several hours or even days to vacate a homesite (Banfield 1954; Stephenson 1974; Peterson 1974). In 1975 at the Echooka den three of five pups were moved on 2 July, the other two on 8 July; and in 1976 it took 8 hrs to remove all pups from a second homesite back to the whelping den on the Hulahula River.

### *Duration and Termination of Secondary Homesite Occupancy*

After wolves vacate whelping dens, pups are moved to secondary dens or rendezvous sites. One or more of these secondary homesites may be used during summer. Duration of occupancy of secondary homesites is quite variable and has ranged from 2-90 days (Stanwell-Fletcher 1942; Murie 1944; Joslin 1967, Kolenosky and Johnston 1967; Haber 1968; Rutter and Pimlott 1968; Clark 1971; Voigt 1973; Carbyn 1974; Peterson 1974; Van Ballenberghe et al. 1975). In this study secondary homesites were occupied for 2, 6±3, 17, and 25 days. Period of occupancy tends to be longer earlier in summer, when pups are relatively small.

It appears that termination of rendezvous site use occurs during September and October at all latitudes (Murie 1944: Haber 1968: Pimlott et al. 1969: Clark 1971: Voigt 1973: Peterson 1974: Van Ballenberghe et al. 1975).

### *Conclusions*

Disturbance of den areas prior to whelping may greatly influence den selection since pregnant females can easily move to another location (Stephenson and Johnson 1973; Stephenson 1974). This argues for limiting human use of areas near established dens approximately 4 weeks prior to whelping. In Mount McKinley National Park it would seem wise to establish closed areas by 1 April. Most closed areas around active wolf dens should remain closed until 1 August unless circumstances dictate that they be opened at earlier or later dates.

Since duration of occupany of secondary homesites is quite variable, it may prove difficult to effectively manage closed areas throughout the summer. If it is possible to implement closed areas around secondary homesites, the area should remain closed for as long as pups are at the secondary homesite. No closed areas need be established after 1 October.

## SIZE OF CLOSED AREAS

### *Sensory Abilities of Wolves*

Wolves are generally regarded as having excellent senses of vision, scent, and hearing. This section will attempt to consolidate the available information on their sensory acuity.

The greatest distance reported at which wolves visually detected other animals is only 1.6 km (Clark 1971, present study). Wolves, however, can probably visually detect other animals at greater distances. Clark (1971) stressed the importance of movement in visual detection and identification of other animals.

For wolves the importance of hearing in detection of other animals is not known. Experiments with dogs (*Canis familiaris*) have demonstrated that they respond to sounds that humans cannot hear. The ability of dogs to locate the source of a sound is also superior to that of man (Dangerfield et al. 1971:229-230).

In forest areas scenting is probably the most common and important method of detecting prey (Mech 1970; Peterson 1974). The greatest distance reported at which wolves scented other animals is only 0.6 km (Mech 1966).

The greatest distance reported at which wolves detected other animals is 2.4 km (Mech 1966), though method of detection was unknown and the incident was in part interpreted from tracks. The greatest distance at which wolves have been known to detect humans near a homesite, visually or by scent, is less than 1.5 km (Stephenson and Ahgook 1975).

TABLE 1. Distances at which wolves howled and/or barked at humans near pups.

| Locale | Distance from human(s) to pups (m) | Distance from human(s) to howling wolves (m) | Distance from pups to howling wolves (m) | Source |
|---|---|---|---|---|
| McKinley | 1 | 91 | 91 | Murie (1944) |
| McKinley | 0 | 400 | 400 | Murie (1944) |
| McKinley | 0 | 137 | 137 | Murie (1944) |
| McKInley | 400 | 91-183 | 400 | Murie (1944) |
| McKinley | 91 | 183 | ? | Murie (1944) |
| McKInley | 69 | ? | ? | Murie (1944) |
| McKInley | 183 | 800 | <800 | Murie (1944) |
| McKinley | <2400 | ? | 1600 | Murie (1961) |
| Algonquin | few hundred | 30-150 | few hundred | Joslin (1966) |
| McKinley | 400, 30 | 15-70 | 400, 100 | Haber (1968) |
| McKinley | 400-800 | 700 | 200-300 | Haber (1968) |
| McKinley | few hundred | few hundred | ? | Haber (1968) |
| McKinley | few hundred | few hundred | nearby | Haber (1968) |
| McKinley | few hundred | few hundred | few hundred | Haber (1968) |
| Algonquin | 152 | 15-400 | 152-400 | Theberge and PImlott (1969) |
| Brooks Range | 2400 | 400 | 2000 | Stephenson (1974) |
| Brooks Range | <800 | few hundred | few hundred | Stephenson (1974) |
| Baffin Island | <25 | 400 | 400 | Theberge (1975) |
| McKinley | 0 | 400 | 400 | Dean (pers. comm.) |
| McKinley | close-300 | 300 | 300 | Tracy (pers.comm.) |
| McKinley | close | 500 | 500 | Tracy (pers. comm.) |
| Brooks Range | 450 | 100-200 | 300 | Present study |
| Brooks Range | 1000 | 1000 | 50-75 | Present study |
| Brooks Range | 1300 | 1300 | 500 | Present study |
| Brooks Range | 1000 | 600 | 520 | Present study |
| Brooks Range | 250-1400 | 250-1000 | 100-400 | Present study |
| Brooks Range | 1200 | 1200 | 200 | Present study |
| Brooks Range | human scent possible visual stimulus (1.6 km) | 100 | <50 | Present study |
| Brooks Range | 600-800 | 600 | <200 | Present study |
| Brooks Range | 400-100 | 400 | <50 | Present study |

TABLE 2. Wolf-human interactions away from pups.

| Number of wolves | Distance of wolves from pups (km) | Distance of humans from pups (km) | "Disturbance" | Behavior prior to detecting humans | Behavior after detecting humans | Source |
|---|---|---|---|---|---|---|
| 1 | 2.4 | 3.2 | scent, and 1 human | leaving den | briefly curious, continues | Stephenson (1974) |
| 1 | 0.6-1.2 | 0.5, 1.2 | 2 humans | leaving den | investigates, continues | Present study (1975) |
| 1 | 2.0 | 1.6 | 2 humans | returning to den | briefly curious, continues | Present study (1976) |
| 3 | 1.6 | 1.6 | 2 humans | leaving den | briefly curious, continues | Present study (1976) |
| 1 | 1.4 | 1.4 | 1 human | returning to den | lopes toward den | Present study (1976) |
| 3 | 1.4 | 1.4 | human tracks | leaving den | sniffs area, continues | Present study (1976) |
| 1 | 0.8 | 1.6 | 1 human | leaving den | watches for several min, continues | Present study (1976) |
| 1 | 0.2(?)-0.9 | 1.2 | 1 human | leaving den | watches for several min, continues | Present study (1976) |
| 1 | 1.2 | 1.2 | 1 human | leaving den | briefly curious, continues | Present study (1976) |
| 1 | 0.8 | 1.0 | unoccupied tent | leaving den | briefly curious, continues | Present study (1976) |
| 1 | 1.0 | 1.0 | unoccupied tent | returning to den | briefly curious, continues | Present study (1976) |
| 3 | 1.4 | 1.4 | base camp | leaving den | briefly curious, continues | Present study (1976) |
| 1 | 1.2 | 1.2 | observation tent | leaving den | looks, continues | Present study (1976) |
| 1 | 1.4 | 1.4 | base camp | leaving den | investigates, continues | Present study (1976) |
| 1 | 1.4 | 1.4 | 1 human and base camp | leaving den | watches for several min, continues | Present study (1976) |
| 1 | 0.8 | 0.8 | 1 human | at whelping den, cannot locate pups | briefly curious, leaves area | Present study (1976) |
| 1 | 2.4 | 2.4 | 1 human | on hunt | leaves area | Present study (1976) |
| 1 | 1.2 | 1.2 | 1 human | leaving den | briefly curious, continues | Present study (1976) |
| 4 | 1.2 | 1.2 | 1 human | leaving den | briefly curious, continues | Present study (1976) |
| 1 | 1.0 | 1.2 | observation tent | returning to den | briefly curious, continues | Present study (1976) |

For animals to be scented they must usually be upwind of wolves. Vision and hearing are effective over a wider area. Wolves can probably identify an animal more accurately by scent than by vision (Pruit 1965). For identifying animals hearing is probably unreliable except when characteristic vocalizations or other sounds are involved, such as the clicking of caribou (*Rangifer tarandus*) hooves. Information from two or more senses probably results in more rapid identification of an animal.

Wolves do not always detect animals within sensing range. I have observed several instances where wolves failed to detect humans, and also a grizzly bear (*Ursus arctos*), within 0.4 km. Mech (1966) found that 29 of 85 groups of moose (*Alces alces*) went undetected by wolves despite the fact that some were within 150 m. Many animals are simply discovered by chance at extremely close range (Mech 1970, personal observations). Topography, cover, weather conditions, and the behavior of both wolves and other animals influence the probability of an animal being detected by wolves.

### *Distances from Homesites at Which Wolves React to Human Presence*

The greatest distance from pups to humans at which human presence has caused adult wolves to howl and/or bark is 2.4 km (Table 1). In only two of the 30 cases was the distance greater than 1.4 km. The greatest distance from pups to adult wolves at which adults howled and/or barked at humans is 2.0 km. In all but two cases, wolves were within 0.8 km of pups.

Twenty cases (Table 2) were observed when adult wolves were from 0.8 to 2.4 km from pups when they detected humans a similar distance from pups. In none of these cases did the adult wolves vocalize or significantly alter their behavior.

Several biologists during summer have observed wolves at close range over extended periods. Most attempted to be as unobtrusive as possible. In open country wolves are usually not disturbed by observers who are 0.8 km or more from homesites (Banfield 1954; Murie 1944, present study). At closer distances wolves may react to the presence of observers (Haber 1968; Clark 1971, present study). In forest areas observers cause little or no disturbance while remaining within 0.4 km of homesites (Joslin 1966, 1967; Voigt 1973; Carbyn 1974; Peterson 1974).

### *Movements of Pups Following Human Disturbance*

The distances that adult wolves move pups from homesites following human disturbance may provide some indication of the distance at which adult wolves feel their pups are safe from human. In eight of the ten reported cases adults moved pups from 1.6 to 3.2 km from the disturbance (Bailey 1930; Murie 1944; Joslin 1966; Wayman 1967; Carbyn 1974; Stephenson 1974). One case was less than 1.6 km (Kelsall 1960), and in this study pups were moved more than 16.9 km from the whelping den on the Echooka River following human disturbance. Additional cases of homesite abandonment following human disturbance have been reported, but the distance that pups were moved was unknown (Joslin 1966; Haber 1968; Carbyn 1974; Stephenson 1974; Stephenson and Ahgook 1975; Theberge 1975). Perhaps these litters were not found again because pups were moved relatively great distances.

### *Wolf Homesites Near Human Activity Centers*

In Mount McKinley National Park 11 of 12 dens known to be active since 1966 are located within 6.4 km of a human activity center (road or campground). The average distance to the human activity center for these 11 dens is 2.8 km and seven are within 2.4 km. The average distance from a human activity center for six dens known to be active in the Park since this study began in 1974 is 3.3 km and three are within 2.4 km.

Comparable distances reported by others include a den 2.8 km from a road (Stebler 1951), two dens 1.2 km from a trail, one of which was 2.8 and the other 3.2 km from a wilderness campground (Carbyn 1974), a rendezvous site 0.4 km from an occupied cabin (Stanwell-Fletcher 1942), and a rendezvous site located 0.8 km from a highway (Rutter and Pimlott 1968).

### *Relocation Movements of Wolf Litters During Summer*

In 1974 pups at the East Fork den were moved 0.3 km to a second den. Reported movements of pups from whelping dens to second dens have ranged from 0.3 to 11.2 km (average=3.0 km, n=14) (Bailey 1930; Murie 1944; Banfield 1954; Kelsall 1960; Wayman 1967; Haber 1968; Clark 1971; Carbyn 1974; Stephenson 1974). Sixty-four percent of these moves were less than 2.4 km.

Reported pup moves from dens to rendezvous sites, and between rendezvous sites, have ranged from 0.5 to 11.2 km (average=2.9 km, n=44) (Murie 1944; Joslin 1967; Kolenosky and Johnston 1967; Clark 1971; Voigt 1973; Carbyn 1974; Peterson 1974, present study). In 1975 between 8 July and 11 August tracks of pups from the Echooka den were observed as far as 21 km from the whelping den.

Movements to rendezvous sites early in summer are usually shorter than those later in summer. In 1976 pups on the Hulahula River were moved increasingly greater distances as the summer progressed (0.5, 0.5, 0.8, and 2.4 km). Early moves recorded by Joslin (1967), Carbyn (1974), and Peterson (1974) were shorter than succeeding ones.

### *Conclusions*

There are five factors which are important in determining the size of closed areas around wolf dens. First, in all reported cases wolves have not been known to detect other animals or humans by vision or by scent beyond 1.6 km. Second, most reported movements of pups following human disturbance have been from 1.6 to 3.2 km from the disturbance. Third, in most cases howling by wolves in response to human presence near pups occurred when the humans were within 1.4 km of pups. Fourth, wolves 0.8 km or more from their pups usually do not alter their behavior significantly upon detecting humans similar distances from pups. Finally, wolves regularly den within 2.4 km of established human activity centers in Mount McKinley National Park and other areas.

Based on these considerations, it would be unlikely for wolves to become disturbed if human activity were excluded within a 2.4 km radius of active dens. I consider this to be a minimum "safe" distance in tundra areas. A circle with this radius circumscribes a 18.1 $km^2$ area. In forest areas where visibility is restricted smaller closed areas may be adequate to protect active wolf dens. Conclusions reached by Stephenson (1974:25), based on his own knowledge of wolves and that of the Nunamiut Eskimos are pertinent

to this discussion and are quoted here:

> . . .[for] wolves that are generally shy of humans, such as those around Anaktuvuk, human presence. . . more than about two miles from the den for a limited period of time does not cause any significant alteration in the behavior of wolves. . . At distances less than this, prolonged presence may cause abandonment of the den . . . .

The guidelines discussed for the protection of whelping dens can be followed for secondary homesites. As discussed above, the length of occupancy is variable and sometimes of short duration, and movements between homesites can be quite substantial. In some cases secondary homesites may be used in two or more consecutive years and re-use in non-consecutive years has been noted (Voigt 1973; Carbyn 1974; Peterson 1974). It is usually very difficult, however, to predict with any certainty where wolves will move. In cases where the first move after wolves leave the whelping den is 2.4 km or less, the closed area around the whelping den may offer some protection.

If everyone was to observe the boundaries of a closed area, an area of the recommended size would be sufficient to protect wolves at homesites. Unfortunately, there are individuals who will attempt to photograph or observe wolves regardless of closed areas. The policy at Mount McKinley National Park is not to publicize the exact locations of wolf homesites. A vigilant observer, however, should be able to locate most dens in open country within a few days even if he remains outside a radius of 2.4 km. One solution to this problem is to make the closed areas asymmetrical by extending the boundaries to include larger areas that offer good hiking routes and exceptionally good visibility such as gravel bars. This would make it more difficult for a person to locate a den in a closed area. Another solution which is replete with public relations problems is to leave the reason for the closed area unannounced. These precautions would probably not be necessary in forest areas where visibility is restricted.

Is an area of approximately 18 $km^2$ manageable? In Mount McKinley National Park closed areas around active wolf dens are currently based on backcountry-unit boundaries. Six dens active since 1974 were located in temporary closed areas ranging between 72 and 99 $km^2$ in size. These closed areas are approximately four times the size recommended in this paper. The current closed areas are also of irregular shape, and, therefore, do not pinpoint dens. Since the boundaries of the backcountry-units are usually divides or rivers, and since overnight users of these units are assigned an area on a permit basis, such visitors can easily be directed away from backcountry-units containing active wolf dens. "WARNING - Hiking Prohibited - Special Wildlife Closure" signs are posted to deter day-hikers from entering den areas.

The closed areas around wolf homesites as established under current policies in Mount McKinley National Park appear to be manageable and are of more than sufficient size to protect denning wolves. A closed area successfully managed to protect grizzly bears in Mount McKinley National Park is 21 $km^2$ in size, but human access to the area is permanently restricted. It is not known if temporary closed areas of approximately 18 $km^2$ in size will prove manageable.

## LITERATURE CITED


BAILEY, V. 1930. Animal life of Yellowstone National Park. Charles C. Thomas, Springfield, Ill. 241 p.

BANFIELD, A. W. F. 1954. Preliminary investigation of the barren ground caribou. Part II. Life history, ecology, and utilization. Can. Wildl. Serv., Wildl. Mgmt. Bull. Ser. 1, No. 108. 112 p.

CARBYN, L. N. 1974. Wolf predation and behavioural interactions with elk and other ungulates in an area of high prey diversity. Can. Wildl. Serv. Rept. 233 p.

CHAPMAN, R. C. The effects of human disturbance on wolves (*Canis lupus* L.). M.S. Thesis, Univ. Alaska. (In preparation.)

CLARK, K. R. F. 1971. Food habits and behavior of the tundra wolf on central Baffin Island. Ph.D. Dissertation, Univ. Toronto. 223 p.

DANGERFIELD, S., E. HOWELL, and M. RIDDLE (eds.). 1971. The international encyclopedia of dogs. McGraw-Hill, Inc., New York. 480 p.

GARCEAU, P. 1960. Wolf population studies in southeastern Alaska. Alaska Dept. Fish and Game, Juneau, p. 445-457. (Ak. W-06-R-01/Wk. Pl. K/Job 01.)

HABER. G. C. 1968. The social structure and behavior of an Alaskan wolf population. M.S. Thesis, Northern Michigan Univ. 198 p.

JORDAN, P. A., P. C. SHELTON, and D. L. Allen. 1967. Numbers, turnover, and social structure of the Isle Royale wolf population. Am. Zool. 7:233-252.

JOSLIN, P. W. B. 1966. Summer activities of two timber wolf (*Canis lupus*) packs in Algonquin Park. M.S. Thesis, Univ. Toronto. 99 p.

_____. 1967. Movements and home sites of timber wolves in Algonquin Park. Am. Zool. 7:279-288.

KELSALL, J. P. 1960. Co-operative studies of barren-ground caribou 1957-58. Can. Wildl. Serv., Wildl. Mgmt. Bull. Ser. 1, No. 15. 145 p.

_____. 1968. The migratory barren-ground caribou of Canada. Can. Wildl. Serv., Ottawa. 340 p.

KOLENOSKY, G. B. and D. H. JOHNSTON. 1967. Radio-tracking timber wolves in Ontario. Am. Zool. 7:289-303.

KUYT, E. 1962. Movements of young wolves in the Northwest Territories of Canada. J. Mammal. 43:270-271.

LENTFER, J. W. and D. K. SANDERS. 1973. Notes on the captive wolf (*Canis lupus*) colony, Barrow, Alaska. Can. J. Zool. 51:623-627.

MECH, L. D. 1966. The wolves of Isle Royale. Fauna Natl. Parks U.S. Fauna Ser. 7. 210 p.

_____. 1970. The wolf: the ecology and behavior of an endangered species. The Natural History Press, New York. 384 p.

MURIE, A. 1944. The wolves of Mount McKinley. Fauna Natl. Parks U.S. Fauna Ser. 5. 238 p.

_____. 1961. A naturalist in Alaska. Devin-Adair Co., New York. 302 p.

PETERSON, R. O. 1974. Wolf ecology and prey populations on Isle Royale. Ph.D. Dissertation, Purdue Univ. 368 p.

PIMLOTT, D. H., J. A. SHANNON and G. B. KOLENOSKY. 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ont. Dept. Lands and Forests Res. Rep. (Wildl.) No. 87. 94 p.

PRUITT, W. O., JR. 1965. A flight releaser in wolf-caribou relations. J. Mammal. 46:350-351.

RAUSCH, R. A. 1967. Some aspects of the population ecology of wolves, Alaska. Am. Zool. 7:253-265.

RUTTER, R. J. and D. H. PIMLOTT. 1968. The world of the wolf. J. B. Lippincott, Philadelphia. 202 p.

SOPER, J. D. 1942. Mammals of Wood Buffalo Park, northern Alberta and District of Mackenzie. J. Mammal. 23:119-145.
STANWELL-FLETCHER, J. F. 1942. Three years in the wolves' wilderness. Nat. Hist. 49:136-147.
STEBLER, A. M. 1951. The ecology of Michigan coyotes and wolves. Ph.D. Dissertation, Univ. Michigan. 198 p.
STEPHENSON, R. O. 1974. Characteristics of wolf den sites. Alaska Dept. Fish and Game, Juneau. (Ak. W-017-R-02, 03, 04, 05, 06/Job 14.6R) 27 p.
STEPHENSON, R. O. and L. JOHNSON. 1972. Wolf report. Alaska Dept. Fish and Game, Juneau. (Ak. W-017-R-03/Jobs 14.3R, 14.4R, 14.5R, 14.6R.) 52 p.
_____. 1973. Wolf report. Alaska Dept. Fish and Game, Juneau. [AK. W-017-R-04/Jobs 14.3R, 14.4R, 14.5R, 14.6R, 14.7R; W-017-R-05/Jobs 14.3R, 14.4R, 14.5R, 14.6R, 14.7R (1st half)] 52 p.
STEPHENSON, R. O. and R. T. AHGOOK. 1975. The Eskimo hunter's view of wolf ecology and behavior, p. 286-291. *In* M. W. Fox (ed.) The wild canids: their systematics, behavioral ecology and evolution. Van Nostrand Reinhold Co. 508 p.
THEBERGE, J. B. 1975. Wolves and Wilderness. Dent Canada, Ltd., Toronto. 159 p.
THEBERGE, J. B. and D. H. PIMLOTT. 1969. Observations of wolves at a rendezvous site in Algonquin Park. Can. Field-Nat. 83:122-128.
VAN BALLENBERGE, V., A. W. ERICKSON, and D. BYMAN. 1975. Ecology of the timber wolf in northeastern Minnesota. Wildl. Monogr. No. 43. 43 p.
VAN BALLENBERGHE, V. and L. D. MECH. 1975. Weights, growth, and survival of timber wolf pups in Minnesota. J. Mammal. 56:44-63.
VOIGT, D. R. 1973. Summer food habits and movements of wolves (*Canis lupus* L.). in central Ontario. M.S. Thesis, Univ. Guelph. 76 p.
WAYMAN, S. 1967. A family of white wolves. Life 62:50-57, 59-60.
YOUNG, S. P. and E. A. GOLDMAN. 1944. The wolves of North America. Am. Wildl. Inst., Wash., D.C. 636 p.

# THE ROLE OF WOLF PREDATION IN A MOOSE POPULATION DECLINE[1]

Rolf O. Peterson[2]

Over the past decade and a half, intensive study of wolves both in the wild and in captivity has produced a wealth of knowledge about these controversial predators. As a result there has been a considerable public awakening to the value of wolves in ecosystems and increased interest in wolves themselves as fascinating creatures. Nonetheless, many people are concerned over competition between wolves and human hunters for limited or declining populations of big game, especially moose. There is the danger that such competition may lead to permanent wolf control programs that might eliminate wolves forever from large portions of their remaining range.

It is not entirely coincidental that several moose populations in Alaska and Canada have recently declined. A number of factors have contributed to synchronous changes in these populations. Fires during the first half of this century created thousands of square miles of young forests with abundant moose browse, leading to high moose populations during the 1950s and early '60s throughout much of their range (Krefting 1974a; Bishop and Rausch 1974; LeResche et al. 1974). Research indicated that, on good range, moose could be highly productive (Pimlott 1959; Simkin 1965), and this led to liberalized hunting regulations and greatly increased moose harvests (Bausch et al. 1974; Ritcey 1974). Moose hunting programs were usually governed by a desire to maximize yield to hunters and stimulate productivity (Ritcey 1974). This resulted in younger populations and heavy reliance on high annual calf crops to maintain moose density and human harvest (Cumming 1974; Addison and Timmerman 1974).

A series of severe winters in many parts of northern North America in the early 1970s resulted in critical shortages of food and led to malnutrition deaths, increased predation, and very low calf survival (e.g., Bishop and Rausch 1974; MacLennan 1974). These effects were especially serious for heavily hunted, young populations, since hard winters are particularly difficult for calves and young adults.

The moose population of Isle Royale National Park, a Lake Superior island, is not hunted and therefore has a more diverse age structure (Peterson 1974). Isle Royale moose were also heavily dependent on post-fire forests, but by the 1960s these seral communities had largely grown out of reach of the moose. Isle Royale experienced the same series of severe winters in the early 1970s, and the wolf population was quick to respond to increased moose vulnerability.

## STUDY AREA AND METHODS

The limited fauna of Isle Royale and its isolation from man create an ideal situation for predator-prey studies, and its wolves and moose have, since 1958, been the focus of a continuous study directed by Durward L. Allen of Purdue University (Mech 1966; Jordan, Shelton and Allen 1967; Wolfe and Allen 1973; Peterson 1974). Moose colonized the island in the early part of this century (Murie 1934), and, before the arrival of wolves from mainland Ontario, the moose ran a cycle of rapid growth followed by large losses from malnutrition (Mech 1966). Since the arrival of wolves in the late 1940s, predation has shaped the moose herd and large-scale die-offs have not occurred.

Wolves and moose are censused in midwinter from light aircraft. The major wolf packs are visually tracked in snow, and an attempt is made to maintain a continuous record of their movements and kills for at least 40 days each winter. Data obtained on an annual basis include a direct count of wolves in winter, analysis of their spatial and social organization and predation rates, and examination of a large number of moose carcasses, mostly wolf-kills.

## RESULTS AND DISCUSSION

Since the early 1960s, several factors have caused a general reduction in browse availability, especially in winter. The most important change, yet perhaps the most subtle, has been declining browse production in the 1936 burn, which covered one-fifth of the island (Krefting 1974b). High moose densities were recorded in this burn as recently as 1957 (Cole 1957) and 1960 (Mech 1966), but since that time moose have not made extensive use of the area except when snow depths were very low. Instead, moose have been forced to use more mature forest types, which are probably marginal habitats. Highest winter moose densities are now found in old forests with a high percentage of coniferous cover, especially balsam fir (Peterson 1974). Browse in these areas is very limited, however, and moose suffer nutritionally during winters of deep snow.

There are recent indications of increased nutritional stress and lower productivity among Isle Royale moose. The incidence of bone marrow fat depletion among calves in midwinter has increased since the early 1960s, malnutrition deaths have become more frequent (although still rare compared to frequency of wolf-kills), and productivity, as reflected in twinning rates, has declined during the same time period (Peterson 1974). All of these changes point to the critical role played by winter food supply in the dynamics of the moose population, an element that was not apparent during early years of the study when browse conditions were somewhat more favorable and winters were noticeably milder.

Winter severity on Isle Royale generally increased through the 1960s, culminating in a series of four hard winters beginning in 1969 (Figure 1). Winter precipitation records indicate that Isle Royale receives about 40% more snow than the nearby Minnesota mainland, and the high humidity and frequent thaws produced by the moderating effect of Lake Superior frequently produce local crusting conditions which greatly restrict moose mobility and generally aid wolves (Peterson and Allen 1974).

[1]Financial support for this study between 1970 and 1976 was provided by the National Park Service, Boone and Crockett Club, Carnegie Museum, Defenders of Wildlife, National Audubon Society, National Rifle Association, and National Science Foundation.

[2]Department of Biological Sciences, Michigan Technological University, Houghton 49931.




FIGURE 1. Total snowfall and index of snow depth at Grand Marais, Minnesota, 1959-74 (Peterson 1974).

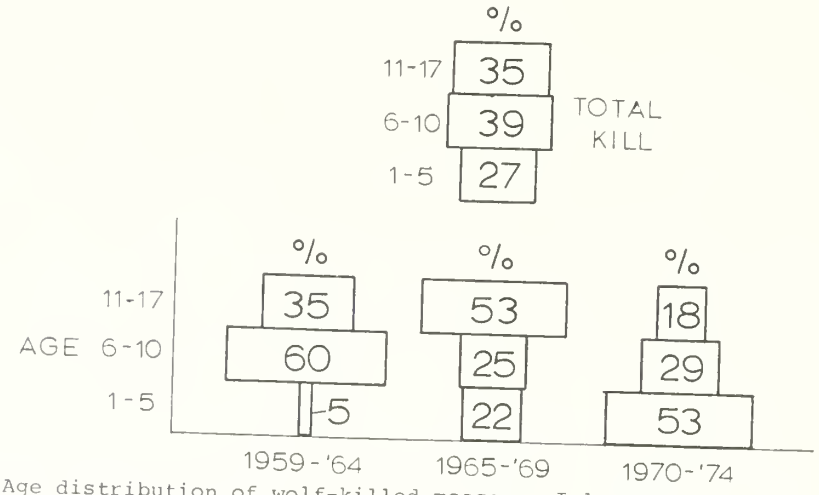



FIGURE 2. Age distribution of wolf-killed moose on Isle Royale, 1959-74 (Peterson 1974).

TABLE 1. Estimated number of wolves on Isle Royale in mid-winter, 1959-76.[a]

| Year | Best estimate | Year | Best estimate | Year | Best estimate |
|---|---|---|---|---|---|
| 1959 | 20 | 1965 | 28 | 1971 | 20 |
| 1960 | 22 | 1966 | 25 | 1972 | 23 |
| 1961 | 22 | 1967 | 22 | 1973 | 24 |
| 1962 | 23 | 1968 | 22 | 1974 | 31 |
| 1963 | 20 | 1969 | 17 | 1975 | 41 |
| 1964 | 26 | 1970 | 18 | 1976 | 44 |

[a]Data from Mech (1966, Jordan et al. (1967), Wolfe and Allen (1973), Peterson (1974 and unpubl. data).

## CHANGING PREDATION PATTERN

Beginning in 1969 we witnessed a rapid rise in vulnerability of calves and young adult moose to wolf predation in winter. Belly-deep snow rendered calves especially vulnerable; calves usually comprise 25-30% of all wolf-kills, but this proportion jumped to over 50% when snow depths exceeded 75 cm. Simultaneously, wolves suddenly began to kill large numbers of moose between the ages of one and six years. Moose in this age group comprised only 13% of all the kills examined before 1970, but this proportion rose to 53% between 1970 and 1974 (Figure 2).

Almost every one of the young adult moose killed by wolves in the early 1970s was born after a severe winter. It appears that they were unable to adequately defend themselves because of adverse long-term effects of malnutrition early in life, probably in the fetal stage. Bone measurements of calves indicate that moose born early in the 1970s were physically small at birth, and subsequently suffered from delayed growth and development (Peterson 1974). Variations in metatarsus length seem to depend primarily on prenatal nutritional plane (Palsson and Verges 1952), and there exists an approximately inverse relationship between winter severity and metatarsus length of Isle Royale moose calves (Figure 3).

During the same period when moose vulnerability was exceptionally high, wolves also preyed to a significant extent on beaver during the open water season. During the early 1970s beaver comprised about half of the total prey occurrences recorded in wolf scats (Peterson 1974). Reliance on beaver during summer tripled from the level recorded in the early 1960s, and beaver research by Philip C. Shelton (pers. comm.) indicated that during approximately the same period (1962-74) the beaver population doubled. Since moose calves, the principal age group killed by wolves during the summer, have become less available during this same period, beaver have consequently become an extremely important summer prey species.

## WOLF POPULATION RESPONSE

In the early 1970s Isle Royale wolves exhibited an immediate response to high moose vulnerability by increasing their kill rate. As kill rate went up, wolf utilization of carcasses declined, leaving a bonanza of food for scavenging foxes and ravens. During these years it was easier for wolves to kill another moose rather than dig out the frozen remains of an old carcass (Peterson and Allen 1974).

Surplus killing in the early 1970s was also shown by estimates of food availability for Isle Royale wolves in winter. These estimates are derived from known kill rates of wolves and estimated carcass weights. Using kill statistics from Mech (1966) for the period 1959-61 plus revised estimates of edible weights from each kill, each wolf in the original large pack on Isle Royale had 4-5 kg of food available per day (Figure 4). From 1971 through 1973 food availability for the two principal packs ranged from 6-10 kg per wolf per day. Since then this figure has fallen back to the more usual 5 kg/wolf/day.

The spatial organization of Isle Royale wolves has undergone radical change since 1970. Previously the population was typically a single large pack plus several smaller social units and loners. In 1959 and 1960 the large pack traveled over the entire island (Figure 5), but subsequently during the 1960s the primary pack limited itself to the southwestern two-thirds of the island (Jordan et al. 1967; Wolfe and Allen 1973). By 1971, evidently because of an abundant food supply, the territory of this pack (West Pack) had shrunk to less than half of the island, leaving the rest of the island to a number of wolf pairs and loners. The following year (1972) a new pack 8-19 wolves occupied this area, the result of a very successful litter of pups. This pack became known as the East Pack and by 1975 had grown to 18 wolves.

In 1975 a third major pack of 7 wolves appeared in the middle of the island, again resulting from successful raising of a litter of pups, and these 3 packs, plus a number of peripheral groups, persisted into 1976. In seven years the wolf population more than doubled, increasing from a low of 17 to a high of 44 (Table 1). Wolf density in 1976 was one per 12 $km^2$, one of the highest populations ever documented.

## IMPLICATIONS FOR THE MOOSE POPULATION

It has not been possible to accurately document changes in the number of moose on Isle Royale. Based on their work in the 1960s, Wolfe and Jordan (unpub. data) believed that the moose population may have been at a peak level in the late 1960s, with perhaps 1300-1400 animals present in 1969. Aerial counts in 1972 and 1974 indicated a mid-winter population of about 1000 moose (Peterson 1974). Aerial composition counts and mortality estimates since 1974 provided the basis for a midwinter estimate of 800-900 moose in 1976 (Peterson unpub. data). This suggests an overall decline of 30-40% between 1969 and 1976. The rate of decline of moose on Isle Royale has been substantially less than that of some heavily hunted moose populations in Alaska; in the early 1970s moose density declined about 50% over a four-year period in both Unit 20A south of Fairbanks (Region III Status Report, Alaska Department of Fish and Game) and the Kenai National Moose Range (Kenai National Moose Range files).

The ratio of wolves to moose on Isle Royale changed from about 1 wolf per 80 moose in 1969 to 1 wolf per 20 moose in 1976, a four-fold increase. While winter weather has moderated in recent years, calf production and survival remain at a very low level. Although predation is once again concentrated on the oldest age classes (Peterson unpub. data), kill rates remain high because of the high wolf population. With wolves at a peak, we expect the current rate of decline in the moose population to be maintained for the next few years. We also expect that the reduced prey base will eventually lead to a downward adjustment in the wolf population.

## CONCLUSIONS

In recent years we have seen a number of dramatic and surprising changes in the Isle Royale wolf population resulting from increased moose vulnerability. This is an ample illustration of the sensitivity to prey condition that is characteristic of wolf predation and of the variability that is possible in wolf-prey interaction. Although wolves can probably accelerate natural declines of ungulates, there is little or no evidence that wolves independently regulate prey populations. However, wolf predation has developed as an extremely efficient and repsonsive means of adjusting prey populations to their underlying resource base in a way that human hunters could never duplicate.

There has been a tremendous positive change in public attitude toward wolves in the past 10-15 years. Unfortunately, this change has occurred particularly in areas where there are no wolves left, and anti-wolf sentiment is still very strong where wolves and man compete for limited prey.

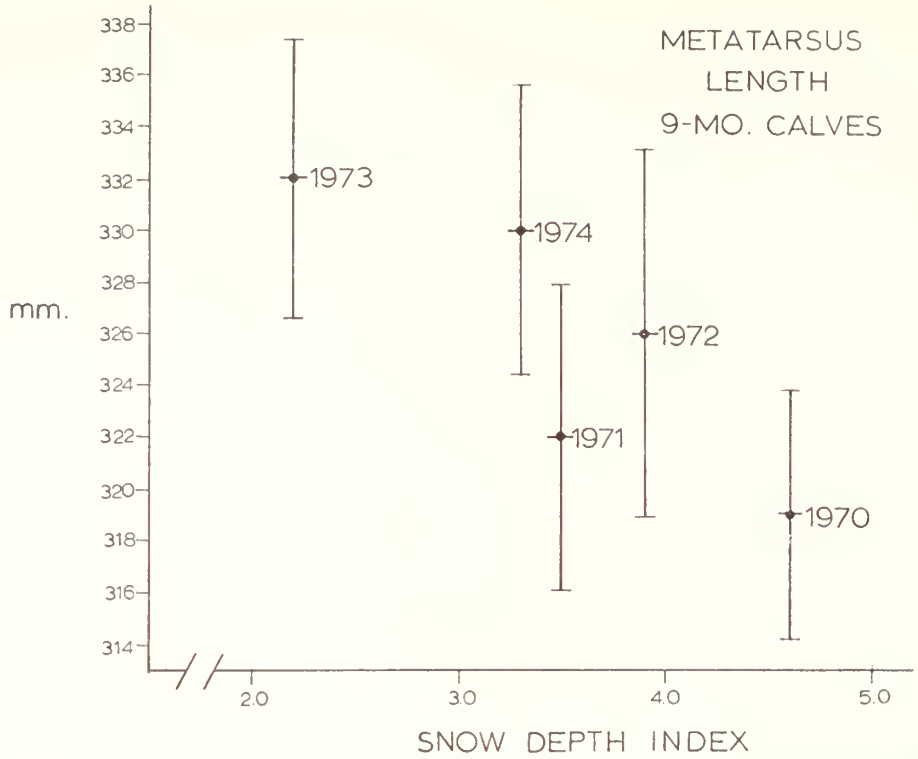



FIGURE 3. Isle Royale moose calf metatarsus length vs. index of snow depth for winter prior to birth of calf. Snow depth index corresponds to that in Figure 1. Mean metatarsus length and 95% confidence interval shown.

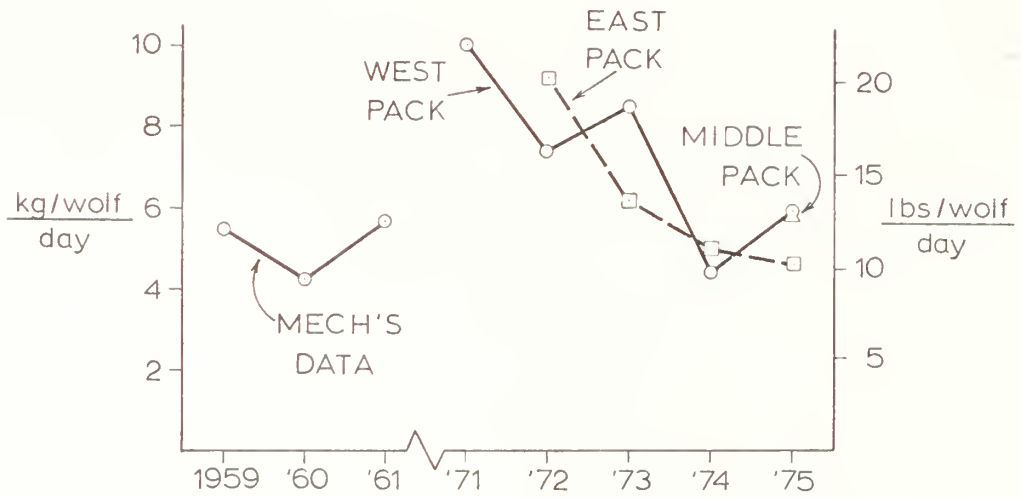



FIGURE 4. Food availability for Isle Royale wolves in midwinter. Method of calculation follows Peterson (1974).

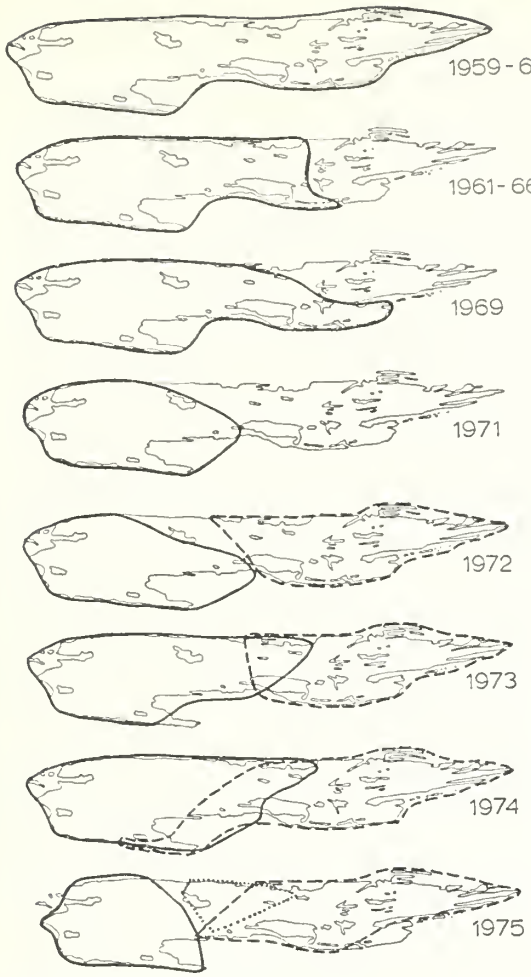



FIGURE 5. Spatial relationships of Isle Royale wolf packs in midwinter.

As we have seen, moose populations have declined in many parts of North America in the past decade because of habitat and weather factors, yet many people view wolves as the principal culprits. The seriousness of wolf-human competition is increasing rapidly as northern areas are opened up to development and large influxes of people. Wolves will survive in these areas only if people understand the importance of habitat and also respect the right of these predators to exist. This will require moose management programs that tolerate use by more than just human hunters, and hunting regulations that are flexible and sensitive to prey condition. If wolves are to persist, human hunters will inevitably have to accept lower harvests in many areas.

## LITERATURE CITED

ADDISON, R. B. and H. R. TIMMERMAN. 1974. Methods of aging and moose population analysis. Proc. 10th N. Am. Moose Workshop, Duluth, MN (in press).

BISHOP, R. H. and R. A. RAUSCH. 1974. Moose population fluctuations in Alaska, 1950-72. Naturaliste can. 101:559-593.

COLE, J. E. 1957. Isle Royale wildlife investigations, winter of 1956-57. Isle Royale National Park files. 42 pp (typewritten).

CUMMING, H. G. 1974. Moose management in Ontario from 1948 to 1973. Naturaliste can. 101:673-687.

JORDAN, P. A., P. C. SHELTON and D. L. ALLEN. 1967. Numbers, turnover, and social structure of the Isle Royale wolf population. Amer. Zool. 7(2):233-252.

KREFTING, L. W. 1974a. Moose distribution and habitat selection in North Centeral North America. Naturaliste can. 101:81-100.

_____. 1974b. The ecology of the Isle Royale moose with special reference to the habitat. Tech. Bull. 297, Forestry Ser. 15, Univ. of Minn. Ag. Exp. Sta., 75 pp.

LERESCHE, R. E., R. H. BISHOP and J. W. COADY. 1974. Distribution and habitats of moose in Alaska. Naturaliste can. 101:143-176.

MACLENNAN, R. 1974. Reasons for the decline in moose populations in Saskatchewan. Proc. 10th N. Am. Moose Workshop, Duluth, MN (in press).

MECH, L. D. 1966. The wolves of Isle Royale. U.S. National Park Service Fauna Series No. 7, 210 pp.

MURIE, A. 1944. The wolves of Mount McKinley. U.S. National Park Service Fauna Series No. 5, 238 pp.

PALSSON, G. and J. B. VERGES. 1952. Effects of the plane of nutrition on growth and development of carcass quality in lambs. Part I. The effects of high and low planes of nutrition at different ages. J. Agric. Sci. 42(1):1-92.

PETERSON, R. O. 1974. Wolf ecology and prey relationships on Isle Royale. Ph.D. thesis, Purdue University. 368 pp.

PETERSON, R. O. and D. L. ALLEN. 1974. Snow conditions as a parameter in moose-wolf relationships. Naturaliste can. 101:481-492.

PIMLOTT, D. H. 1959. Reproduction and productivity of Newfoundland moose. J. Wildl. Manage. 23:381-401.

RAUSCH, R. A., J. SOMERVILLE, and R. H. BISHOP. 1974. Moose management in Alaska. Naturaliste can. 101:705-721.

RITCEY, R. W. 1974. Moose harvesting programs in Canada. Naturaliste can. 101:631-642.

SIMKIN, D. W. 1965. Reproduction and productivity of moose in northwestern Ontario. J. Wildl. Manage. 28:740-750.

WOLFE, M. L. and D. L. ALLEN. 1973. Continued studies of the status, socialization, and relationships of Isle Royale wolves, 1967-70. J. Mammal. 54(3):611-635.

# SUMMER SCAVENGING ACTIVITY IN NORTHEASTERN ALASKA

Audrey J. Magoun[1]

## INTRODUCTION

Most biologists recognize that many species of animals, from lemmings to lions, are scavengers to some degree; yet, there has been relatively little scientific study of the scavenger role and of the conditions which govern scavenging activities.

With few exceptions, the most comprehensive studies on the role and the behavior of scavengers have been done in Africa.

The sporadic nature of scavenging activity and unpredictable sources of carrion in the Arctic reduce the chances for observing scavengers in this ecosystem; yet, the eastern Alaskan Arctic is one of the few areas in North America where natural predator-prey and predator-scavenger relationships still exist undistorted by intensive human activity and by "artificial" food supplies available to scavengers in recent human settlements.

It was the purpose of this study to describe scavenging activity at large mammal carcasses in the eastern Alaskan Arctic and to discuss factors which affect an animal's role as a scavenger and influence its activity patterns. A more comprehensive account than can be presented here of the study and the results may be found in Magoun (1976).

## STUDY AREA

### *Physiography and Vegetation*

The study was conducted during the summers of 1972 and 1973 in two adjacent areas essentially encompassing the upper Canning River drainage (Figure 1). This river is located on the Arctic Slope about 200 km west of the U.S.-Canadian border and flows north 161 km to the Arctic Ocean.

The habitat of the study area is typical of the northern foothills and mountains of the Arctic Slope. The major plant forms are ericaceous shrubs, willow, and sedges. Visibility was almost unlimited in the study area due to the lack of forested habitat.

## METHODS AND MATERIALS

### *Data Collection*

During the summers of 1972 and 1973, 15 large mammal carcasses were used for observing scavenging activity. Eleven of the animals were shot under special permit provisions made by the Alaska Department of Fish and Game and the U.S. Fish and Wildlife Service. An attempt was made to space these carcasses in time and distance to simulate a natural situation. Three additional carcasses were of animals that had died of natural causes; another was shot by a hunter.

Whenever a carcass was located, a green 4-man tent was set up at the most suitable vantage point for observation. The tent was located in a position that would allow good observation with a minimum of potential disturbance. A variable power Redfield scope (15x to 60x) and 10x40 Leitz binoculars were used to watch the carcass for the longest period of time possible. Observation distances ranged from 92 m to over 1.5 km. Detailed notes of all that occurred at the carcass or in the surrounding area were kept in field notebooks. The exact time of day was recorded before each entry in the notebook. Three observers were sometimes available, but only two observers were used most of the time. Mainly because of physical limitations and weather conditions, it was not possible to obtain a constant watch of the carcasses at all times. When the carcasses were not being watched continually, an attempt was made to check activity at the carcass at regular intervals. These intervals usually ranged from a few minutes to an hour.

Whenever possible, individuals of the same species at a carcass were identified in the notes and given a specific code number for data analysis.

### *Data Analysis*

The activity patterns for all scavengers were analyzed with the aid of a series of COBOL programs in 5-minute sections of observation time for each day of each carcass. For each 5-minute period, there is a record of all scavengers present with their respective activities in the vicinity of the carcass, the number of times certain activities occurred, and those activities which occurred simultaneously.

## RESULTS

Extended observations were made at 11 of 15 carcasses totaling 11,643 observation periods or approximately 970 hours of total observation time. Attempts to make observations during 999 potential periods were unsuccessful because the carcasses were obscured by rain, fog, snow, heat waves, or darkness. No observations were attempted during 11,752 additional potential observation periods. The observed activity by scavengers occurred during 30% of the total observation time (3,465 observation periods). There was no visible activity during 70% of the total observation time (8,179 observation periods). The majority of inactivity at a carcass occurred during the first days after a carcass became available, before scavengers had begun to feed on it. (A breakdown of actual observation time and activity time by carcass is given in Table 1.)

The nine species which scavenged at carcasses included four mammals (grizzly bear, wolf, red fox, and arctic ground squirrel) and five birds (golden eagle, raven, glaucous gull, long-tailed jaeger, and parasitic jaeger). The number of individual animals which visited the carcass vicinities varied from 3 to 12.

Not all of the animals that visited a carcass actually fed on it, and particular individuals spent much more time at the carcass than others.

Ravens, wolves, and bears each scavenged at over 50 percent of the 11 carcasses that were observed for extended lengths of time (100%, 72%, and 63% respectively). All other species scavenged at less than 30 percent of the carcasses (jaeger

[1]Cooperative Park Studies Unit, University of Alaska, Fairbanks 99701

and gulls, 27%; foxes and eagles, 18%; and ground squirrels, 9%). Ground squirrels could have been present at other carcasses without being seen, but this probably did not occur often, if at all.

Except for the red fox and the raven, the order of arrival at the carcass site of each scavenger species was variable. The red fox only visited two carcasses but was one of the first two scavengers to appear at these carcasses; the raven was the first species to arrive at 8 of 11 carcasses (73%) and was one of the first two species to arrive at 100 percent of these 11 carcasses.

An average of 1.25 days passed before a fox arrived at a carcass; for the raven, the average was 2.00 days (0.00-4.50). The average for glaucous gulls was 2.25 days (0.25-4.50), for bears 3.25 days (1.25-6.00), and for jaegers 3.50 days (2.50-4.75). Wolves averaged 3.75 days (0.50-7.50) and golden eagles 4.75 days (4.00-5.50). Ground squirrels visited only one carcass, arriving after 3.50 days.

For the particular species which I observed and at the numbers I observed them, the following hierarchy existed at the carcasses in descending order of dominance: single adult bear, sow with cub, wolf, adult eagle, immature eagle, adult raven, immature raven, glaucous gull, and jaeger. Foxes and ground squirrels were not seen at carcasses with other species.

The three major activities of scavengers at a carcass site are feeding, moving, or resting. The length of an average session of continuous feeding was nearly the same for all species, approximately 20 minutes. The average session of continuous movement not involving feeding varied from 7 minutes for the jaeger to 17 minutes for the glaucous gull. The average session of continuous resting was most variable, ranging from 10 minutes for the jaeger to 60 minutes for the grizzly bear.

The behavior of scavengers at a carcass site was influenced mainly by the presence or absence of other scavengers in the vicinity of the carcass. Some scavengers such as foxes and eagles avoided a carcass site if more dominant scavengers were present while others such as wolves, gulls, and ravens were more adaptable to the presence of dominant scavengers near a carcass.

The dominant animal was usually the largest individual present and it maintained its dominance by displaying an aggressive attitude. The more passive acts of aggression included raising the head and facing the subordinate, lifting the wings, opening the mouth toward the subordinate, and changing position at the carcass resulting in displacement of the subordinate. More active aggressive behavior included a lunge or short chase, a swipe with the paw, and actual bodily contact. Of 28 pairs of subordinate and dominant scavengers, 54 percent of the subordinates did not visit a carcass site or did not attempt to feed at all if a dominant scavenger was near the carcass (see Table 2).

Human presence or scent may also affect the behavior of scavengers at a carcass. Because carcass no. 3 had been handled by several people, the wolf that found the carcass was afraid to approach it and would not feed on it for over 39 hours. Over 65 percent of the wolf's time at the carcass site was spent lying down. Despite a plague of mosquitoes and a heavy rainstorm, it did not leave the carcass vicinity. Once it moved higher up the slope above the carcass where it lay down again. On several occasions it spent short periods investigating the area around the carcass site, sometimes catching mice and occasionally finding raven caches to eat. Only the awareness of an approaching grizzly, still a mile or more upstream, induced the wolf to start feeding on the carcass.

In addition to the three major activities of feeding, moving, and resting, minor or short term activities occurred of which caching and scraping were two of the most interesting.

Only two species of scavengers were observed catching meat from carcasses, the wolf and the raven. During 839 observation periods in which ravens were feeding, these birds made 382 caches or 1 cache per 2.1 observation periods. Wolves made 28 caches in 259 observation periods in which wolf feeding occurred or 1 cache per 9.2 observation periods.

The amount of caching activity is not always the same from one carcass to another. The rate of caching by ravens varied from one cache per 1.3 observation periods in which feeding occurred to one cache per 4.0 ovservation periods.

The rate of caching by wolves varied from one cache per 3.8 observation periods in which feeding occurred to one cache per 16.7 observation periods.

Of the total 382 caches made by ravens, 316 were cached away from the carcass (i.e., the raven flew to the caching location) and 66 caches (17%) were made in the proximity of the carcass (i.e., the raven walked, hopped, or glided to the caching location usually within 46 m of the carcass).

Wolves only made 1 of 28 caches (3%) in the proximity of the carcass (i.e., 46 m from the carcass).

Raven caches were made in several different types of locations. When a carcass was lying on a riverbed, ravens would often cache meat under pieces of flotsam or cover the caches with sand, small stones, or debris. They were seen caching meat on rocky hillsides, in sedge meadows, and among vegetation on moist slopes. It was not always possible to see whether ravens covered the caches with material, tucked it under vegetation or rocks, or merely left it partly exposed among the vegetation or rocks. But in many cases, ravens were definitely seen covering their caches with material.

Wolves nearly always cached meat in loose soil, usually along streams or sand bars or under willows. One wolf cached a legbone in a snowbed. The method used to cache meat was typical of many canids. A hole was dug with the forefeet, the meat placed in the hole, and soil or snow pushed over the meat with the nose.

Ravens carried food both in the bill and in a buccal pouch from which they later regurgitated it for caching. Wolves carried meat in the mouth and in the stomach and also regurgitated meat for caching.

Ravens generally made only one or two caches during a caching trip. Ravens at carcass no. 1 were timed during an extensive feeding session to determine the time required for a caching trip. The average for 15 caching trips was 120 seconds with 50 seconds being minimum and 206 seconds being the maximum time observed to complete a caching trip. During 2 of the 15 trips, two caches were made (averaging 172 seconds per trip) and during the remaining 13 trips, only one cache was made (average 105 seconds per trip). The actual time to make a cache once the raven was on

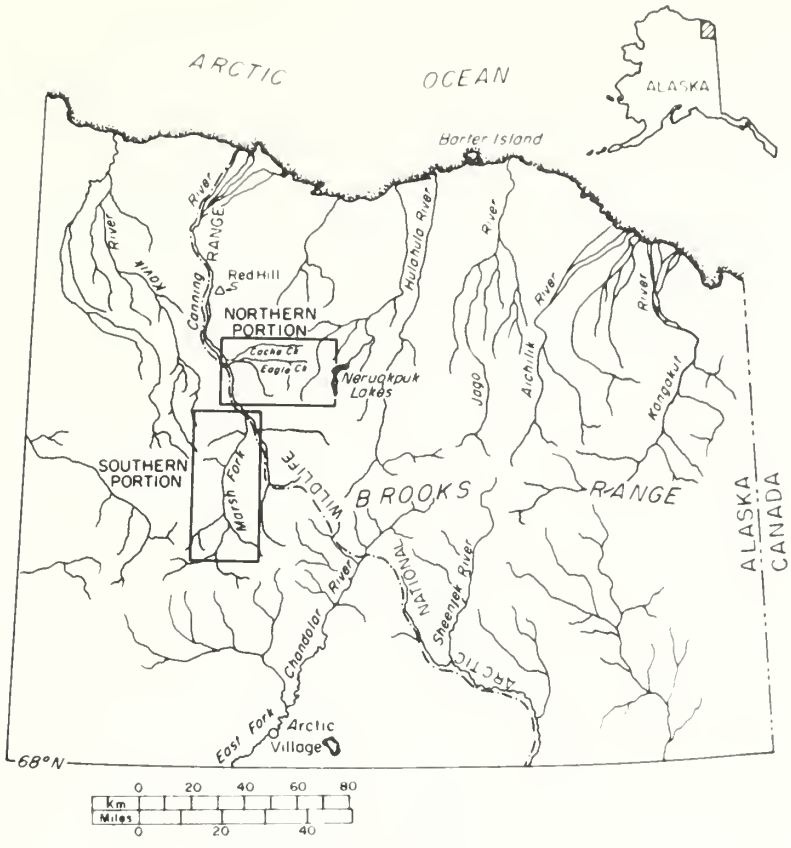



FIGURE 1. Study area.

TABLE 1. Summary of observation time and activity time for each carcass.[1]

| Carcass number | Total time of carcass (TTC) | Observation time (OBT) | OBT as % of TTC | No activity (NACT) | NACT as % of OBT | Activity (ACT) | ACT as % of OBT |
|---|---|---|---|---|---|---|---|
| 1 | 4,763 | 2,108 | 44 | 669 | 32 | 1,439 | 68 |
| 2 | 2,082 | 1,054 | 50 | 850 | 81 | 204 | 19 |
| 3 | 1,602 | 1,133 | 71 | 750 | 66 | 383 | 34 |
| 4 | 1,920 | 1,280 | 67 | 1,124 | 88 | 156 | 12 |
| 6 | 2,586 | 1,631 | 63 | 1,541 | 94 | 90 | 6 |
| 7 | 2,779 | 1,783 | 64 | 1,448 | 81 | 335 | 19 |
| 8 | 2,772 | 1,499 | 52 | 1,003 | 67 | 496 | 33 |
| 9 | 1,154 | 179 | 16 | 143 | 80 | 36 | 20 |
| 10 | 1,159 | 276 | 24 | 214 | 78 | 62 | 22 |
| 12 | 574 | 284 | 49 | 197 | 69 | 87 | 31 |
| 13 | 3,003 | 416 | 14 | 240 | 58 | 176 | 42 |
| | 24,394 | 11,643 | 48 | 8,179 | 70 | 3,464 | 30 |

[1]Observation time and activity time expressed in number of 5-minute observation periods.

TABLE 2. Feeding by subordinates while dominant scavengers were in the proximity of the carcasses.[1]

| Dominant | Subordinate: Jaeger | Gull | Raven | Eagle | Fox | Wolf | Bear |
|---|---|---|---|---|---|---|---|
| Bear | NV | NV | 0-1-38 (81) | NV | NV | 0-4-1 (173) | 16-8-9 (84) |
| Wolf | NV | NF (1) | 2-18-69 (119) | NV | NF | ---- (87) | |
| Fox | NV | NV | NV | NV | NV | | |
| Eagle | 0-0-1 (5) | NF (7) | 4-6-1 (11) | 0-1-0 (3) | | | |
| Raven | 1-0-1 (27) | 15-75 (51) | ---- (291) | | | | |
| Gull | 3-4-0 (33) | NF (4) | | | | | |
| Jaeger | ---- (22) | | | | | | |

[1]Calculations were not made for two wolves, two ravens, or two jaegers feeding together because subordinates and dominants were indistinguishable. These intraspecific pairs fed together without interference with each other.

( ) = Number of observation periods in which the pair was in the proximity of a carcass imultaneouslv.

1-2-3 = The first numeral is the number of observation periods in which the pair fed together at the carcass; the second is the number of observation periods in which the subordinate fed on carcass fragments while the dominant was in the proximity of the carcass; the third is the number of observation periods in which the subordinate fed on the carcass while the dominant moved or rested nearby.

NV = No visits to the carcass by the subordinate while dominant was present.

NF = No feeding by the subordinate while dominant was present.

the ground averaged 28 seconds and ranged from 15 seconds to 56 seconds.

Usually it was difficult to observe wolves caching because they often disappeared into willows or went out of sight behind a hill. On one occasion, one wolf made six separate caches during one caching trip after feeding for 20 minutes. All six caches were completed within 10 minutes after the wolf left the carcass. The caches were dug in sandy soil along the river about 137 m from the carcass. All but one were placed beneath willow bushes. At one of the caches, the wolf deposited three ti five pieces of meat in the hole before covering it over with sand.

Scraping refers to a bear's behavior of covering a carcass with vegetation and dirt scraped from the area around a carcass. Scraping occurred at four of eight carcasses that bears were known to have visited.

The way the bear covered the carcass with litter was usually by standing on the carcass and scraping material onto it or standing beside the carcass facing away from it and scraping material backward onto the carcass. Bears consistently used front feet for scraping.

Of the times the bear was observed scraping material onto the carcass, all but four occurred when a raven or wolf was nearby, and often the bear interrupted its scraping to chase the other species away. All four instances when the bear covered the carcass with litter when no other animal was nearby occurred just after the bear had fed on the carcass and before it begin a period of rest.

### *Carcass Disposal and Remains*

Usually within two to six days after a bear or wolf had found a carcass of a caribou, sheep, or bear, most or all of the meat had been consumed. Moose carcasses lasted 7 to 13 days. The average disposal time for all carcasses except the moose was about three days. The time depended upon the species and the number of scavengers as well as upon the amount of time the scavengers spent feeding. For example, the bear at carcass no. 6 did not feed for long periods of time and removed very little meat during its first feeding session. Therefore, the disposal time for this carcass was six days, the longest for any carcass except the moose.

The observers were close enough to only one carcass to observe the order in which the carcass parts were eaten; this was carcass no. 7, the

TABLE 3. Remains of the carcasses.

| Carcass number | Major scavengers | Total days of carcass | Number of days the scavengers fed on the carcass | Remains | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Pieces of hide | Hair | Lenbones-cracked | Legbones-not cracked | Skull intact | Skull in pieces | Lower jawbones | Spinal column intact | Pieces of vertebrae | Ribcage intact | Ribs disconnected | Scapula | Pelvic bones | Remaining meat |
| 1 | Bears Wolves | 13 | 12 | | | | | | | | | | | | | | |
| 2 | Bears Wolves | 7 | 4 | | | X | X | | | X | | | | X | X | | N |
| 3 | Wolf | 5 | 3 | | | | | * | | | * | | * | | | X | S |
| 4 | Bears | 5 | 2 | | | | X | | X | | | X | | X | X | | N |
| 5 | Bear | No observations | | | | X | | X | | X | | X | | X | X | | M |
| 6 | Bear | 10 | 6 | X | | | X | | | | | | | | | | S |
| 7 | Wolves | 9 | 3 | X | | | X | * | | | * | | * | | | | N |
| 8 | Avian Scavengers | 10 | 10 | X | | | X | * | | | * | | * | | X | X | M |
| 9 | Bear | 4 | 2 | X | | | X | | | | | X | | X | | X | N |
| 10 | Bear Wolves | 5 | 4 | X | | | X | | | | | X | | X | X | | S |
| 11 | Wolf? | No observations | | X | | | | * | | | * | | * | | | | N |
| 12 | Wolves | 2 | 2 | | | | | | | | * | | * | | | X | S |
| 13 | Wolves | 9 | 2 | | | | | * | | | * | | * | | | | N |
| 14 | Bear Wolves | ? | 7 | X | | | X | * | | | * | | * | | | | M |
| 15 | Wolves | 3 | 3 | | | | X | | | | * | | * | | | | N |

N = No meat remaining.

S = Small amount of meat remaining (less than 10%).

M = Meat still remaining in some quantity (approximately 10-20%).

* = Parts of the carcass remaining nearly intact.

majority of which was eaten by two wolves. There was no obvious pattern in the order in which the various parts of this carcass were removed. The wolves indiscriminately fed on the meat of the backbone and ribcage, legs, and viscera, alternating frequently from one portion to another. The meat of the neck and head was some of the last to be eaten. Pieces of the hide were eaten throughout the duration of the observation time.

The parts of the carcasses that remained at a carcass site after most meat was removed varied from one carcass to another. (Table 3 is a list of all the carcasses and the parts that were found at the site.) I found no remains at all at carcass no. 1 though I searched the area thoroughly. The odor of decay and of bear excrement was evident. Some areas were found where the bears had scraped dirt and vegetation onto the carcass.

Except for carcass no. 14, none of the carcasses fed on by bears had an intact skull, spinal column, or ribcage, including those checked only two days after the bear began feeding. The bear at carcass no. 14 was shot by hunters before it had removed most of the meat from the carcass.

Those carcasses that were fed on by wolves but not by bears (carcasses no. 3, 7, 11, 12, 13, and 15) had the major portion of the spinal column and ribcage still intact. Even carcass no. 13, a sheep carcass weighing 45 kg or less had an intact ribcage after the wolves had removed most of the meat. All but two of the carcasses also had most of the skull intact. The skull was removed from carcass no. 15 by hunters. The skull of carcass no. 12 was not visible when the site was checked with a spotting scope; the observers could not reach the site due to high water in the river at that time.

## CONCLUSIONS

Through my own observations and from information obtained in the literature, I arrived at these conclusions concerning summer scavenging activity in northeastern Alaska.

1) Bears and ravens are the major scavengers on the Arctic Slope of the eastern Brooks Range. Wolves have high potential as a scavenger but probably have few opportunities to scavenge on large mammal carcasses in the study area. Red foxes, golden eagles, glaucous gulls, long-tailed and parasitic jaegers, and arctic ground squirrels are among the minor scavengers. Other species such as the wolverine and the gray jay are so few in numbers that they are insignificant scavengers in the area.

2) Because ungulate populations are only sporadically abundant in this area of the Brooks Range, carrion is not plentiful and most frequently becomes available as a result of wolf and occasionally bear predation. Large mammal carcasses which become available from causes other than predation must still be opened by the larger scavenger before the smaller, particularly the avian scavenger, can feed on the flesh.

3) The degree to which carcasses are utilized by the various scavengers is an indication of the scarcity or abundance of prey and alternate food resources.

4) Scraping litter onto carcasses is a means by which bears inhibit other scavengers from gaining access to the flesh of the carcass.

5) Carrion is most important to the grizzly in the spring and fall and to the raven in the winter; little else is available as food for these species during those seasons.

6) Though ravens are predatory to some extent, most of the flesh in their diet is probably carrion. The numbers of ravens in the area are directly related to the predator population that provides this carrion.

7) Wolves and ravens do not make the maximum number of caches possible from the carcasses they visit; there may be an upper limit to the number of caches these species will make regardless of the scarcity or abundance of carrion. Ravens distribute their caches within several specific areas; they later revisit the areas and relocate the caches through a "trial and error" method of search.

8) Red foxes are not important scavengers during the summer; alternate sources of food are abundant making scavenging unnecessary, and carcasses are avoided due to the potential harrassment by wolves. Foxes are likely to scavenge more often during winter months.

9) Carrion is likely to be an important source of food for golden eagles during early spring when they first arrive in the Arctic, but this raptor does not depend on scavenging during summer months. Alternate food supplies are plentiful enough to make scavenging an unnecessary strategy for the glaucous gull. Scavenging by glaucous gulls does not occur in areas away from the larger bodies of water, and does not appear to be an important method of obtaining food. Jaegers also do not rely on scavenging in the study area but scavenging may be important during some years.

10) The behavior of scavengers at carcass sites is particularly influenced by competition with other scavengers, by human interference, and by alternate food supplies.

## LITERATURE CITED

MAGOUN, A. J. 1976. Summer scavenging activity in northeastern Alaska. Unpubl. M.S. Thesis. Univ. Alaska. 168 p.

# PRODUCTION OF AQUATIC MACROPHYTES AND ITS UTILIZATION BY MOOSE ON ISLE ROYALE NATIONAL PARK[1]

Robert W. Aho and Peter A. Jordan[2]

There may be little sodium available for herbivores living in regions where sodium is mostly leached from the soil and where marine aerosols have no influence; inability to obtain an adequate supply of this essential macronutrient may limit further growth of herbivore populations. In their initial measurements of mineral flux within the Isle Royale soil-vegetation-moose system, Jordan et al. (1973) and Botkin et al. (1973) concluded that woody plants, which comprise some 85% of the diet of moose, provide less than 14% of their estimated annual sodium requirement. On the other hand, they found that aquatic macrophytes contained from 50 to 500 times as much sodium as terrestrial vegetation in the same watershed. Because moose feed extensively on aquatic macrophytes and no other sufficient source of sodium intake was identified, they concluded that aquatics are the moose's primary source of sodium. This led to further questions: 1) What is the net production or standing crop of aquatic macrophytes in aquatic habitats used by moose? 2) What portion of standing crop is removed by moose each year? 3) Does the sodium concentration in aquatics vary with time, location, taxa, or life form, and do patterns in aquatic feeding by moose correlate with such variations? 4) What is the impact of moose grazing on short- and long-term productivity of aquatic macrophytes? and 5) How do moose maintain sodium homeostasis during the 9-10 months when they do not eat or do not have access to aquatics?

This paper presents estimates of production of aquatic macrophytes and its utilization by moose based on exclosure experiments. It discusses the implications of current removal rates with respect to future productivity of aquatics and to the potential limitation of the moose population because of declining sodium availability. Associated studies, to be reported elsewhere, include the inventory of aquatic macrophyte biomass throughout the Park, further determinations of sodium concentrations in plants, and sodium dynamics in moose.

## STUDY AREA

Isle Royale National Park is a 550-km$^2$ archipelago located in northwestern Lake Superior about 30 km off the Ontario shore. Vulcanism, tectonic movements of the earth's crust, glaciation, and a large beaver (*Castor canadensis*) population have created a diverse abundance of aquatic habitats (Huber 1975; Shelton 1966). Summers are generally cool and moist; ponds are frozen from November through April. Above normal temperatures and below normal precipitation prevailed during May through September 1976.

Moose immigrated from Canada to Isle Royale in the early 1900's and underwent an irruptive growth followed by declines and general instability. Wolves (*Canis lupus*) arrived, also from Canada, about 1948 and appeared to have a stabilizing effect upon the moose (Mech 1966). Nevertheless there have been some recent increases from an estimated 600 in 1960 (Mech 1966) to 1500 in 1970 (Wolfe and Jordan, submitted). Peterson (1974, 1977) estimated a population of about 1000 moose in 1974, and has since observed trends of low calf production, high winter predation rates, and low recruitment; he estimated the 1976 pre-partum population to be 800.

Beaver ponds of two drainages at the western end of Isle Royale had been used by J. C. Cannon (unpublished data) for studies of moose grazing in 1973, and there remained remnants of several moose exclosures that he constructed. We selected these pond systems, both of which are used extensively by moose, as study sites: they are convenient to our camp, previous data were accumulated for them, and we could incorporate some exclosure remnants. The flow rates and other characteristics of the sites are representative of the variation among beaver ponds on Isle Royale. Grace Creek Pond is a 1.5-ha, active beaver pond on Grace Creek, a major drainage with a relatively constant flow. Located in a mature yellow birch (*Betula lutea*) forest, it has water depths up to 1.5 m, noticeable current, substrates of fine gravel or as much as 1 m of silt, numerous sedge-grass hummocks, and standing and fallen snags. Dominant macrophytes are nitella (*Nitella flexilis*) and red pondweed (*Potamogeton alpinus*). The other study site, "Coastal Pond," is a contiguous pair of active beaver ponds totaling about 0.8 ha on an intermittent stream north of outer Washington Harbor. Located in a forest of white spruce (*Picea glauca*), balsam fir (*Abies balsamea*) and paper birch (*Betula papyrifera*), it has water depths up to 1.5 m, negligible current, 0.1-1-m deep silt subtrates, sedge-grass hummocks, and standing and fallen snags of mostly speckled alder (*Alnus rugosa*). Dominant macrophytes are slender pondweed (*Potamogeton pusillus*) and (*Nitella flexilis*).

## METHODS

Within each study pond, four experimental blocks of 10-200 m$^2$ were selected. Location and size of two of the four were determined by Cannon's exlosure remnants that tended to extend from shore to deeper water. The other two blocks were randomly located away from shore in deeper water, but their size was assigned arbitrarily.

Blocks comprised an exclosure (treatment) unit paired with an unprotected (control) unit. Where exclosure remnants were reconstructed, an adjacent, unfenced area of equal size was designated; where new exclosures were established, a fence was constructed around one randomly-selected half of the block. Paired units appeared to have similar biotic and abiotic characteristics. Exclosures were constructed of rectangular-mesh hog wire nailed to pulp logs which had been collected from Lake Superior beaches, packed into the ponds, and sledge-hammered into the substrate at 2.5-3.0-m intervals. These heavy-duty posts (ca. 15cm diam. by 2.4 m) were used because the previous

[1]We thank the National Park Service and the University of Minnesota Agricultural Experiment Station for funding; John M. Morehead, Superintendent, and the staff of Isle Royale National Park for their extensive cooperation and logistical support; David V. Hinkley for statistical advice; and Walter R. Amble, Louanne S. Ditchett, Bruce Folley and Kraig A. Klungness for field assistance.

[2]Department of Entomology, Fisheries, and Wildlife, University of Minnesota, St. Paul 55108.

exclosures, which had incorporated trunks of locally-available speckled alder, had been broken by moose. A layer of poultry wire was added to six of the eight exclosures to discourage moose from probing with hooves and antlers. The "Coastal Pond" and Grace Creek Pond exclosures were completed by 30 June and 12 July 1975 respectively.

Standing crops in paired exclosure and control units was sampled simultaneously at the time of presumed annual maximum of biomass (late August-early September). Sample plots and the transects on which they were located were determined by systematic randomization; inter-transect distance was 1.0 m and inter-plot distance was 0.5 or 1.0 m in proportion to unit size. At each sample point, a 0.12-$m^2$, circular, metal frame was placed on the bottom, and all plants rooted within it were pulled up by hand. This procedure simulated aquatic grazing by moose; the samples contained foliage, tubers, rhizomes, roots, winter buds, seeds, and inorganic and dead organic material. The researcher wore a wet suit, weight belt, mask, snorkel, and fins or boots. Sampling was essentially done "blind" by the tactile sense because turbidity limited visibility.

In 1975, samples were sorted by species for drying and weighing. This proved unduly time consuming, and, because our data suggested that moose grazing is unselective, samples were not sorted in 1976; species were simply identified and ranked by abundance by visual inspection. In both years, samples were cleaned of inorganic and dead organic material by agitating them in the water and removing remaining pieces by hand. [While eating aquatics, moose do ingest some of this material--fragments of mostly terrestrial foliage and twigs, plus organic detritus, and some inorganic sediments--which contains up to 300 ppm sodium (Jordan et al. 1973). In summer 1976, Hennings and Jordan (in prep.) observed moose in northeastern Minnesota that were apparently feeding solely on the bottom material.] Samples were transported to camp in airtight plastic bags to prevent decomposition, transferred to paper bags, oven-dried at 75-100 degrees C for at least 48 hours, and weighed to the nearest 0.1 g.

Secchi disk transparencies (Ruttner 1963) were measured at "Coastal Pond" and Washington Creek during 18-19 June 1975.

## RESULTS

### *Production and Utilization*

Our observations indicate that the annual maximum of biomass occurs during late August-early September; therefore the aquatic macrophytes were measured at that time. The standing crop that we sampled approximates total biomass in that it includes foliage, seeds, winter buds, and tubers, rhizomes, and roots within about the top 15 cm of substrate. Little foliage persists from the previous growing season (mostly *Nitella* and *Chara*), and because that which does probably decays before the annual maximum biomass, the maximum standing crop in exclosure units gives a good estimate of annual net production (Wetzel 1965; Westlake 1965). The maximum standing crop in control units is a measure of net community production: net primary production minus heterotrophic consumption (Odum 1971:43). Thus the average difference between standing crop of exclosure and control units estimates utilization of macrophytes by moose.

Exclusion of moose appeared to account for a marked increase in standing crop. Despite variations between and within ponds and between years, peak standing crop of macrophytes was significantly and consistently greater in exclosure units than control units ($P < 0.001$, Table 1). In Coastal Pond this was accompanied by a significant increase in the frequency of *Potamogeton pusillus* and *Lemna minor* in exclosures, as well as a significant decrease in the frequency of plots devoid of vegetation ($P < 0.005$ and $P < 0.05$, Table 2). In Grace Creek Pond, however, frequency of plant species and empty plots did not differ significantly between exclosures and controls (Table 3). The paired units in both beaver pond systems were intensively sampled: plots comprised an average of 24% and 17% of a unit's area in 1975 and 1976 respectively (Table 4).

### *Between- and Within-Site Differences*

Production of macrophytes was significantly greater in Grace Creek Pond than in Coastal Pond ($P < 0.05$ in 1975, $P < 0.01$ in 1976, Table 1), resulting perhaps from one or both of the following: 1) Higher flow rates in Grace Creek may increase the supply of photosynthetic metabolites, carbon dioxide and bicarbonate ions (Westlake 1975:111-112); and 2) Allochthonous sources of organic nutrients, leaves and woody materials from the surrounding forest, may differ in quality and/or quantity (Ruttner 1963:191).

Production of macrophytes also varied significantly within the ponds, i.e., among the experimental blocks ($P < 0.05$ or $P < 0.01$, Table 5), resulting perhaps from variations in microclimate, soils, hummock density, and/or previous herbivory.

### *Inter-Year Differences*

Standing crop increased significantly from 1975 to 1976 in both exclosure and control units ($P < 0.001$, Table 1). One or both of the following factors may have been operative, although individual effects cannot be separated: 1) The warmer, longer 1976 growing season probably favored more growth in both exclosure and control units; and 2) A reduced intensity of moose grazing, associated with the decline in moose numbers, may have contributed to higher standing crops in control units.

Protection in 1975 probably resulted in increased production and survival of propagating structures (seeds, winter buds, roots, rhizomes, tubers; and oogonia of *Nitella* and *Chara*) to initiate new growth in 1976; the higher number of propagating structures probably accounted for a substantial portion of the increased standing crop in exclosure units in 1976. Such a phenomenon would have resulted in a greater 1976 standing crop in exclosure units than in control units even in the absence of moose grazing in the latter in 1976. Therefore the apparent removal of macrophytes by moose in 1976 (Table 1) is more correctly an index of the cumulative impact of moose on aquatic macrophytes.

### *Grazing Selectivity*

In two of the three blocks where moose had a choice between two species of plants, species were removed in proportion to their availability in 1976. However, moose appeared to select *Chara vulgaris* and *Potamogeton alpinus* in Block 4 of Grace Creek Pond ($P < 0.025$, Table 6). We believe that in this block, distribution and growth form are such that harvestability of the two species is similar. The apparent selection would not maximize sodium intake; *C. vulgaris* contained 534.0 ± 162.5 ppm NA, whereas *P. alpinus* contained 3346.0 ± 323.1 ppm (mean ± SE, n = 5 samples of each species). However, *C. vulgaris* may be a superior source of calcium, having greater external deposits of $CaCO_3$ on the plants than *P. alpinus*; perhaps it

TABLE 1. Peak standing crops of aquatic macrophytes in Grace Creek Pond and Poastal Pond, and its estimated removal by moose in 1975 and 1976 (Mean ± SE).

| Study site and year | No. samples[a] | Peak standing crop ($g/m^2$)[b] Exclosure | Control | Estimated removal by moose ($g/m^2$)[c] | % removed |
|---|---|---|---|---|---|
| Grace Creek | | | | | |
| 1975 | 116 | 84.9±17.4 | 31.4±11.1 | 53.5± 9.3 | 63.0 |
| 1976 | 242 | 268.7±50.7 | 70.7±20.8 | 198.0±13.0 | 73.7 |
| Coastal | | | | | |
| 1975 | 246 | 13.7± 8.8 | 1.0±0.6 | 12.7±2.1 | 92.6 |
| 1976 | 284 | 54.2±23.5 | 2.4±0.4 | 51.7±3.2 | 95.4 |

[a]Distributed among 3 (1975) or 4 (1976) blocks. See Table 4 for details of sampling.

[b]The variance of the mean is estimated from the analysis of variance based on the random effects model (Table 5); it is the mean square between blocks divided by the total number of samples (Snedecor and Cochran 1967:281), divided by the sample plot size. Differences between exclosure and control units, and within study sites-between years are significant ($P < 0.001$), by a t test of the form

$$t = \sum_{j=1}^{J} (\bar{A}j - \bar{B}j) / \sqrt{\sum_{j=1}^{J} [(SE(\bar{A}j))^2 + (SE(Bj))^2]} \text{ with } df = n-J$$

where J = number of blocks sampled

$\bar{A}j$ = mean standing crop in unit A of block j

$\bar{B}j$ = mean standing crop in unit B of block j

Because df > 50, t was compared with the normal (z) distribution to determine the level of significance.

Differences within years-between study sites are significant (t test of independent samples; $P < 0.05$ in 1975, $P < 0.01$ in 1976).

[c]See Inter-Year Differences of RESULTS for clarification of 1976 data.

TABLE 2. Frequency (%) of aquatic-macrophyte species present in plots in exclosures (E) and in controls (C) in Coastal Pond, 1975 and 1976.[a]

| | Frequency of species | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Occurring alone | | Ranked 1 | | 2 | | 3 | | Total | | Chi-square |
| Year and species | E | C | E | C | E | C | E | C | E | C | (1 df) |
| 1975 [n = 136 (E) and 110 (C)] | | | | | | | | | | | |
| Potamogeton pusillus | 45.2 | 33.6 | 19.0 | 7.3 | 3.6 | 3.6 | 0.0 | 0.0 | 67.8 | 44.5 | 13.54** |
| Lemna minor | 0.0 | 0.9 | 0.0 | 0.0 | 14.6 | 6.4 | 0.7 | 0.0 | 15.3 | 7.3 | 3.77 |
| Nitella flexilis | 4.4 | 7.3 | 3.6 | 3.6 | 4.4 | 0.0 | 0.0 | 0.0 | 12.4 | 10.9 | 0.13 |
| Callitriche palustris | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.7 | 0.0 | 0.7 | 0.0 | c |
| Equisetum fluviatile | 0.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.9 | 0.7 | 0.0 | 1.4 | 0.9 | c |
| Empty plots | | | | | | | | | 27.0 | 47.3 | 10.07** |
| 1976 [n = 142 (E) and 142 (C)] | | | | | | | | | | | |
| P. pusillus | 23.7 | 29.5 | 39.1 | 14.0 | 3.4 | 4.2 | 0.0 | 0.0 | 66.4 | 47.8 | 10.02** |
| L. minor | 6.2 | 16.1 | 2.7 | 0.0 | 34.2 | 7.7 | 9.7 | 0.7 | 53.2 | 24.6 | 24.43** |
| N. flexilis | 1.3 | 3.5 | 5.5 | 4.2 | 4.1 | 2.8 | 0.0 | 0.0 | 11.1 | 10.5 | 0.33 |
| Sparganium chlorocarpum | 2.0 | 0.7 | 0.6 | 1.4 | 0.6 | 0.0 | 2.0 | 0.0 | 5.5 | 2.1 | 2.24 |
| C. palustris | 0.0 | 0.0 | 0.0 | 0.0 | 4.1 | 5.6 | 1.3 | 0.7 | 5.5 | 6.3 | 0.06 |
| Empty plots | | | | | | | | | 14.6 | 23.9 | 3.9 * |

[a]Data are separated by plots according to whether the species occurred alone, or, if with other species, it was ranked 1 through 3 in decreasing order of abundance among species in the plot.

[b]$P = 0.053$.

[c]Not testable; expected values are less than 5.

*$P < 0.05$.

**$P < 0.005$.

TABLE 3. Frequency (%) of aquatic-macrophyte species present in plots in exclosures (E) and in controls (C) in Grace Creek Pond, 1975 and 1976.[a]

| Year and species | Frequency of species: Occurring alone | | Ranked 1 | | Ranked 2 | | Ranked 3 | | Total | | Chi-square (1 df) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | E | C | E | C | E | C | E | C | E | C | |
| 1975 [n = 58 (E) and 58 (C)] | | | | | | | | | | | |
| Nitella flexilis | 60.3 | 65.5 | 17.2 | 12.1 | 0.0 | 0.0 | 0.0 | 0.0 | 77.5 | 77.6 | 0.0002 |
| Potamogeton alpinus | 1.7 | 0.0 | 0.0 | 13.8 | 25.9 | 8.6 | 0.0 | 0.0 | 27.6 | 22.4 | 0.41 |
| Chara vulgaris | 3.4 | 1.7 | 17.2 | 3.4 | 0.0 | 13.8 | 0.0 | 0.0 | 20.6 | 18.9 | 0.05 |
| Sparganium chlorocarpum | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.7 | 0.0 | 1.7 | 0.0 | b |
| Callitriche palustris | 0.0 | 0.0 | 0.0 | 0.0 | 1.7 | 5.2 | 0.0 | 0.0 | 1.7 | 5.2 | b |
| Empty plots | | | | | | | | | 0.0 | 3.4 | b |
| 1976 [n = 123 (E) and 119 (C)] | | | | | | | | | | | |
| N. flexilis | 54.0 | 62.2 | 33.1 | 22.7 | 0.0 | 2.5 | 0.0 | 2.5 | 87.1 | 89.9 | 0.46 |
| P. alpinus | 0.0 | 0.0 | 11.3 | 13.4 | 25.0 | 14.3 | 1.6 | 0.8 | 37.9 | 28.5 | 2.40 |
| C. vulgaris | 0.0 | 0.0 | 0.8 | 0.0 | 11.3 | 12.6 | 0.0 | 0.0 | 12.1 | 12.6 | 0.01 |
| S. chlorocarpum | 0.0 | 0.0 | 0.0 | 1.7 | 4.0 | 2.5 | 0.8 | 2.5 | 4.8 | 6.7 | 0.40 |
| C. palustris | 0.0 | 0.0 | 0.0 | 0.0 | 3.2 | 4.1 | 1.6 | 0.0 | 4.8 | 4.1 | 0.07 |
| Utricularia sp. | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.8 | 3.2 | 0.0 | 3.2 | 0.8 | b |
| Equisetum fluviatile | 0.0 | 0.0 | 0.0 | 2.5 | 1.6 | 4.2 | 0.8 | 0.8 | 2.4 | 7.5 | 3.36 |
| Empty plots | | | | | | | | | 0.8 | 0.0 | b |

[a]Data are separated by plots according to whether the species occurred alone, or, if with other species, it was ranked 1 through 3 in decreasing order of abundance among species in the plot.
[b]Not testable; expected values are less than 5.

TABLE 4. Intensity of sampling in paired exclosure and control units in Grace Creek Pond and Coastal Pond, 1975 and 1976.

| Study area & Block | Area of unit ($m^2$) | Mean no. of plots harvested from unit: 1975 | 1976 | Sampling fraction: 1975 | 1976 |
|---|---|---|---|---|---|
| Grace Creek Pond | | | | | |
| 1 | 5.2 | 15 | 12 | .36 | .27 |
| 2 | 16.7 | 30 | 20 | .22 | .14 |
| 3 | ca. 100 | - | 74 | - | .09 |
| 4 | 8.1 | 13 | 15 | .20 | .22 |
| | Total | 58 | 121 | Mean .26 | .18 |
| Coastal Pond | | | | | |
| 1 | 11.2 | 25 | 17 | .28 | .18 |
| 2 | 9.3 | 16 | 15 | .22 | .19 |
| 3 | ca. 20 | - | 24 | - | .14 |
| 4 | 79.5 | 82 | 86 | .13 | .13 |
| | Total | 123 | 142 | Mean .21 | .16 |
| | | | | Grand Mean .24 | .17 |

TABLE 5. Analysis of variance of the peak standing crop of Aquatic macrophytes[a] in Grace Creek Pond and Coastal Pond in 1975 and 1976.

| Study site, year, and unit | Source of variation | df | SS | MS | F |
|---|---|---|---|---|---|
| Grace Creek Pond | | | | | |
| 1975 | | | | | |
| Exclosure | Blocks | 2 | 551.00 | 275.50 | 6.58** |
| | Plots | 55 | 2303.43 | 41.88 | |
| | Total | 57 | 2854.43 | | |
| Control | Blocks | 2 | 223.08 | 111.54 | 5.24** |
| | Plots | 55 | 1170.91 | 21.29 | |
| | Total | 57 | 1393.99 | | |
| 1976 | | | | | |
| Exclosure | Blocks | 3 | 13236.61 | 4412.20 | 46.09** |
| | Plots | 120 | 11485.98 | 95.72 | |
| | Total | 123 | 24722.59 | | |
| Control | Blocks | 3 | 2147.09 | 715.70 | 41.78** |
| | Plots | 115 | 1969.63 | 17.13 | |
| | Total | 118 | 4116.72 | | |
| Coastal Pond | | | | | |
| 1975 | | | | | |
| Exclosure | Blocks | 2 | 334.30 | 167.15 | 4.95** |
| | Plots | 134 | 4522.40 | 33.75 | |
| | Total | 136 | 4856.70 | | |
| Control | Blocks | 2 | 1.34 | 0.67 | 3.35* |
| | Plots | 107 | 21.33 | 0.20 | |
| | Total | 109 | 22.67 | | |
| 1976 | | | | | |
| Exclosure | Blocks | 3 | 3276.83 | 1092.28 | 16.44** |
| | Plots | 139 | 9232.07 | 66.42 | |
| | Total | 142 | 12508.90 | | |
| Control | Blocks | 3 | 0.80 | 0.26 | 0.48 |
| | Plots | 138 | 74.97 | 0.54 | |
| | Total | 141 | 75.77 | | |

[a]Expressed as g/plot.

*P < 0.05, **P < 0.01; a significant F-value indicates significant among-blocks variation in productivity of aquatic macrophytes.

TABLE 6. Production of aquatic-macrophyte species and its removal by moose in Grace Creek Pond and Coastal Pond, 1975.

| Study site | Block | Species | Production ($g/m^2$) | Proportion of total production | Removal by moose ($g/m^2$) | Expected removal by moose ($g/m^2$)[a] | Chi-square (1 df) |
|---|---|---|---|---|---|---|---|
| Grace Creek Pond | 2 | Nitella flexilis | 96.7 | 0.99 | 45.2 | 45.6 | |
| | | Potamogeton alpinus | 1.2 | 0.01 | 0.9 | 0.5 | |
| | | Total | 97.9 | 1.00 | 46.1 | 46.1 | 0.32 |
| Grace Creek Pond | 4 | Chara vulgaris | 96.9 | 0.88 | 82.2 | 75.0 | |
| | | P. alpinus | 13.5 | 0.12 | 3.0 | 10.2 | |
| | | Total | 110.4 | 1.00 | 85.2 | 85.2 | 5.77* |
| Coastal Pond | 1 | N. flexilis | 5.6 | 0.63 | 5.0 | 5.1 | |
| | | P. pusillus | 3.3 | 0.37 | 3.1 | 3.0 | |
| | | Total | 8.9 | 1.00 | 8.1 | 8.1 | 0.005 |

[a]Calculated by multiplying (proportion of total production) x (total removed by moose); e.g., 0.37 x 8.1 = 3.0.

*P < 0.025; a significant chi-square value indicates that removal of species was not in proportion to their availability.

simply tastes better than *P. alpinus*.

*Water Transparency*

The mean Secchi disk transparency at Coastal Pond was 0.50 ± 0.07 m (95% confidence interval, n = 4). The disk did not disappear from view in Washington Creek (maximum depth ca. 1.3m).

*Evaluation of the Exclosure Technique*

Interpretation of production and removal by moose grazing could be biased by several factors. In 1975, because the exclosures were not completed until almost mid-July, about five weeks after moose generally commence aquatic feeding, estimates of standing crop inside, hence of production and utilization, could have been lower than had protection been in effect all season. There would not be a similar problem for 1976 estimates. Here, however, if 1975 protection led to inclusion of the previous season's foliage in the 1976 samples, an overestimate of 1976 production, hence, utilization would have occurred. As stated above, however, we believe residual growth, while present in spring, disappeared by the time of sampling. Long-term effects of protection upon production is a separate issue and is discussed below.

Other herbivores--beaver, muskrat (*Ondatra zibethicus*), waterfowl, fish, and invertebrates--could bias production and possible moose-removal estimates. Because all these animals had approximately the same access inside as outside the exclosures, their removals should have been correspondingly uniform. Our estimated "standing crop in exclosure units" more accurately should be termed "net residual available to moose," and the calculated amount removed by moose would not differ. The issue is complicated, however, because beaver, muskrats, and waterfowl might have been partially discouraged from entering the exclosures; this would be especially true for the mammals, which could only find access under the poultry wire, ca. 1 m below the surface. On the other hand, if removal by moose outside left the protected stands as the most easily grazed, this might attract the mobile herbivores to the exclosures. In general, neither beaver nor muskrats appeared to us to be present in such numbers as to be having even one tenth of the effect of moose. In 1973, however, Cannon believed that beaver grazing inside the Grace Creek Pond exclosures was accounting for a sizable removal. While we recognize the potential biases due to other herbivores, we conclude that during these experiments no effect was sufficient to alter the general pattern attributable to moose. We plan to test for effects of other herbivores in the future.

The exclosure technique assumes that productivity in paired units is identical. However, Westlake (1956:245) states, "Grazing may stimulate productivity, so when it is important the exclusion of grazers from an experimental site may give underestimates of the productivity." Such stimulation of productivity may be achieved through continued growth of remaining portions of cropped plants or through enhanced growth of uncropped plants because of reduced competition for nutrients and light and space. We observe, however, that moose usually remove most of the above-substrate (photosynthetic) portions, eliminating further growth of cropped plants; also, because grazing during a given feeding period is often localized in a small area, few uncropped plants are left. We doubt that moose grazing measurably increased productivity in control units compared to exclosure units. We conclude, in summary, that while a number of possible biasing factors were not accounted for, the exclosure studies essentially accomplished the intended objective--to demonstrate the approximat magnitude of the impact of moose grazing on aquatic macrophytes.

## DISCUSSION

Based on Cannon's (unpublished) data from the single experimental block in Grace Creek Pond whose exclosure was not broken into by moose in 1973, we calculate that the peak standing crop was 47.4 ± 7.8 g/m$^2$ and 3.8 ± 0.6 g/m$^2$ (mean ± SE) in the exclosure and control unit, respectively--considerably less than our standing crop in 1975 and 1976 (Table 1). The disparity with our data results in part from within-pond variation in productivity (Table 5), and it may also reflec a higher moose population in 1973 as well as inter-year climatic variation.

There is little published data on the production of aquatic macrophytes in other, relatively moose-free portions of the Lake Superior region. Westlake (1963) states that sites in infertile lakes may only produce about 1 metric ton/ha (100 g/m$^2$) per year, citing Potzger and van Engel (1942). However, the presentation of the latter' data on macrophytes in Weber Lake, located about 190 km south of our area in Vilas County, Wisconsin, is confusing. Westlake (1963) also notes that fertile, temperate rivers in Great Britain have been found to produce 100-200 g/m$^2$ per year Comparisons with our data are tenuous because of variations in climate, geography, time and techniques.

The relatively low production of macrophytes in 1975 (Table 1) probably reflects some 70 years of intensive moose grazing. When released from it, the plants responded with a surge of growth, but it may take many years before a new equilibrium of growth is attained within the exclosures.

Apparently aquatic macrophytes are resilient to herbivory. Steiglitz (1967) reported that waterfowl consumed 32.3% of the standing crop of two preferred aquatic plant species in Florida, and he believed that at least 50% of the vegetation could be removed annually without decreasin productivity. Sterling (1970) reported that waterfowl removed 52% of the fall crop of sago pondweed (*Potamogeton pectinatus*) tubers at Bear River Migratory Bird Refuge in Utah, and he believed that such removal had no significant effe on subsequent productivity. On the other hand, Anderson and Low (1976) found that removal by waterfowl of more than 60% of sago pondweed resulted in significant declines (up to 80%) in the following year's production on the Delta Marsh, Manitoba.

Both moose and waterfowl mechanically destroy aquatic macrophytes that are not eaten. Anderso and Low (1976) estimated that waterfowl may eat as little as 25% of the vegetation they disrupt. Although we believe that moose eat the majority of vegetation that they disrupt, plants may be broken off by hooves and mouths and carried away by currents, and plants may be destroyed when pushed deeply into soft substrates by hooves.

More importantly, as moose walk through aquat habitats, they stir up sediments which remain in suspension for many hours. These intercept and scatter light and thus impair photosynthesis. Robel (1961) reported that the standing crop of sago pondweed in Utah varied inversely with turbidity. Krull (1969) believed that a massive die-off of pondweeds at Montezuma National Wildlife Refuge in New York was caused by turbidity from carp and from precipitation. Bellrose (1941

stated that a Secchi disk transparency less than 9 inches (0.23 m) precluded development of submerged macrophytes in Illinois. McCombie and Wile (1971) observed heaviest growth of macrophytes in southern Ontario impoundments at transparencies of 0.9-2.6 m. In comparison, Secchi disk transparencies averaged 0.50 m at Coastal Pond on 18 June 1975. However, this preceded maximum moose use of the Pond, and we believe that transparencies would have decreased with increased moose activity.

Murie (1934) and Brown (n.d.) reported that in the early 1930's the 1000-3000 moose were causing severe destruction of aquatic habitats, including the virtual extirpation of several macrophytes, i.e., *Nuphar variegatum, Nymphaea odorata,* and *Potamogeton* spp. Their photographs, and those taken by Dr. Frank R. Oastler, show aquatic habitats more disturbed by moose than that observed recently. Jordan et al. (1973) reported that with a population of about 1200 moose, ponds appeared virtually cleared of aquatic vegetation by September during the early 1970's. Current use appears to be less. Many well-used aquatic habitats such as Grace Creek Pond and the mouth of Washington Creek appeared to contain a substantial biomass of macrophytes at the termination of aquatic feeding by moose in mid-September. It appears that the present moose population is leaving a sufficient quantity of plants to assure adequate plant reproduction under normal climatic conditions.

The 1976 drought emphasized the dependence of aquatic habitats, especially beaver ponds, on adequate precipitation. Water levels dropped considerably and many ponds dried up. Production of macrophytes probably decreased because of desiccation of foliage seeds (Muenscher 1936), and tubers (Yeo 1965). Beard (1973) reported that lowering the water level of a northern Wisconsin impoundment during the winter resulted in a significant reduction in the relative abundance and acreage of aquatic vegetation. Lowered water levels interfering with vegetative reproduction, rather than frost damage, were responsible, although *Nuphar* rhizomes were severely damaged by the latter. We observed that many areas still retaining water, formerly in the profundal zone, usually contained no vegetation in late summer 1976. Moose concentrating on remaining stands of macrophytes probably removed an extraordinary amount and probably caused abnormally high turbidity. The beaver population, which had about doubled in the past decade to about 2000 animals in the fall (Shelton 1975), probably suffered increased mortality because of malnutrition (reduced availability of aquatic macrophytes and of proximal stands of aspen and birch), of increased vulnerability to wolf predation, and of loss of habitat. Although extirpation of beaver in major drainages such as Grace Creek is unlikely, it conceivably could occur in the Coastal Pond and similar systems supplied by relatively small drainages.

A decline in beaver impoundments is detrimental to moose due to loss of good, widely distributed habitats for growth of aquatic macrophytes. Reestablishment of extirpated beaver colonies may be indirectly limited to the suppression of preferred aspen and birch regeneration by moose browsing (de waal Malefyt 1974; Snyder and Janke 1976), and directly by wolf predation on dispersing beaver. Colonization of new or reoccupied beaver ponds by aquatic macrophytes is dependent on a suitable upstream source of reproductive structures for water-borne dispersal, or on dispersal by birds or mammals (Hutchinson 1975; DeVlaming and Proctor 1968). Colonization may be slow. Harris and Silvey (1940) suggested that it may require 10-25 years to achieve the maximum number of species in certain Texas impoundments. Hutchinson (1975:256), extrapolating from Godwin's (1923) data, suggested that certain ponds in Great Britain achieved 90% of the maximum number of species in 222 years. Droughts, therefore, have short- and long-term detrimental effects on the productivity and diversity of aquatic macrophytes, with potentially serious repercussions for a moose population at the density found in the Park.

Isle Royale National Park has a moose density as high as any site within the species' circumpolar range. Moose there reduce the productivity of aquatic food resources that apparently are the only sufficient source of the essential macronutrient, sodium. Plant productivity appears to adequately fulfill the moose's requirements at the present moose density and under normal climatic conditions. However, it is conceivable that a lengthy drought, a marked decline in the beaver population, an increase in the moose population, or any combination of these may greatly reduce the availability of aquatic macrophytes. Were this to occur. the moose would experience a nutritional limitation attributable to a single mineral; unfortunately, sodium-deficiency symptoms are not obvious, so if and when it did occur its identification would require a careful monitoring of a number of variables in sodium dynamics in order to show that insufficient sodium, independent of the dynamics of other nutrients, was the limiting factor.

## LITERATURE CITED


ANDERSON, M. G. and J. B. LOW. 1976. Use of sago pondweed by waterfowl on the Delta Marsh, Manitoba. J. Wildl. Manage. 40(2):233-242.

BEARD, T. D. 1973. Overwinter drawdown: impact of the aquatic vegetation in Murphy Flowage, Wisconsin. Wisc. Dept. of Nat. Resources, Tech. Bull. No. 61. 14 pp.

BELLROSE, F. C. 1941. Duck food plants of the Illinois River Valley. Ill. Nat. History Bull. 21(8):235-280.

BOTKIN, D. B., P. A. JORDAN, A. S. DOMINSKI, H. S. LOWENDORF and G. E. HUTCHINSON. 1973. Sodium dynamics in a northern ecosystem. Proc. Natl. Acad. Sci. 70(10):2745-2748.

BROWN, C. A. (N.d., ca. 1935). Ferns and flowering plants of Isle Royale, Michigan. U.S. Dept. of the Interior, Emergency Conservation Field Survey, Univ. of Michigan Herbarium. 90 pp.

DEVLAMING, V. and V. W. PROCTOR. 1968. Dispersal of aquatic organisms: viability of seeds recovered from the droppings of captive killdeer and mallard ducks. Am. J. Bot. 44(1):20-26.

DE WAAL MALEFYT, J. J. 1974. Abundance of moose, hares and red squirrels as related to various seral stages of the spruce-fir-birch forest type of Isle Royale National Park, Michigan. M.S. Thesis, Mich. Tech. Univ., Houghton. viii + 72 pp.

GOODWIN, H. 1923. Dispersal of pond floras. J. Ecol. 11:160-164.

HARRIS, B. B. and J. K. G. SILVEY. 1940. Limnological investigations on Texas reservoir lakes. Ecol. Monogr. 10:111-143.

HUBER, N. K. 1975. The geologic story of Isle Royale National Park. U.S. Geol. Surv. Bull. 1309. 66 pp.

HUTCHINSON, G. E. 1975. A treatise on limnology, volume III-limnological botany. John Wiley and Sons, New York. 660 pp.

JORDAN, P. A., D. B. BOTKIN, A. S. DOMINSKI, H. S. LOWENDORF and G. E. BELOVSKY. 1973. Sodium as a critical nutrient for the moose of Isle Royale. Proc. N. Am. Moose Conf. Workshop 9:13-42.

KRULL, J. N. 1969. Factors affecting plant tie-offs in shallow water areas. Am. Midl. Nat. 82(1):293-295.
MCCOMBIE, A. M. and I. WILE. 1971. Ecology of aquatic vascular plants in southern Ontario impoundments. Weed Sci. 19:225-228.
MECH, L. D. 1966. The wolves of Isle Royale. U.S. Natl. Park Serv. Fauna Series. 7. 210 pp.
MUENSCHER, W. C. 1936. The germination of seeds of *Potamogeton*. Ann. Bot. 50:805-822.
MURIE, A. L934. The moose of Isle Royale. Misc. Publ., Mus. Zool., Univ. of Michigan, No. 25. 44 pp.
ODUM, E. P. 1971. Fundamentals of ecology. W.B. Saunders Co., Philadelphia. 574 pp.
PETERSON, R. O. 1974. Wolf ecology and prey relationships on Isle Royale. Ph.D. Thesis. Purdue Univ., W. Lafayette, Indiana. 368 pp.
_____. 1977(1976). The role of wolf predation in a moose population decline. Proc. First Conf. on Sci. Research in the Natl. Parks.
POTZGER, J. E. and W. A. VAN ENGEL. 1942. Study of the rooted aquatic vegetation of Weber Lake, Vilas County, Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. 34:149-166.
ROBEL, R. J. 1961. Water depth and turbidity in relation to growth of sago pondweed. J. Wildl. Manage. 25(4):436-438.
RUTTNER, F. 1963. Fundamentals of limnology. Univ. of Toronto Press, Toronto. 295 pp.
SHELTON, P. C. 1966. Ecological studies of beavers, wolves, and moose on Isle Royale National Park. Ph.D. Thesis, Purdue Univ., W. Lafayette, Indiana. 308 pp.
_____. 1975. Beaver studies, 1973 and 1974, p. 17-20. In R. O. Peterson and D. L. Allen, Ecological studies of the wolf on Isle Royale. Annual report, 1974-1975, Purdue Univ., W. Lafayette, Indiana. Isle Royale Natl. Park files. 20 pp.
SNEDECOR, G. W. and W. G. COCHRAN. 1967. Statistical methods. Iowa State Univ. Press, Ames. 593 pp.
SNYDER, J. D. and R. A. JANKE. 1976. Impact of moose browsing on boreal-type forests of Isle Royale National Park. Am. Midl. Nat. 95(1): 79-92.
STEIGLITZ, W. O. 1967 (1966). Utilization of available foods by diving ducks on Apalachee Bay, Florida. Proc. Southeastern Assoc. Game and Fish Comm. 20:42-50.
STERLING, M. R. 1970. Seasonal utilization of sago pondweed by waterfowl at Bear River Migratory Bird Refuge, Utah. M.S. Thesis, Utah State Univ., Logan. 121 pp.
WOLFE, M. L. and P. A. JORDAN. The number of moose at Isle Royale: a comparison of inventory methods. Submitted for publication, 1974.
WESTLAKE, D. F. 1963. Comparisons of plant productivity. Biol. Rev. 38:385-425.
_____. 1965. Some basic data for investigations of the productivity of aquatic macrophytes. p. 229-248. *In* C. R. Goldman (ed.), Primary productivity in aquatic environments. Mem. First Ital. Idrobiol., 18 Suppl., Univ. California Press, Berkeley.
_____. 1975. Macrophytes, p. 106-128. *In* B. A. Whitton (ed.), River ecology. Univ. of California Press, Berkeley. 725 pp.
WETZEL, R. G. 1965. Techniques and problems of primary productivity measurements in higher aquatic plants and periphyton. p. 249-267. *In* C. R. Goldman (ed.), Primary productivity in aquatic environments. Mem. First Ital. Idrobiol., 18 Suppl., Univ. of California Press, Berkeley.
Yeo, R. R. 1965. Life history of sago pondweed. Weeds 13:314-321.

# STREAM FLOW EFFECTS ON BEAVER POPULATIONS IN GRAND TETON NATIONAL PARK[1]

Thomas C. Collins[2]

Portions of the four major river systems of the western United States arise from northwest Wyoming, and the benefits of beavers in water conservation on these headwaters have been recognized (Grasse and Putnam 1950). The National Park System provides a sanctuary for rare and endangered or otherwise protected species and the beavers on National Park lands are often attracting these species by providing attractive pond habitats. The beaver, therefore, is an important component of the riparian ecosystem in the National Parks. Since beaver populations in northwest Wyoming are largely unexploited, being under the auspices of Federal agencies including the National Park Service, the delineation of the ecology of these beavers in relation to the apparently unexploited conditions would help insure the protection of these important headquarter populations as well as provide insight into the implementation of sound management of adjacent populations.

Data reported in this paper are for one aspect of a much larger investigation conducted over the past four years concerning beaver ecology on the Snake River floodplain in Grand Teton National Park. The specific objectives of this aspect of the study were to assess the influence of stream flow regimes on beaver population abundance, distribution, and movements.

## METHODS

The influence of stream flow on population abundance, distribution, and movements was assessed by observing colony response in changes in stream flow. Delineation of territorial boundaries and observations of ear tagged beavers facilitated close scrutiny of colony movements. Rates of abandonment and subsequent movement to new dwelling sites due to seasonal high and low stream volumes were compared for a regulated and two unimpeded streams. Discharge data for the Jackson Lake Dam and daily flow rates for the Snake River, Buffalo River, and Pacific Creek were obtained from Bureau of Reclamation records for the period of the study.

## RESULTS AND DISCUSSION

Seasonal fluctuations in flow rates are typical of most streams in Grand Teton National Park. Most streams in the study area carry their maximum volumes in June and minimum volumes in midwinter.

The Snake River in the park is regulated by the Jackson Lake Dam while flows of the Buffalo River and Pacific Creek are relatively unimpeded. The location of these streams in the study area is shown in Figure 1. Table 1 shows the number of beaver colonies on these streams between 1974 and 1976 while average monthly stream flows for these streams are correlated with beaver dwelling abandonment in Figure 2. Observations of movements were facilitated by following 88 ear tagged beavers in the study area.

The number of beaver colonies on these streams was nearly constant between 1974 and 1976 (Table 1). However, there were fewer colonies occupying the Snake River in the fall and 75 percent of the colonies that abandoned territories at low water were colonies that had established the previous spring or early summer. These colonies may have dispersed from the study area after abandonment since their whereabouts was not determined. It is probable that the fall-winter colony totals represent carrying capacity for each of the streams in the study area.

Maximum flow rates on the Snake River at the Jackson Lake Dam occur several weeks earlier than on the Buffalo River and Pacific Creek. Low flow rates on the Snake River at the Jackson Lake Dam occur five to seven weeks later than on the Buffalo River and Pacific Creek. Beavers abandoning dwellings at low flow rates on the Snake River thus have a short critical period of time before winter climatic conditions.

Beaver colonies are unequally distributed on the Snake River. They are absent from sizable sections of stream with good willow or cottonwood habitat. Swift water and lack of suitable banks for establishing lodges or dens were probably a major influence. Six of the eight colonies that permanently abandoned their territories on the Snake River between 1974 and 1976 apparently did so because of the complete lack of dwelling sites at low water.

Beaver abandonments of dwellings due to changes in stream volume were more common than Figure 2 indicates. Some colonies were forced to abandon their dwellings during high water periods. For example, the lodge at site 22 was completely inundated and washed away by high water in 1975. The lodge at site 25, after withstanding high water in 1973-75, was totally removed by high water in 1976 after a channel shift increased the volume in the lodge channel. These beavers reestablished dwellings within their territories when flow rates decreased. Dwelling abandonment at high water was not uncommon on any of the streams in the study area.

A dramatic population movement occurred at low water when numerous colonies were forced to leave summer dwellings. On the Snake River, colony movements due to low stream flows occurred in 1975

[1]This study was financed by the National Park Service and the State of Wyoming through the Northern Rocky Mountain Cooperative Park Study Program and by the New York Zoological Society. The University of Wyoming's Scott Memorial Fund provided travel funds to present this paper. All research was conducted from the Jackson Hole Biological Research Station of the University of Wyoming, Dr. Oscar H. Paris, Director. The data presented here were part of a doctoral dissertation completed under the supervision of Dr. Jack Turner of the Department of Zoology and Physiology, University of Wyoming. I would like to express my sincere gratitude to Robert Wood, Charles McCurdy, and Peter Hayden of Grand Teton National Park for their invaluable assistance throughout this study.

[2]Department of Zoology and Physiology, University of Wyoming, Laramie. Present Address: Wildlife Technology, Pennsylvania State University, The DuBois Campus, DuBois, Pennsylvania 15801.

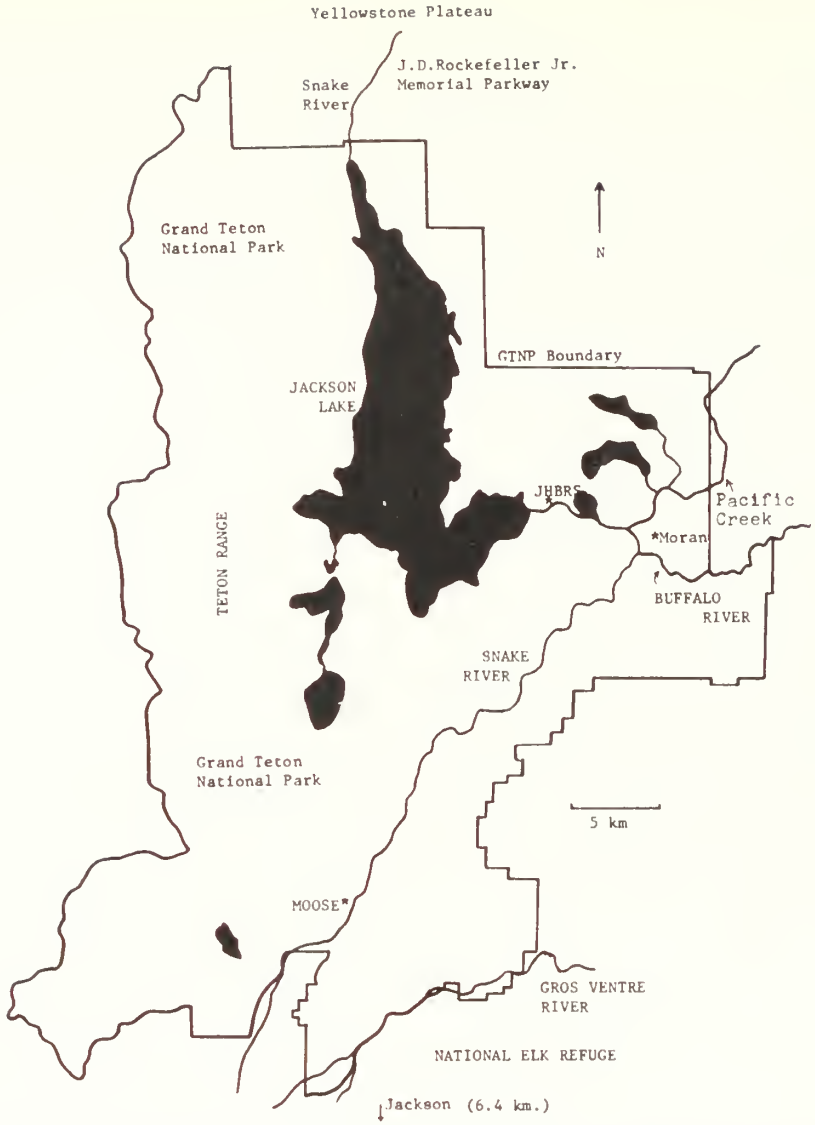



FIGURE 1. Location of study area in Grand Teton National Park.

TABLE 1. Beaver colony abundance on three streams in streams in Grand Teton National Park between 1974 and 1976.

| | Number of Colonies | | | | | |
|---|---|---|---|---|---|---|
| | Snake River | | | Buffalo R.-Pacific Ck. | | |
| | 1974 | 1975 | 1976 | 1974 | 1975 | 1976 |
| Spring-Summer | 45 | 44 | 44 | 9 | 9 | 9 |
| Fall-Winter | 40 | 41 | 40 | 9 | 9 | 9 |

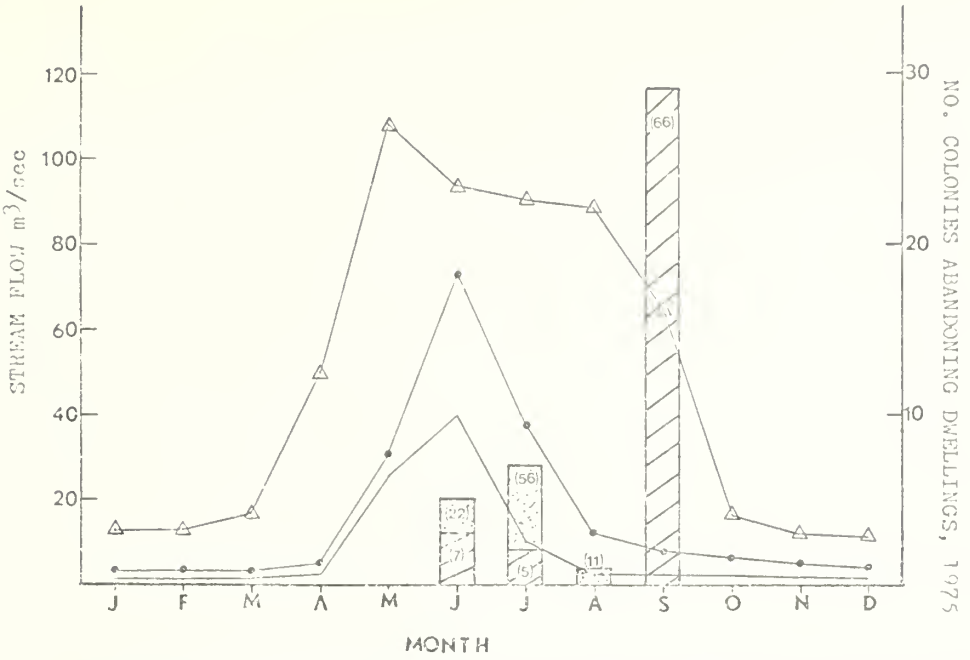



FIGURE 2. Average monthly stream flow for Pacific Creek, Buffalo River, and the Snake River at the Jackson Lake Dam correlated with number of beaver colonies abandoning dwellings in response to high or low stream flows. All stream flow data are from USGS-Bureau of Reclamation summaries (1966-75). Averages for the Snake River are for 5 years (1970-75) and averages for Pacific Creek and Buffalo River are 8-year averages (1966-73).

——— Stream flow, Pacific Creek

—•—•— Stream flow, Buffalo River

—△—△— Stream flow, Snake River at Jackson Lake Dam

▒ No. colonies abandoning dwellings on Pacific Creek and Buffalo River, 1975

▨ No. colonies abandoning dwellings on Snake River, 1975

Numbers in parentheses are percents of colonies of each population abandoning.

between September 14 and 19 when discharge at the Jackson Lake Dam was reduced from over 100 $m^3$/sec to nearly 30 $m^3$/sec (Figure 3). During this period, 29 of 44 colonies (66%) between the Jackson Lake Dam and Moose, Wyoming, abandoned their dwellings (Figure 2). A similar pattern of abandonment occurred on other streams but these low water abandonments took place in late July of 1975, leaving sufficient time for reestablishment before winter conditions.

Colonies that were forced to leave summer dwellings at low stream flows on the Snake River were not located until the second week of October when colonies began reappearing in bank dens on the main channels. Previously occupied side channels of the Snake River in GTNP were dry in many instances. Floodplain populations concentrated on the main river channels and built new dens or lodges where suitable dwelling sites became available. The average distance of movement to reestablish was 262 m for 11 different colonies that did not abandon their territories. Of the 29 colonies forced to abandon dwellings at low water on the Snake River in 1975, 24 reestablished in bank dens, two in lodges, and three abandoned their territories completely.

At low water, the majority of stream banks observed were unsuitable for building lodges or dens because of shallow water adjacent to the banks, unstable banks in deep water, or cobblestone substrate. Twenty-three of the reestablished colonies on the Snake River and all colonies on the Buffalo River and Pacific Creek built bank dens in relatively unstable, eroding stream banks. Many of these dens were behind fallen trees or other debris that afforded some stability to the dens. All of these winter dens were abandoned when stream volumes increased the following spring.

Winter ice bound conditions were evident on most ponds by October 28, 1975. Colonies that abandoned at low water on the Snake River in September had only five weeks before winter conditions occurred to rebuild a dwelling and cut a food cache. An early freeze could have been detrimental to the Snake River population. Thirty-one of the 33 colonies (94%) on the three streams that abandoned their dwellings at low water and reestablished within their own territories cut food caches for the winter while only two of the 17 colonies not forced to abandon built caches.




FIGURE 3.

Abandonment rates and subsequent movements to new dwelling sites due to seasonally high and low stream volumes were similar on all three streams studied. The major difference was the time when these changes occurred. Seasonal movements are typical of beaver populations on the streams in Grand Teton National Park. The lack of winter dwelling sites due to reduced stream flows in the fall and winter greatly restricted potential colony density and dictated the carrying capacity of the floodplains. Since all the reestablished colonies built within their territorial boundaries, the territorial integrity of the population as a whole was maintained.

Berghofer (1961) observed that two causes of beaver territorial abandonment and movement were destruction of dwellings by high water and changing water conditions. In four years of study, no permanent territory abandonments were observed in Jackson Hole beaver colonies that had dwellings destroyed. Changing water conditions (e.g., shifts in channels) were observed on occasion but they never resulted in permanent abandonment. Causes of abandonment appear to be stream specific and may relate to population density in some way. That is, in filled habitat, catastrophes to a colony dwelling may more regularly result in rebuilding within territorial boundaries since adjacent habitat is unavailable. The single major cause of permanent territorial abandonment in the study area was the absence of low water dwelling sites.

Methodologies for assessing stream flow requirements of wildlife populations were discussed by Kadlec (1976). The impact of flow regimes on critical limiting habitat variables affecting the species population were considered to be areas requiring elucidation. Winter dwelling site availability is a measurable habitat variable that can be related to stream flow. It appeared to be one of the more important variables influencing beaver carrying capacity on major streams in the study area. This variable was not limiting for all stream populations and results reported here should not be extended to other localities. However, it is possible that this habitat variable is critical to other beaver populations in other localities.

The long term effects of the Jackson Lake Dam on beaver and other wildlife populations are unknown. Extensive flooding of the floodplain is prevented by the dam. There may be a long term trend toward stability of stream channels which would definitely be detrimental to many floodplain wildlife species. Additionally, some willows require periodic flooding and drying (Houston 1968). The dam, by reducing extensive flooding, could cause the reduction of willow habitat by retarding reproduction. The availability of historic aerial photos, daily stream flow records, and a diversity of relatively unexploited wildlife species make the Snake River in Grand Teton National Park a unique study area. This drainage is especially feasible for examining long term effects of altered flow regimes on wildlife populations.

## LITERATURE CITED

BERGHOFER, C. B. 1961. Movement of beaver. Proc. 41st Ann. Conf. W. Assoc. Game Fish Comm., p. 181-184.

GRASSE, J. E. and E. F. PUTNAM. 1950. Beaver management and ecology in Wyoming. Fed. Aid Wildl. Restoration Proj., Wyo. 31-D and 30-R. Wyo. Game Fish Dept., Bull. No. 6. 52 pp.

HOUSTON, D. B. 1968. The shiras moose in Jackson Hole, Wyoming. Grand Teton Nat. Hist. Assoc., Moose, Wyo. Tech. Bull. No. 1. 110 pp.

KADLEC, J. A. 1976. Methodologies for assessing instream flows for wildlife. *In* C. B. Statnaker and J. L. Arnette, eds. Methodologies for the determination of stream flow requirements: an assessment. U.S. Fish and Wildl. Serv.

U.S. Geological Survey. 1965-1975. Water resources data for Wyoming. Surface water records. USGS Water Res. Div.

# POPULATION STUDIES OF BEAVERS IN ISLE ROYALE NATIONAL PARK, MICHIGAN

Philip C. Shelton[1]

This summarizes the history of Isle Royale beaver populations through 1974, based on historical records and recent investigations. My contributions to this study, beginning in 1960 and extending through 1974, were part of long-term studies of the island's major mammals, initiated in 1958 by Durward L. Allen of Purdue University. His continued support of my involvement in these studies is appreciated immeasurably. Financial support came from the National Science Foundation (G-13236), the National Park Service, and the Wildlife Management Institute. The excellent cooperation of numerous Park Service staff made the study possible. Especial thanks are due Robert M. Linn for continuing advise and support. Other aspects of my study, especially the physical characteristics of Isle Royale beavers and their interactions with moose, wolves, and with the island's vegetation, are being prepared for publication elsewhere.

The history of beavers on Isle Royale is one of probable extermination by trapping, followed first by habitat changes highly favorable to beavers, and later by abundantly successful natural reestablishment.

Information from before 1900 is scarce, possibly reflecting the scarcity of beavers. John Tanner (James 1830:24) mentioned that beavers and otters were abundant on Isle Royale when he visited it briefly about 1790. However, most early reports indicated that beavers were scarce in streams on the north shore of Lake Superior during the fur trading era, probably because the forests were predominantly coniferous (Longley and Moyle 1963:17). Posts established on Isle Royale by the American Fur Company, and possibly others, beginning about 1835, dealt mainly with fish, rather than furs (Nute 1944; Rakestraw 1968), hence their presence does not necessarily indicate an abundance of beavers. Tanner's brief account, based on a verbal report some three decades after his visit, cannot be taken as more than an indication of the possibility of beaver abundance in the late 18th century.

William Ives' maps (Isle Royale National Park files), based on the linear survey of 1847 and 1848 show old beaver works in only three places, all on the southwest end of the island. During the 1890's, Scott (1925:408) found old beaver cuttings near Windigo. Adams' (1909:402) party knew of no one on the island in 1904 or 1905 who had information on recent occurrence od beavers, although a few people remembered signs of beavers found in the 1870's. It was not clear whether the signs were fresh or old when they were seen.

Thus whatever the population may have been earlier, there is no evidence of beaver abundance in the 19th century, and they probably were absent for most of that century.

During the absence of beavers most of the northeast two-thirds of the island was burned by copper miners and prospectors. On these burns grew extensive stands of quaking aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*), the two most important beaver food trees in this region. The absence of moose and beavers allowed these forests to develop uninhibited.

Earliest reestablishment of beavers on Isle Royale was not documented, but they were well established by 1920 (Krefting 1963:4).

A crude estimate of the population in 1930 was made by combining data from Adolph Murie's work in 1929 and 1930 with data from aerial photographs taken in 1930.

Murie (n.d.) described 28 sites where beavers or beaver signs were seen. Of these, 19 were known to be occupied in 1929 or 1930. The set of over 600 aerial photographs, covering the entire island, made in 1930 for the Park Service by Abrams Aerial Photo Corporation (Isle Royale National Park files) show 27 sites with signs of beaver activity, mostly full ponds with dams clearly visible. Only five of these were the same as ones described by Murie.

If the ratio of sites common to Murie's report and the photographs (5) to the total Murie described (28) were the same as the ratio of the total number on the photographs (27) to the actual number present, then this number would have been 151. Assuming further that the percentage of sites known to be active in Murie's sample were representative of the entire island, then 102 of the 151 sites would have been active in 1930. If the number of beavers per colony were in the range 5 to 6.4 reported for Michigan by Bradt (1947:18) and for Isle Royale in the present study respectively, then there would have been 500 to 650 animals in 1930.

Obviously, these calculations must be taken with considerable reservation, for several assumptions are questionable. However, the figures probably are in the right order of magnitude, and they are the only approximation available.

Murie (n.d. and pers. comm.) felt that beavers would have been more abundant in 1930 except for widespread poaching.

No further data are available from the 1930's, but beavers became abundant within a few years after the island became a national park in 1940. Gilbert (1946:1) reported that no noticeable increase occurred until 1943, but that by the fall of 1945 beavers were ". . . present in numbers in all streams, in practically all of the inland lakes, in practically every swamp regardless of its isolation from other bodies of water, and along the shorelines of protected harbors and bays were [*sic*] natural food is accessible." There was an increase in nuisance complaints against beavers by island residents, and several park service trails had to be rerouted because of beaver flooding. Studies made by Gilbert and by Fish and Wildlife Service personnel (Gensch 1946; Krefting and Lee 1948) indicated rapid use of beaver food supplies, and a decline in beaver numbers was predicted on the basis of this rapid use of resources.

Krefting (1963:6) estimated that during the period 1945-50 there were 150 to 200 active colonies on the island. Using Bradt's (1947:17-21) figure of four beavers per colony with one lodge, he calculated that there were 600 to 800 animals. If, however, the number per colony was similar to that found on Isle Royale in the 1960's (6.4) then the

[1]Clinch Valley College, Wise, Virginia 24293.

1945-50 population would have been 1000 to 1300 animals.

Following a peak reached about 1948 the beaver population did decrease. Krefting (1963:8) thought that between 1949 and 1958 there was a steady decline that may have been as great as 75%, caused by ". . . a depleted food supply although the coyote or disease may have been secondary causes . . ." If the 75% reduction was accurate, the population was reduced to perhaps 300.

Interviews with island residents and one biologist's report (Cole 1954) indicated that the decline was more rapid, occurring mainly between 1950 and 1955.

By the early 1960's the beaver population had recovered to the levels indicated before the die-off occurred (see below) and at that time abandoned sites were found where food and physical factors did not appear to be deficient for beavers. Reoccupation of many such sites through the 1960's and early 1970's indicated that they had not been depleted, for the beavers were feeding on trees that were present when the sites were abandoned. This is evidence that food depletion was not the primary cause of the decline.

Circumstantial evidence indicates that epizootic disease may have played a critical role in the beaver decline. An epizootic of tularemia (*Pasturella tularensis*) spread from central Canada across the upper lake states, beginning in 1948 in Manitoba and northern Ontario (Labzoffsky and Sprent 1952), later including Minnesota (Strenland 1953) and Wisconsin (Knudsen 1953) and reaching upper Michigan by 1953 (Lawrence et al. 1956). Isle Royale lay directly in the path of this epizootic and there is no reason to believe that the 12.5 to 15 miles of open water separating Isle Royale from the north shore of Lake Superior would be an effective barrier against the spread of tularemia, for numerous potential vertebrate and arthropod vectors were present.

Direct evidence of disease in the Isle Royale beaver population is absent, but one Park Service employee, John Rose, remarked that he did not find dead beavers any more like he used to (pers. comm. 1961). The potential significance of this remark was not evident to me at the time, and I did not press for more details. Mr. Rose died the following winter. He would have been more likely than anyone else to find dead beaver if such existed, for he was one of the few non-professional park employees whose interest in natural history went beyond idle conversation. He spent much time in the woods, both on and off duty, and his observations usually were accurate, if his interpretations were at times imaginative. During the period in question he was a member of the trail crew and would have been one of the few people out in early spring, when dead beavers would have been most likely found. In the reports of die-offs in other areas, dead animals were found during trapping seasons in February, March, and April. In a separate conversation, it was learned that Mr. Rose was well aware of the beaver decline, and thought that coyotes and wolves were responsible.

Other residents interviewed, mostly commercial fishermen and park employees, had no recollection of dead beaver. However, these people seldom saw inland lakes and less often visited inland beaver ponds, where most of the mortality would have occurred. Krefting (pers. comm.) thought most of the decrease occurred on inland ponds.

Predation was not likely a factor in this population decline. Although Packard (1940) and Murie (1940) found coyotes capable of killing beavers, and Krefting (1963:8) reported that 41% of Isle Royale coyote scats, probably collected in the late 1940's, contained beaver remains, the highest number of beavers (prior to the 1960's) occurred on Isle Royale when coyotes were also numerous. It therefore appears that the most coyotes could have done was slow the buildup of beavers.

The decline in beavers closely followed the arrival of timber wolves on the island, but no causal relationship can be inferred. As shown below, beavers have since increased to levels higher than those occurring before the decline of the 1950's. Wolves were present throughout this period of beaver increase.

Live-trapping and aerial surveys constitute the bases for population estimates made during the 1960's and 1970's. Details of live-trapping results will be presented elsewhere; the pertinent figure for this discussion is the average number of beavers per colony, which can be multiplied by the number of active colonies found in aerial surveys to arrive at an estimate of the total population. This figure, 6.4, is based on live-trapping done in 1961-63, and in 1974.

Aerial surveys were made to count and map as accurately as possible all active sites on the island. These surveys were made in October after most leaves had fallen and when beavers had been cutting and storing winter food for several weeks. Fresh cutting, fresh mud on houses and dams, and food piles were reasonably conspicuous from the air and served as indications of current activity.

Counts attempted on 1960 and 1961 were incomplete and afforded little useful information. The first satisfactory count was made during 17 hours flying time 17-20 October 1962 in a 90 hp Aeronca Champion, piloted by Jack Burgess. A partial count was made 19 and 21 October 1969 during 3.5 hours flying time in a J-3 Cub piloted by William Martilla. The latest counts were made during 12.5 hours 15, 17, and 18 October 1973, and 16, 17, and 18 October 1974 in a J-3 Cub piloted by Dale Chilson.

The 1962 and 1969 counts combined the beaver survey with a sample count of moose to determine sex and age ratios. The division of attention between moose and beavers and the differences in optimum flight patterns for gathering the two kinds of information required more flying time than was found necessary for beaver counting alone in later years. Moose counting required lower altitudes and more circling, while beaver colony counting was most efficiently done by flying higher and maintaining straight flight paths.

Results of these counts follow:

| Year | Flying time (hours) | Number tallied | Number estimated |
|---|---|---|---|
| 1962 | 17 | 117 | 140 |
| 1969 | 3.5 | 141 | 175-200 |
| 1973 | 12.5 | 213 | 300 |
| 1974 | 12.5 | 286 | 315 |

During the 1962 count, 117 active sites were found from the air and an additional 23 sites not seen from the air were known through ground work. A few of these were in areas covered from the air. but most were in areas worked heavily on the ground on which air time was not spent. Most of those missed from the air but found in ground work had only a scant amount of beaver signs, indicating the presence of no more than one to three beavers. The effect of 10 to 20 more of these in areas not covered on the ground would not affect the total population estimate significantly.

Thus for 1962 the figure used was 140 colonies, with an average of 6.4 beavers per colony, the total estimated population was 896, or approximately 900.

In 1969 a total of 141 active sites were known from the 3.5 hours flying and three weeks of ground work. It was estimated that a few more hours of aerial work would have brought the total number of known active colonies to 175 to 200, an increase of at least 25% over the 1962 figure.

During the 1973 count 213 active sites were mapped, and estimates of probable error made by intensively recounting selected areas indicated that the actual number present probably was about 300.

The 1974 count revealed 286 sites with visible food piles or sufficient recent cutting or other signs to indicate the probable presence of one. About 30 additional sites had fresh mud on the house or dam or a small amount of fresh cutting, but no food piles visible. Most of these probably represented sites occupied by lone beavers or pairs rather than colonies with reproducing adults and their offspring. The total number of active sites recorded for 1974 was thus a minimum of about 315. That this figure is slightly higher than the 1973 estimate probably reflects the excellent conditions under which the 1974 survey was flown, and the additional experience of both pilot and observer, rather than any real increase in number of colonies.

The 1974 count was made almost entirely (12 hours) on 17 and 18 October. These were days with high, thin overcast and light to moderate winds--nearly ideal conditions for observing freshly felled trees, food piles, and fresh mud on houses and dams. These conditions, plus the experience gained by the same pilot and observer working together two consecutive years, gave us confidence that we had approached the practical limits of accuracy for such a count.

If the 286 colonies known or thought to have food piles averaged 6.4 beavers per colony, and the approximately 30 additional colonies with less sign averaged two beavers each, then the total population for the fall of 1974 would have been (286 X 6.4) + (30 X 2) = 1905 beavers for the entire island, or, roughly 1900 beavers. This represents an increase of slightly over 100% from the 1962 figures, and 60 to 70% from the 1969 estimate.

These figures should not be interpreted to indicate that most of the increase occurred between 1969 and 1974, because the 1969 figure was a conservative estimate, based on only 3.5 hours flying and three weeks ground work. There is some evidence to indicate that most of the increase occurred before 1969. On Tobin Creek, for example, there were two or three active colonies in 1962, five colonies in 1969 and 1973, and six in 1974.

The increase in colonies was confined almost entirely to stream habitats rather than to lakes or harbors. For comparison, on Tobin and Rock Harbors and the islands northeast of Tobin Harbor there were six colonies in the early 1960's, seven in 1969 and 1973, and eight in 1974. Sargent Lake had six colonies in 1961, but only three in 1974. Other large inland lakes appeared to have about the same number in the 1970's as they had in the early 1960's.

That the increase was primarily in stream habitats is consistent with the hypothesis that the decline in beaver numbers that occurred during the 1940's and early 1950's was caused by epizootic tularemia. Harbor and lake dwelling animals may have been less susceptible to this disease, because of the much larger volume of water with which they would come into contact, resulting in massive dilution of any contamination, especially as compared with beavers living in ponds on slow-moving streams or in stagnant swamps or bogs.

Consequently harbor sites have been occupied more continuously during the last 30 to 40 years than have any known stream sites. Beavers have continued to harvest food trees throughout this period and some now have comparatively little left to sustain them. They do, however, demonstrate a remarkable tenacity and ability to survive on birch and a variety of herbaceous and shrubby species when their preferred aspen is depleted.

Stream dwelling beavers, by contrast, still have remaining considerable aspen and birch trees, mostly stands dating from fires of the late 19th and early 20th centuries. Regeneration of aspen and birch is severely inhibited by moose browsing and the natural shade intolerance of these seral stage species. Thus as supplies dwindle, beavers will be forced to move farther from water to feed and will become more vulnerable to wolf predation.

Wolves are now taking significant numbers of beavers. Beaver remains occurred in only about 11% of wolf scats examined in 1958-63 (Mech 1966; Shelton 1966) when wolves numbered in the low 20's. Peterson's (1977) wolf studies indicate that wolves increased to 44 by 1976, and about half the prey occurrence in wolf scats examined in the early 1970's were beaver remains. Thus beavers may have contributed to the wolf increase, although increased moose vulnerability was thought to be the major factor involved. That beavers were numerous when wolves were at their lowest point in 1969 would indicate that moose were indeed the critical prey item for wolves.

The future of beavers in this dynamic community will depend upon their continued ability to forage from water in the face of increased wolf predation, and on their ability to depend increasingly on less preferred food species. At what point these factors act to bring the population into equilibrium or start it downward remains to be seen. Recurrence of disease is increasingly probable as the population increases. The present population is probably well above that of the late 1940's and early 1950's when the last decline occurred. The finding of three spec ies of parasites in 1974 may indicate a density dependent buildup. No parasites were found on or in beavers handled in the early 1960's. The species found were tentatively identified as the beetles, *Leptinillis validus* and *Platypsylla castoris* one or both of which were found on four of the 63 beavers caught in 1974, and the roundworm *Travassosius americanus* which was numerous in the stomach of the only beaver autopsied.

## LITERATURE CITED


ADAMS, C. C. 1909. An ecological survey of Isle Royale, Lake Superior. A report from the University of Michigan Museum, published by the State Biological Survey as a part of the Report of the Board of the Geological Survey for 1908. Wynkoop Hallenbeck Crawford Co., Lansing. 468 p.

BRADT, G. W. 1947. Michigan beaver management. Mich. Dept. Cons. Game Div. 56 p.

COLE, J. E. 1954. Report on investigation of Isle Royale National Park. U.S. Nat. Park Serv. Isle Royale Nat. Park files. (typewritten).

GENSCH, G. H. 1946. Observations on the beaver of Isle Royale National Park, Michigan from May 8 to June 6, 1946. U.S. Fish and Wildl. Serv. Isle Royale Nat. Park files. 18 p. (typewritten).

GILBERT, K. T. 1946. Memorandum for the Superin-

tendent, Isle Royale National Park, Feb. 15, 1946. Isle Royale Nat. Park files. 3 p. (typewritten).
JAMES, E. 1830. A narrative of the captivity and adventures of John Tanner during 30 years residence among the Indians in the Interior of North America. Reprinted 1956. Ross and Haines, Inc. Minneapolis, Minn. 427 p.
KNUDSEN G. J. 1953. Beaver die-off. Wisc. Cons. Bull. 18(9):20-23.
KREFTING, L. W. 1963. Beaver on Isle Royale. Naturalist 14(2):1-11.
KREFTING, L. W., and F. B. LEE. 1948. Beaver food investigation of Isle Royale National Park, May 2-26, 1948. U.S. Fish and Wildl. Serv. Isle Royale Nat. Park files. (typewritten).
LABZOFFSKY, N. A., and J. A. F. SPRENT. 1952. Tularemia among beaver and muskrat in Ontario. Can. J. Med. Sci. 30:250-255.
LAWRENCE, W. H., L. D. FAY, and S. A. GRAHAM. 1956. A report on the beaver die-off in Michigan. J. Wildl. Mgmt. 20(2):184-187.
LONGLEY, W. H., and J. B. MOYLE. 1963. The beaver in Minnesota. Minn. Dept. Cons., Tech. Bull. No. 6. 87 p.
MECH, L. DAVID. 1966. The Wolves of Isle Royale. Fauna of the National Parks of the United States Fauna Series 7. 210 p.
MURIE, A. 1940. Ecology of the coyote in the Yellowstone. Nat. Park Serv., Fauna Ser, No. 4 206 p.
MURIE A. Undated. Annotated list of the mammals of Isle Royale. 12 p. (typewritten).
NUTE, G. L. 1944. Lake Superior. The Bobbs-Merrill Co. Indianapolis, 376 p.
PACKARD, F. M. 1940. Beaver killed by coyotes. J. Mammal. 21(3):259-360.
PETERSON, ROLF O. 1977. The role of wolf predation in a moose population decline. Proceedings of the First Conference on Scientific Research in the National Parks, Zoology section 2.
RAKESTRAW, LAWRENCE. 1968. Commercial Fishing on Isle Royale. Isle Royale Natural History Association. 24 p.
SCOTT, W. P. 1925. Reminiscences of Isle Royale. Mich. History Mag. 9(3):398-412.
SHELTON, PHILIP C. 1966. Ecological studies of beavers, wolves, and moose in Isle Royale National Park, Michigan. Ph.D. thesis, Purdue University. 308 p.
STENLUND, M. H. 1953. Report of Minnesota beaver die-off, 1951-1952. J. Wildl. Mgmt. 17(3):376-377.

# BEHAVIOR OF THE EUROPEAN WILD BOAR IN THE GREAT SMOKY MOUNTAINS NATIONAL PARKS[1]

Mark L. Shaffer[2]

## INTRODUCTION

The establishment of European wild boar (*Sus scrofa* L.) in the Great Smoky Mountains National Park has created a serious management problem in terms of their effects on populations of native plants and animals as well as potential impacts on visitor usage. Although the National Park Service has had a control program in operation since 1959, the boar are apparently more numerous and continue to expand their range (Bratton, 1974).

To be successful, a control program requires practical and reliable methods both for affecting the abundance of the target species, and for measuring the extent of that effect. Such methods must be based on a thorough knowledge of the biology of the species, particularly its ecology and behavior.

Most of the ecological and behavioral studies of *S. scrofa* have dealt with the subspecies or populations native to Europe and central Asia (but see Diong, 1973; Eisenberg and Lockhart, 1972). While some work has been done on the populations of introduced wild stock and feral domestics in the United States (Bratton, 1974) their ecology and behavior is still poorly known (NPS, 1976). Moreover, detailed studies of boar behavior have, until recently, been lacking for any wild population (Hafez, 1962; Fradarich, 1974; Beuerle, 1975).

In addition to the lack of detailed knowledge on boar behavior and ecology, the control program has been hampered by a lack of adequate censuses of the park's population. Estimates of the boar's abundance range from 500 to 2400 (Bratton, 1974). Part of the problem in getting good estimates has been the difficulty of employing standard mark-recapture techniques on this animal in *this* environment. While boar are not particularly difficult to trap, the use of traps in the park's back country presents man-power and logistics problems.

The primary purpose of this study was to make a preliminary survey of boar behavior in at least two areas of the park during the summer season. Of particular interest was the size, composition, and fidelity of groups; their daily activity and movement patterns; habitat utilization; and individual and group interactions.

In addition, an attempt was also made to carefully describe individuals according to a number of characteristics. It was hoped that such descriptions would reveal phenotypic variation sufficient to recognize individuals and thus, in effect, mark them. Resighting such individuals would then be equivalent to the recapture of marked individuals but without the necessity of actual trapping. Such data could then be used to make a population estimate for the area sampled by any of a number of models (Seber, 1973).

## THE STUDY AREA

Figure 1 shows a generalized map of the Great Smoky Mountains National Park and surrounding region. The approximate locations of the study areas are indicated by shading. The Spence Field-Little Bald study area consisted of a corridor .5 miles wide by 1 to 1.25 miles long and bisected by that portion of the Appalachian Trail running from the eastern edge of Spence Field to the western edge of Little Bald.[3] The total area was approximately 320-400 acres. The Cades Cove study area amounted to approximately 3000 acres bounded by the Cades Cove Loop Road.[4]

Adequate descriptions of the geology, climate, and vegetation of the park and region are available elsewhere (King et al., 1968; Henry, 1962; Whittaker, 1956). Very generally the Spence Field-Little Bald area is a high elevation (5070 ft. to 4885 ft.) ridge top while the Cades Cove area is a valley (1720 ft. to 2000 ft.) of gently rolling topography surrounded by high mountain ridges. No attempt was made at detailed vegetation classification, but general habitat types were recognized. These were: high elevation fields (Lindsay, 1976), and high elevation beech forest (Whittaker, 1956) in the Spence Field-Little Bald area; and field, mixed hardwood, and mixed evergreen forest in the Cades Cove area.

## METHODS

The ideal way to study the behavior and much of the ecology of many species is simply to spend time with them. There are principally two approaches to doing this. One way is to follow an individual or group, continually observing and recording information. The other way is to monitor specific areas and observe the species when it is active in that area or at a particular site. Because of the shy, nocturnal habits of the boar and the rugged topography and dense vegetation of the Smokies the latter approach was chosen.

Within the two study areas regular cruises were made along existing trails. In addition,

[1]The author would like to asknowledge those who aided in this research, including Dr. Susan Bratton and Mr. Frank J. Singer of the National Park Service's Uplands Field Research Laboratory, GSMNP; and Dr. Raymond Herrman of the NPS Southeast Regional Office, Atlanta, Georgia. This work was supported nu NPS Contract No. CX5000-61040.

[2]School of Forestry and Environmental Studies, Duke University, Durham, N.C. 27706.

[3]See USGS 7.5 Minute Series (Topographic), Thunderhead Mtn. Quadrangle, North Carolina-Tennessee.

[4]See USGS 7.5 Minute Series (Topographic), Cades Cove Quadrangle, Tennessee-North Carolina.

two tree-blinds were constructed in Cades Cove for long term observations at baited foraging sites. For both cruises and long-term observations the location, time and duration, number of boar (by sex and age), activity, foods taken, interspecific and intraspecific interactions, and direction of travel were recorded to the extent possible. All photography was done during the long-term observations at the tree blinds.

To supplement this information a notebook was placed in the Spence Field Shelter with a request for hikers to record their observations of boar in the Spence Field-Little Bald area.

During each sighting or observation an attempt was made to look for and record any outstanding features or characteristics of the boars which might aid in "recognizing" them if seen again. Characteristics checked were: size and build, pelage color and length, special pelage markings, group composition, offspring, behavior, and other characteristics such as type of tail, tusk development, scars, and deformities.

The long term observations and photographic work were done from simple platform tree blinds lashed 12-15 ft. off the ground. Sour mash corn was the principal bait and was put out fresh daily once a blind had been visited. Boar take the mash readily while most other species (except for bear and raccoon) seem to leave it alone. Apples, rotten meat, and vegetable scraps were also used occasionally.

The photographs were taken at a distance of 18-25 ft. using a Nikkormat FT-2 camera equipped with a Vivitar 75-260 mm zoom lens and a Soligor M2-A strobe unit. High Speed Ektachrome film was used at an ASA of 400 and processed by Kodak Labs.

Besides the cruises and long-term observations most of the Spence Field-Little Bald area and much of the Cades Cove area were covered on foot at least once and boar sign recorded. Record sheets were used to make preliminary notes on sightings, observations, and habitat cruises. This information was then rewritten in the field notes in a more complete, expanded form.

## RESULTS

During the course of the study 22 days were spent in the Spence Field-Little Bald (SFLB) study area while 39 days were spent in the Cades Cove (CC) area. In this time 74 census cruises (23 at SFLB and 51 at CC) were made. In addition 16 habitat cruises were done (5 at SFLB and 11 at CC). Approximately 110 1/2 man-hours were spent in long term observation sessions (6 1/2 at SFLB and 104 at the blinds in CC). A total of 29 sightings (SFLB = 17, CC = 12) and 24 observations[5] (SFLB = 3, CC = 21) amounting to 955 minutes (SFLB = 150, CC = 805) were made. Another 46 sightings/observations were recorded by hikers in the notebook at the Spence Field Shelter. An additional 8 sightings and 4 observations totaling 125 minutes were made in other areas of the park.

[5]A sighting was defined as a visual contact of less than 5 minutes while and observation lasted longer than 5 minutes.

Of the 53 sightings/observations in the two study areas, 19 involved the resighting or reobservation of identifiable individuals or groups. The total number of "marked" groups was 9 containing 21 individuals. An additional 7 solitary boar were considered "marked." Unfortunately, the number of resightings was insufficient to allow reliable population estimates by standard mark-recapture models. Therefore, phenotypic variation will not be discussed in detail.

## SIZE AND COMPOSITION OF GROUPS

Table 1 presents a summary of the sex and age group composition of boar from all sightings and observations. There were four recognized age groups: young, shoats, sub-adults, and adults. These somewhat arbitrary groupings are based on pelage, weight, and association with other boars. Detailed accounts of these characteristics by age are available elsewhere (Conley et al., 1971; Fradarich, 1974; Sludskii, 1974). For the purposes of this study young refers to boar of 30 lbs. or less with buff colored, black striped coats. Shoats are boar of 60 lbs. or less, with adult pelage, and accompanied by an adult female. Sub-adults are boar between 60-90 lbs., with adult pelage, and in the company of other sub-adults, adults, or adults with young. An adult was any boar over 100 lbs.

Part 1 of Table 1 is a full listing of all sightings and observations. Part 2 of Table 1 omits sightings and observations, involving previously identified animals. This represents the number of different animals sighted/observed. Of eighty-six different individuals 45 (52%) were adults, 12 (14%) were sub-adults, and 27 (32%) were either young or shoats. Sex could only be reliably determined for adults; 14 of 45 (31%) were males and 16 (36%) were females with 15 (33%) of unknown sex. The female:offspring ratio is 1:1.68.

These figures are in agreement with those found for the wild boar inhabiting the nearby Tellico Wildlife Management Area (Conley et al., 1971).

Table 2 is a listing of all groups sighted/observed and the sex and age composition of each. Table 3 is a summary of these groups by size and type. Four types of groups were recognized: family, extended family, multi-family, and others. A family group is a sow and offspring of the year (either young or shoats). An extended family group is a sow with offspring of the year and sub-adults (probably offspring from the previous year--Fradarich, 1974). Multi-family groups are those containing at least two sows, each with offspring of the year. Such groups, termed sounders, are commonly reported for wild boar from various areas and are usually thought to form after the offspring are weaned (Fradarich, 1974; Eisenberg and Lockhart, 1972).

Table 3 shows that, of the 22 different groups, 11 (50%) were family groups; 3 (14%) were extended family groups, and 1 (4%) were multi-family groups. The 7 groups classed as *other* included 2 (9%) of sub-adults, and 5 (23%) whose composition could not be determined. The most frequent group size was 2, with 6 groups of 3 and 1 group each of 7 and 8 animals. Average group size was 3. The hiker's reports from the Spence Field Shelter notebook indicate that groups of up to 5 or 6 were occasionally seen. Again, these results agree with those for the Tellico area (Conley, et al., 1971).

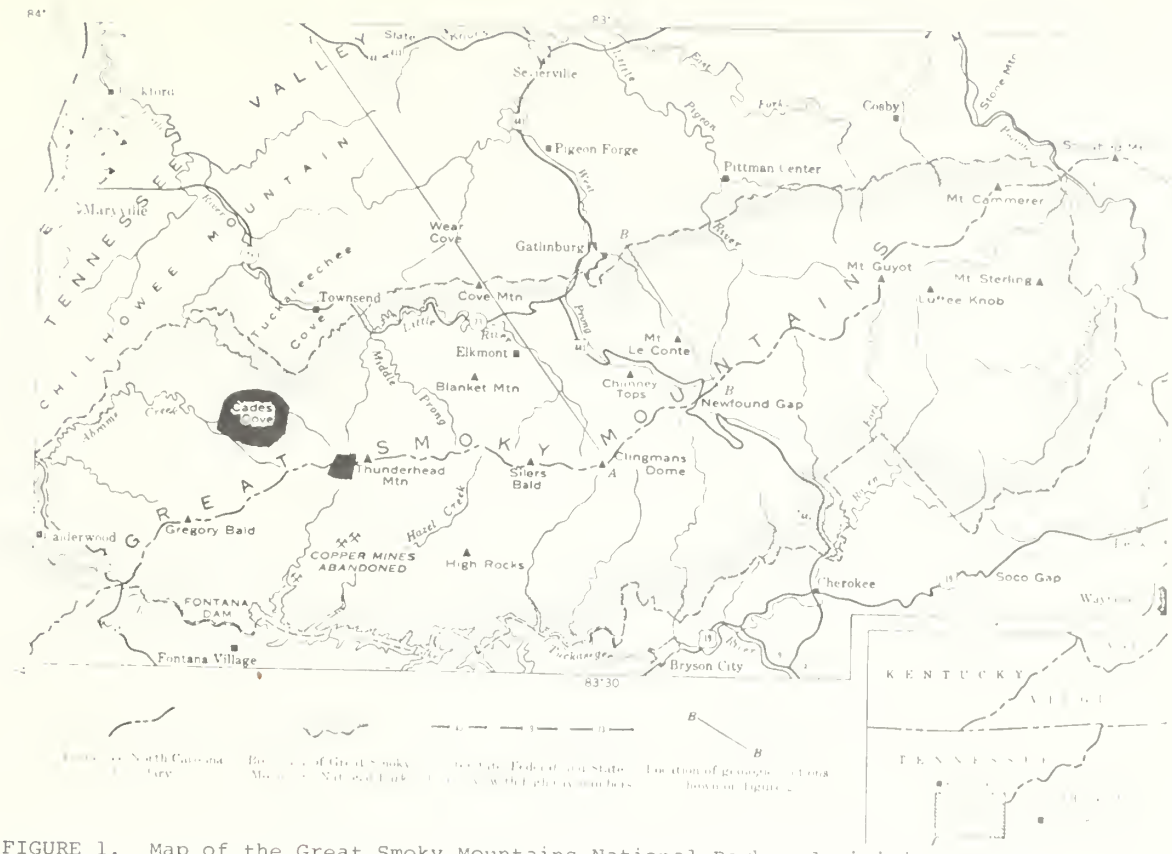



FIGURE 1. Map of the Great Smoky Mountains National Park and vicinity. The two study areas are indicated by shading. (Map from USGS, Map of Great Smoky Mountains National Park and Vicinity, Tennessee and North Carolina.)

## DAILY ACTIVITY AND MOVEMENT PATTERNS

Boar proved to be difficult to follow (there were some exceptions) and, as mentioned earlier, the number of resightings of "marked" individuals was not great. Consequently, little detailed information was obtained on daily activity and movement patterns. Nevertheless, some general findings may be of interest.

Most sightings and observations were made from 7:30 - 9:30 PM (EDT) with the frequency dropping off gradually through the night. Only 9 of 63 sightings/observations were made between 7:30 AM and 7:30 PM (EDT). This, in part, reflects the distribution of time spent searching or waiting for boar but they definitely are primarily crepuscular to nocturnal. The hiker's reports also indicate that, while boar may be active any time of day, the majority of sightings were in the evening and night. The boar did seem to be active earlier in the evening and later in the morning in the Spence Field-Little Bald area than in Cades Cove. Of 9 day time sightings/observations, 7 were in the backcountry. Boar from other areas are known to be less nocturnal where their contacts with man are limited (Sludskii, 1974; Fradarich, 1974).

Boar were flushed from their beds three times; once at 8:00 AM, once at 9:00 AM, and once at 10:30 AM. All three beds were located just off the ridge top; one in a rhododendron (*Rhododendron maximum* L.) thicket, another in a blackberry (*Rubus* sp.) patch, and the other beneath a white pine (*Pinus strobus* L.).

Rainstorms appear to increase the activity of boar. Three of the 9 daytime sightings/observations were made just prior to or during rainstorms. Whether the rain aids in locating or obtaining foods (such as earthworms), or simply decreases human interference is not known.

Boar were observed on several occasions to feed in a small area for extended periods of time. One day a mother and two young spent 5 1/2 hours feeding along a 100 yard stretch of a small stream. The next day one or two boar were heard rooting the same area most of the morning and afternoon. Hikers report that boar fed around the shelter for up to 3 to 4 hours. The boar visiting the blinds in Cades Cove usually stayed until the bait was totally consumed, about 40 to 90 minutes. One night a very shy mother and young visited one of the blinds three times (11:20 PM, 1:20 AM, and 5:00 AM) but somehow sensed the observer and left after only 10-15 minutes of feeding.

Boar do use trails in their movements but all the trails examined in both study areas showed sign of use by deer as well as boar. In some cases, bear sign was also present. At night, the Appalachian Trail is heavily used as a route of movement between feeding areas and wallows.

## HABIT UTILIZATION

Little detailed information was gathered on specific food items utilized due to the conditions under which most sightings occurred.

TABLE 1. Sex and age group composition of boar by area. (A = adult, F = female, M = male, S = sub, SH = shoat, U = unknown, Y = young.)

All Sightings, Resightings, and Observations

| Area | AM | AF | AU | SAM | SAF | SAU | SH | Y | U | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Spence Field-Little Bald | 3 | 9 | 12 | 0 | 0 | 2 | 5 | 8 | 2 | 41 |
| Cades Cove(T)[1/] | 4 | 6 | 1 | 0 | 0 | 6 | 13 | 1 | 0 | 31 |
| Cades Cove(B)[2/] | 9 | 10 | 0 | 0 | 0 | 3 | 10 | 0 | 0 | 32 |
| Other | 4 | 4 | 2 | 0 | 0 | 4 | 1 | 8 | 0 | 23 |
| | 20 | 29 | 15 | 0 | 0 | 15 | 29 | 17 | 2 | 127 |
| % Total | 16 | 23 | 12 | 0 | 0 | 12 | 23 | 13 | 1 | |

Sightings and Observations

| Area | AM | AF | AU | SAM | SAF | SAU | SH | Y | U | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Spence Field-Little Bald | 2 | 7 | 12 | 0 | 0 | 2 | 4 | 7 | 2 | 36 |
| Cades Cove(T)[1/] | 3 | 3 | 1 | 0 | 0 | 3 | 4 | 1 | 0 | 15 |
| Cades Cove(B)[2/] | 6 | 2 | 0 | 0 | 0 | 3 | 2 | 0 | 0 | 13 |
| Other | 3 | 4 | 2 | 0 | 0 | 4 | 1 | 8 | 0 | 22 |
| | 14 | 16 | 15 | 0 | 0 | 12 | 11 | 16 | 2 | 86 |
| % Total | 16 | 19 | 17 | 0 | 0 | 14 | 13 | 19 | 2 | |

1/ T refers to sightings/observations made from the trail.

2/ B refers to sightings/observations made from the blinds.

Also, the manner in which boar feed does not allow the differentiation of what is actually consumed and what is simply destroyed in the feeding process. However, some information on habitat usage was gathered.

The most heavily used habitat in the Spence Field-Little Bald area is that of high elevation beech forest with an understory of mesic, mixed herbs. Blackberry patches, both in woodland and field, are rooted to varying degrees. Sedge areas in the forest are rooted, but not heavily. Usually, patches of rooting in these areas range from the size of a single hoof to several square feet. The grassy areas of the balds appear least disturbed though grazing was observed twice and hikers report it frequently. Hiker reports also indicate that boar feed on the refuse common around shelters.

In the Cades Cove area, the most striking feature of boar sign was the lack of intensive rootings. The most prevalent signs were shallow rootings (actually, more like rackings) in pine needle litter and deep, trench-like rootings around the bases and major roots of pines (usually shortleaf--*Pinus echinata* M.). The gutters and ditches along the road and some trails were also "racked-up." Only light scattered rootings occur in the fields. The only other sections showing some activity were mesic areas of mixed herbaceous species along streams.

On three occasions boar were observed feeding in grass or weeds, but not rooting or grazing. This amounted to a quick, continuous pushing of the snout up and down, back and forth over the vegetation. One set of scats found was almost 100% exoskeletous of some sort of beetle, so perhaps this feeding pattern indicated the gleaning of insects from the vegetation. In central Asia boar are known to feed extensively on grasshoppers (Sludskii, 1974).

Another feature of habitat utilization in the Cove was the irregularity of utilization of feeding sites. An area would display no fresh sign for up to several weeks, then intensive use for a period of a few days, then inactivity.

## INDIVIDUAL AND GROUP INTERACTIONS

On only six occasions was more than one individual or group sighted or observed in close proximity to each other. On none of these occasions was there any obvious sign of interactions. There was no evidence of "marked"

TABLE 2. Composition of groups sighted or observed. (Does not include records from the SF Sgelter notebook.)

| Area | Group Composition | Marked | No. of Resights |
|---|---|---|---|
| Spence Field | AF + Y | x | 2 |
| | AF + SH | x | 0 |
| | AF + SH | x | 1 |
| | AF + 2SH | x | 0 |
| | AM + AU + Y(?) | | |
| | 2AF + 5Y + SAU | | |
| | 2AU | | |
| | 1AU + U | | |
| | 1AU + U | | |
| | 3AU + SAU | | |
| | | 4 | 3 |
| Cades Cove(T) | AF + Y | | |
| | AF + SH | x | |
| | AF + 3SH | x | 2 |
| | 3SAU | x | 1 |
| | | 3 | 3 |
| Cades Cove(B) | AF + SH | | |
| | AF + SH | x | 5 |
| | 3SAU | x | 0 |
| | | 2 | 5 |
| Other | AF + Y | | |
| | AF + 2Y | | |
| | AF + 2Y + SAU | | |
| | AF + 3Y + 3SAU | | |
| | | 0 | 0 |

individuals or groups associating with other individuals or groups. No "marked" group was known to lose or gain members. Of course, all of this is based on very limited observation. There was one occasion where a known solitary male was seen feeding within sight of another adult of unknown sex but when frightened they departed in different directions.

Three different times more than one individual or group visited a particular shelter on the same night. One night two groups fed at different times; on another night two individuals fed at different times. Another time one boar was feeding near a shelter when a group of two arrived. Hikers at the shelter frightened off the latter two with a flashlight, but the solitary boar remained.

At the blinds the one multiple visitation was by two groups about 2 hours apart. At least 5 and perhaps 6 different adult males used one of the blinds over the course of the study but each was solitary and there were no multiple visits on any night.

Vocalizations appear to be important for the mother and her young but males were rarely heard. Quite often a mother will make almost continuous soft grunts while feeding with her young. On numerous occasions alarm grunts and snorts were heard from boars that had been surprised. In most cases the animals would run off a few yards (10-30) and, if a female, pause and continue to grunt and snort rapidly and repeatedly. On one occasion an almost growl-like grunt was heard. One time, when snorted at by some deer, a mother and young snorted also and then continued a dialogue of soft grunts.

Only a limited number of interspecific encounters were observed. Hikers report that one boar attempted to chase off some juvenile skunks *(Mephites mephites)* from a pile of trash but eventually gave up. One boar chased a raccoon *(Procyon lotor)* from one of the blinds but the former eventually returned and the two fed on the bait, 15 feet apart, for about 20 minutes.

Boar were never observed close to deer *(Odocoileus virginianus)* at Spence Field but were seen feeding within 50 yards of them in Cades Cove. One night a male boar was frightened from the bait at one of the blinds by a large buck. The deer also ran away. The boar returned but the deer did not. On several occasions deer snorted at boar just as they would at a hiker who surprised them.

Stegeman (1938) reports that boar and black bear *(Ursus americanus)* do not inhabit the same areas at the same time. One hiker reported that a boar appeared at the Spence Field Shelter just after a bear had left. Fresh tracks of both species were found several times at the same places along the Appalachian Trail. Bear visited the blinds several times but never when an observer was there.

TABLE 3. Summary of groups by size and type (does not include records from the SF Shelter notebook).

| Area | Number of Groups | Number of Family Groups[1] | Number of Extended Family Groups[2] | Number of Multi-Family Groups[3] | Number of Other Groups[4] |
|---|---|---|---|---|---|
| Spence Field | 11 | 4 | 1 | 1 | 5 |
| Cades Cove(T) | 4 | 3 | 0 | 0 | 1 |
| Cades Cove(B) | 3 | 2 | 0 | 0 | 1 |
| Other | 4 | 2 | 2 | 0 | 0 |
| | 22 | 11 | 3 | 1 | 7 |

Number in group

| Area | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| Spence Field | 7 | 6 | 3 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| Cades Cove(T) | 3 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Cades Cove(B) | 6 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Other | 7 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| | 23 | 10 | 6 | 3 | 0 | 0 | 1 | 1 | 0 | 0 |

1. A family group is considered to be a sow and young of the year.

2. An extended family group is a sow, young of the year, and sub-adults.

3. Multi-family groups contain at least two sows with some young of the year.

4. Any group containing no sows with young of the year is listed in this category.

## CONCLUSIONS

This preliminary survey of boar behavior yielded too few observations to allow drawing any strong inferences but three pieces of evidence would seem to warrant future work.

1. Though the female:offspring ratio is roughly in accord with that found for a neighboring population it is substantially lower than is reported from other areas (Sludskii, 1974; Diong, 1973; Eisenberg and Lockhart, 1972). It would be worth knowing if the small number of offspring is due to pre-natal mortality or low post-natal survivorship. The latter is apparently the case in the Tellico area (Tennessee Fish and Game Commission, 1971).

2. The lack of large groups, particularly of sounders, is another apparent difference between this population and others. Eisenberg and Lockhart (1972) point out that the formation of these rearing units may depend on the relative age of the offspring of different sows. Most sounders are composed of sows with litters of the same age. The lack of such rearing units in the Smokies may reflect a lack of synchrony in breeding and this should be investigated. In fact, litters may be small because females may be farrowing more than once a year.

3. The prevalence of rootings in leaf litter in Cades Cove probably indicates a search for animal foods (worms, insect larvae, snails, etc.). Considering the lack of evidence of plant food utilization in the area, animal foods may be of critical importance to the boar, at least seasonally. A closer look needs to be taken at the degree to which boar utilize animal foods and their overall importance in the diet--measured in nutritional terms as well as bulk and frequency.

## LITERATURE CITED


BEUERLE, W. 1975. Freilandunterschungen zum Kampfund Sexualverhalten des europaischen Wildschweines (Sus scrofa L.) *Z. Tierpsychol.* 39(1-5):211-258.

BRATTON, S. P. 1974. An integrated ecological approach to the management of European wild boar (Sus scrofa) *In:* Great Smoky Mountains National Park. Management Report No. 3. NPS, Uplands Field Research Laboratory, GSMNP, Gatlinburg, TN. 42 p.

CONLEY, R. H., V. G. HENRY, and G. H. MATCHKE. 1971. Final Report on European Wild Hog Research, Project W-34. Tennessee Game and Fish Commission, Nashville, TN. 259 p.

DIONG, C. H. 1973. Studies of the wild pig in Perak and Johore. Malay. Nat. J. 26:120-151.

EISENBERG, J. F. and M. LOCKHART. 1972. An ecological reconnaissance of Wilpattu National Park, Ceylon. Smithsonian Contrib. Zoology, No. 101. Smithsonian Institution, Wash., D. C. 118 p.

FRADARICH, H. 1974. A comparison of behavior in the Suidae. *In:* v. Geist and F. Walther (eds.) Behavior of Ungulates and its Relation to Management. IUCN Publications, NS No. 24. IUCN. Morges, Switz. 940 p.

HAFEZ, E. S. E. 1962. The Behavior of Domestic Animals. Boilliere Tindall Co., London.

HENRY, B. L. et al. 1962. Climatological Summary of Gatlinburg, TN. U. S. Dept. of Commerce, Wash., D. C.

KING, P. B., R. B. NEWMAN, and J. B. HADLEY. 1968. Geology of the Great Smoky Mountains National Park, Tennessee, North Carolina. U. S. Geol. Survey Prof. Paper 587. USGS, Wash, D. C. 23 p.

LINDSAY, M. 1976. History of the grassy balds in Great Smoky Mountains National Park. Management Report No. 4. NPS, Uplands Field Research Laboratory, GSMNP, Gatlinburg, TN. 217 p.

SLUDSKII, A. A. 1974. The Wild Boar: Its Ecology and Economic Importance. Translated from the Russian by P. Auklund. CSIRO, Melbourne, Australia.

STEGEMAN, L. C. 1938. The European wild boar in the Cherokee National Forest, Tennessee. J. Mammal. 19:279-290.

SEBER, G. A. F. 1973. The Estimation of Animal Abundance. Charles Griffin and Company, London. 506 p.

WHITTAKER, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monog. 26:1-80.

# THE FERAL PIG IN HAWAII VOLCANOES NATIONAL PARK

James K. Baker[1]

The first pigs (*Sus* sp.) in the Hawaiian Islands arrived along with migrations of Polynesian man about 1,200 years ago. Polynesians carried pigs, dogs and jungle fowl on long exploratory voyages as items of food when looking for new lands to settle.

Domesticated pigs were widely distributed throughout the Pacific not only by aboriginal man but in more recent times by European explorers and colonists. Pigs and goats were often released on islands to establish ready food supplies for other explorers and colonists who would follow.

By the time the first Europeans arrived in Hawaii in 1778 Polynesian pigs were already distributed throughout the six major islands of the archipelago. Captain James Cook, an Englishman (1785) noted that these pigs were common about the villages and that they were small in size, weighing about 60 pounds, and were black in color.

In 1778 Cook released the first varieties of European domesticated pigs in Hawaii, and in the nearly 200 years since that time large numbers of other domesticated pigs have been introduced to upgrade the quality of pork raised in Hawaii. Boars of larger breeds were purposefully released into the wild to increase the size of the much smaller Polynesian pig (Judd 1936, Tomich 1969). From these releases and the escape of other domesticated pigs into the wild, such mixtures of European/Polynesian stock occurred that the Polynesian pig is no longer recognizable.

Since domesticated pigs readily revert to a feral state it seems probable that populations of feral pigs became established in Hawaii not long after the first introductions some 1,200 years ago. Ellis (1917) observed in 1823 that Hawaiian people possessed small pigs which were sometimes found wild in the mountains. Today, wild populations of feral pigs--whatever their origin--are common throughout all the major islands. They are especially abundant in forests on the island called Hawaii, and in rain forest habitats of Hawaii Volcanoes National Park.

On the island of Hawaii feral pigs, goats and sheep are abundant game animals which are highly prized for trophies and meat. Despite the popularity of the pig as a game animal free-roaming pigs are pests in grassland, crop, forest and watershed areas, and their damages can be extensive through rooting and foraging, the making of trails and mud wallows, and from causing spread of weedy, non-native plants in areas of disturbance.

Along with other introduced predators in Hawaii such as housecats, rats, dogs and mongooses, pigs are suspect in large part for extinction of native flightless birds, and endangering other ground nesting species such as the nene, or Hawaiian goose. Moreover, the pig is a suspect in spread of avian diseases by creation of aquatic habitats for mosquito vectors, as well as being suspected of spreading root-rot fungi which may be one cause for loss of native trees.

Within the boundaries of Hawaii Volcanoes, pigs are distributed from sea level to about 7,000 feet on the slopes of Mauna Loa Volcano, the upper limits of suitable cover and feeding habitat. At the higher elevations above about 4,000 feet pigs utilize a mountain parkland with mixed forest and grassland. Studies by Mueller-Dombois and Spatz (1972) show that in these grassland areas pigs are causing changes in the composition of species favoring spread of non-native grass.

In areas below about 4,000 feet pigs are abundant in rain forest habitats where they feed largely on hapu or tree ferns (*Cibotium* sp.) and other fern species. Analyses of stomach contents show hapu and other ferns to comprise as much as 85 percent of the diet. Pigs will feed on all age classes of ferns but because they seem to prefer the starchy interior pulp of tree fern trunks, they feed extensively on larger ferns which have toppled from natural causes. We have no observations or evidence to indicate pigs purposefully uproot larger ferns but they do push against or uproot smaller ferns.

Pigs feed upon the interior pulp of tree fern trunks by biting away the hard outer bark-like tissues and scraping out the pulp by use of scoop-shaped lower incisor teeth. A large trunk 12 inches or more in diameter and several feet in length will feed one to several pigs for several days. In time the trunk is hollowed, appearing as a dug-out canoe, and will become a catchment basin for rainwater.

From extensive feeding on a tree fern trunk pigs trample all ground cover around the fern, and establish trails through the forest to and from the trunk. Discovery of new trails in the forest often leads to a fallen tree fern.

Other items of diet in the rain forest are grasses and sedges, comprising as much as 5 to 10 percent of the diet, insects and earthworms, comprising as much as 3 percent, mud and soil litter about 5 percent, and unidentified matter about 2 percent.

It appears that rain forest pigs can subsist almost entirely on ferns and grass and it becomes obvious that since these foods are taken above ground level, the excessive damage done by rooting is done principally in searching for earthworms. While earthworms are a relatively small part of the diet, volume-wise, they are a highly desired delicacy and are found in some amount in nearly all stomachs taken.

Earthworms are searched for in grassy spots where investigations reveal they are often found right at ground level and pigs will uproot and roll back grass while foraging for earthworms much like one would roll back a carpet. One pig stomach analyzed after a period of intensive rooting in grass revealed relatively little grass but the remains of approximately 50 earthworms. Insect remains were also found.

[1]Hawaii Volcanoes National Park, Hawaii 96718.

Wherever fruits and berries are locally abundant pigs feed extensively upon such weedy, non-native species as guava and passion fruits, and the spread of these noxious weeds around Hawaii is probably due in large part to the feeding activities of pigs. Dense tangles of blackberry bushes are also used as hideaways and beds.

Stomach analyses also reveal that pigs are scavengers, feeding on goat, pig and cattle carcasses. Hunter discarded remains of pigs and goats are devoured in a relatively short period of time and observations reveal that pigs prefer remains that are in advanced stages of decomposition when teeming with fly maggots. It is believed maggots are a main attractant since elsewhere we observe that caterpillars and earthworms are readily searched for and consumed.

It is a well known habit of pigs to wallow in mud, and the probable reasons are that mud soothes dry skin; it cools in hot weather; it helps rid skin of lice; and it eases the severe itching from mange caused by mites. In addition to wallowing in mud pigs also scratch and rub themselves against rough rocks and tree trunks and good rubbing trees are landmarks in the forest.

Mud wallows in the park are confined to rain forest habitats where occasional patches of swampy ground occur with boggy soils deep enough to form a body sized depression and wet enough to remain muddy for long periods of time during the summer dry season. In areas outside the rain forest mud wallows are almost non-existent

A well established wallow may be used almost daily by a number of pigs, and pigs use more than one wallow. Several wallows may occur within the home range of a pig and the only trails in the forest which can be considered permanent are trails leading between wallows. Some of these trails may be several hundred meters in length.

In the making of wallows and tree fern hollows, rain catchment basins are formed which become habitats for mosquito larvae and other aquatic organisms. In places pig created aquatic habitats are abundant. In one, one hectare study area 35 tree fern hollows were located which contained mosquito larvae, and in a 25 hectare study plot five mud wallows contained water and larvae. Larvae of four other families of dipterans are also found, as well as numerous species of nematodes, copepods, ostracods, cladocera and protozoa.

There were no mosquitoes in Hawaii before 1826 when *Culex* species were accidentally introduced. Though there was a potential for epizootic diseases among forest birds in Hawaii before introduction of mosquitoes, because of bird migrations from mainland areas, there were no vectors to spread the diseases among non-migratory species. Consequently, Warner (1968) has shown that Hawaiian forest birds never developed immunities to bird malaria and pox, and it is believed that spread of these diseases after arrival of mosquitoes helped cause the extinction of many Hawaiian species.

The Hawaiian rain forests are relatively free of free standing ground water because of the shallow, porous lava soils, but the compaction of soils by pigs in making wallows, and in hollowing out tree ferns, is greatly increasing the potential and occurrence of mosquitoes in the forest, and spread of avian disease. The role of the pig in the spread of mosquitoes is under continuing investigation and the study will be supported in part by work of an avian pathologist beginning sometime later next year.

In studying the impact of pigs upon certain forest trees we found an interesting cause and effect relationship between boars and pilo (*Coprosma* sp.) trees. The pilo is a common understory tree which has soft, succulent, palatable bark which boars slash with their tusks.

Boars slash the bark for two probable reasons: (1) to eat the bark for food and moisture, and/or (2) to mark territory or show size superiority or male dominance. Slash marks appear to be made as high up a trunk as a boar could reach, and tusk marks out of reach of smaller boars may indicate the presence of larger animals.

The pilo is normally a straight, slender, single-trunked tree which grows tall in competition with other trees for available sunlight. On occasion naturally occurring multiple-trunked trees are found but it would appear they are at a disadvantage in competition for sunlight because they spread out and grow less tall. Natural selection would tend to favor the taller single-trunked trees.

In the presence of pigs, however, single trunked trees are at a disadvantage because pigs can remove the bark from around the trunk and kill the tree. Multiple-trunked trees become favored because two or more trunks protect the bark between closely spaced trunks.

A bark damaged pilo responds by sending up sucker growth from the base of the injury usually at ground level. In time, these grow into additional trunks and once established the survival of secondary growth, multiple-trunked trees is enhanced.

Studies of single- vs. multiple-trunked trees in areas free of pigs vs. areas foraged in by pigs show significantly higher percentages of multiple-trunked pilo where pigs are present. It would appear, therefore, that if mutations occur for multiple-trunked trees such mutations would be favored. As new biological pressures in older Hawaiian ecosystems, the pig could well be causing adaptation and evolution in a native tree from one trunk to several trunks better suited for survival.

Since the pig is a destructive, non-native intruder, National Park policy states that the pig should be eliminated. The objective, however, is made difficult because of the secretive nature of the animal in often, almost impenetrable rain forest habitats, and because of the sensitive ethno-political issues in Hawaii favoring the pig as a game animal and its cultural significance to island people. There is an argument that the pig in Hawaii should be considered "native" since it was part of aboriginal culture before the arrival of European man.

Aside from these considerations pig control within the park will be difficult and probably impossible with present techniques of trapping and hunting and the Federal ban on use of poison. The most we can do, and are doing at the present, is to hunt out and trap those pigs in areas of high impact where they are doing the most damage.

## LITERATURE CITED


COOK, J. 1785. A Voyage to the Pacific Ocean. 2nd ed. Vols. I-III, London: Hughs, Vol. II, p, 190-252.

ELLIS, W. 1917. A Narrative of a tour through Hawaii, or Owhyhee. Honolulu: Haw. Gazette (Reprint of the London 1827 edition), 367 pp.

JUDD, C. S. 1936. Hawaii's forests winning their battle with wild animals. Honolulu Star-Bulletin, March 21, 3rd Sec., pp. 1, 7.

SPATZ, G. and D. MUELLER-DOMBOIS. 1972. Succession patterns after pig digging in grassland communities on Mauna Loa, Howaii. Island Ecosystems IRP, Tech. Rept. No. 15; U. S. Internat'l. Biol. Program; 44 pp.

TOMICH, P. Q. 1969. Mammals in Hawaii, Bernice P. Bishop Mus. Spec. Pub. 57. Bishop Museum Press, Honolulu; 81 pp.

WARNER, R. E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. Condor 70(2):101-120.

# THE BEHAVIOR, ECOLOGY, AND SOCIAL ORGANIZATION OF THE FERAL PONIES OF ASSATEAGUE ISLAND[1]

Ronald R. Keiper[2]

## INTRODUCTION

Although some attention has been paid to isolated behavior patterns of equines, such as grooming (Trumler, 1959) and mating behaviors (Zeeb, 1963), few studies have been conducted on the general social organization. Likewise, most available observations refer to domesticated animals or captive animals in zoos. Recent studies have been conducted on the Mountain and Steppe Zebra (Klingel, 1967) and on the New Forest ponies in England (Tyler, 1972), but little scientific information is available on the behavior, ecology, and social organization of the feral ponies that inhabit a number of barrier islands along the Atlantic coast of the United States. These islands include Assateague Island, along the coast of Maryland and Virginia, Shackleford and Ocracoke Island, along the coast of North Carolina, and Cumberland Island, along the coast of Georgia. Since the environments occupied by these ponies are quite different from those inhabited by zebras or New Forest ponies, special adaptations in behavior and ecology might be expected. These barrier island ponies also are of interest since they occupy land that is now, or will become in the near future, part of national seashores. Information obtained on their behavior and ecology can be used to establish appropriate management programs to assure their continued existence.

## MATERIALS AND METHODS

Approximately 200 ponies live on Assateague Island. These include about 45 animals inhabiting the northern (Maryland) portion of the island and owned by the National Park Service, and 155 ponies occupying the Chincoteague National Wildlife Refuge on the southern (Virginia) end of the island. The ponies lead a relatively wild existence in that they roam freely throughout the 35 mile island and obtain their own food throughout the year. The ponies on the southern portion, which are owned by the Chincoteague, Virginia Volunteer Fire Company, are rounded up each year during the last week of July and most of the foals are removed and sold at auction. The Maryland ponies have not been subject to the round-up since the island became a national seashore in 1966.

Because of their exposure to man, the ponies can be observed at close range without affecting their normal behavior. Each pony could be individually recognized on the basis of sex, size, color, and markings. For future reference and for proper recording of data, an identification sheet was completed for each animal indicating the pertinent data for recognition. The pony was assigned a code letter, indicating herd membership, as well as a code number.

During over 1000 hours of field observation, data were collected on the behavior of individual ponies as well as on the entire herd using maps of the area and check sheets where various activities were recorded at 1 minute intervals for each hour of daylight.

## RESULTS AND DISCUSSION

Significant data were collected in three general areas of pony biology: Ecology and Population Dynamics, Behavior of Individual Animals, and Social Organization. With respect to Population Dynamics, the birth rate for the Assateague ponies for 1975 and 1976 was approximately 60% while the death rate was about 15% for the same period. The sex ratio of the 99 foals born during the course of the study was approximately 60% male to 40% female. Births began as early as February and continued until September, but most births (64%) occurred during May.

Ecologically, the ponies utilized all 6 of the different kinds of habitats on Assateague Island (beach, dune zone, inner dune zone, shrub zone, tree zone, and saltmarsh), although they spent most of the time grazing either in the saltmarsh or in the dune and inner dune zone. The shrub and beach zones were used primarily for movement, although the ponies frequently spent long periods of time during the summer standing on the beach utilizing the ocean breezes to ward off the swarms of biting flies. The tree zone was used for resting, although this area also contained a number of permanent waterholes that the ponies visit each day for drinking.

Although a number of other animals are found on Assateague, few interactions occur between them and the ponies. One unique relationship exists between the ponies and birds called Cattle Egrets. As many as 32 of these birds were observed feeding with a herd of ponies for as long as 3 hours. The birds commonly pick insects off the undersides and legs of the ponies, and frequently perch on their backs for as long as 60 minutes. By observing and recording the behavior of these birds during timed 1 minute intervals, it was demonstrated that the birds obtained more food by walking beside grazing ponies than by searching for food on their own (Keiper, 1976).

Interactions also were noted between invertebrates and the ponies, with mosquitoes and biting flies creating the most serious problem. In response to high insect populations, the ponies exhibit several unusual behaviors which can be considered "anti-insect" in nature. The animals wade out into the waters of Chincoteague Bay to a depth of 2-3 feet and remain there for as long as six hours. Another behavior seen at this time that also involves the entire herd is termed "circling". In "circling" the members of the herd stand in close proximity, so that the tail

[1]I wish to thank the National Park Service, the Chincoteague Wildlife Refuge, and the Chincoteague Volunteer Fire Company for granting me access to their lands and permission to observe the Assateague ponies. I also thank the National Park Service for financial support for the research.

[2]Pennsylvania State Universitym Mont Alto, Pennsylvania 17237.

of one pony swishes the body of another. There is constant movement as one pony brushes past other members of the standing group rubbing its body against their bodies. After circling about the herd, the first pony stops and another one begins to move in the same way. The third unusual "anti-insect" behavior seen at times of peak insect levels is "running". At times a herd will be engaged in grazing when suddenly the entire group dashes across the terrain. The animals run for several hundred yards, stop and graze briefly, then run again. Often the ponies move to the shade of the tree zone where insect activity is reduced. In addition to the three behaviors discussed above, head-shaking, blowing (exhaling of air violently through the nostrils), rolling, and rubbing behaviors were also commonly seen at this time.

During each month data were collected on the behavior of individual ponies using check sheets where various activities were recorded at 1 minute intervals for each hour of daylight. As expected grazing activities occupy the major portion of the day, although some resting and grooming behavior can be seen throughout the day. By far the most important food plants were *Spartina alterniflora*, *Spartina patens*, and *Ammophila breviligulata*. In addition to grazing on these grasses, the ponies were observed to feed on a variety of other herbaceous plants and to browse on a number of woody species. In later winter, the animals browse on Marsh Elder and obtain most of their food from this source.

One pattern that seemed to emerge from the data was that resting activities occurred most frequently during the summer between 0600 and 0830 EST, but were most common after 0900 EST in the fall. Ponies rested either standing or lying down, with standing behavior being more typical of adults. Resting behavior was often "contagious", with the resting of one animal triggering the appearance of resting actions in others.

Grooming behaviors were also "contagious" and included rubbing, rolling, and mutual grooming activities. Rubbing was directed against a fixed object such as a tree or post, and was most often observed in the fall, when the thick winter coats were growing in, during the spring, when the winter coats were being shed, and during periods of peak insect activity. Rubbing behavior often continued for 10-15 minutes.

A special type of rubbing behavior was where the back was rubbed against the ground. Such rolling occurred at the end of a resting session, just before a lying animal arose, during periods of high insect activity, and when a pony had just crossed a body of water and had gotten its coat wet. An animal usually rolled 2-6 times before getting back up, and the total duration of such behavior was usually less than 2 minutes.

While mutual grooming may have been used for the same reasons as auto-grooming, this behavior was also an important form of social contact between ponies. It occurred when 2 animals stood facing each other and nibbled at the neck, mane, chest, shoulder, or withers of their partner. Such behavior rarely lasted as long as 5 minutes. Mutual grooming apparently functions to establish and maintain social ties between members of a herd.

A fourth type of maintenance behavior engaged in by each animal during the course of each day was drinking behavior. The ponies were observed to drink from a variety of sources including permanent waterholes, temporary puddles of rainwater, tidal streams, and the waters of Chincoteague Bay. When drinking from salty sources, ponies take only a few short sips, with a total drinking time lasting only 10-15 seconds. In most cases, such drinking followed periods of exertion (after a "forced march" along the beach or an aggressive encounter between stallions) or occurred when the animals were standing for several hours in the Chincoteague Bay to escape the biting flies.

When drinking from primarily fresh water sources, the ponies took long draughts which often lasted for 2-3 minutes. The ponies usually move to waterholes twice daily; just after sunrise and just after sunset. Often these movements are over relatively long distances, and take 10-25 minutes to complete.

The Assateague ponies socially were organized into 17 different herds, ranging in size from 3 to 26 animals. The size and composition of each of the herds, at its maximum population size, is shown in Table 1. The 17 herds fall, however, into 4 basic types with respect to composition. Most of the herds (12) consisted of a dominant stallion, 2-15 mares, and their offspring. Four of the herds (herds D, M, N, and T) contained at least 1 other male in addition to the dominant stallion, although these were young, sexually immature males 1-3 years of age.

Of the remaining 5 herds, 1 (herd G) consisted of 3 young males and 3 young females, 2 herds (herds S and K) were composed entirely of young males, and 2 herds (herds F and R) were made up only of females and their offspring.

This social structure appears similar to the organization of other feral equines. In the Steppe and Mountain Zebra, most groups consisted of a stallion, 1-6 mares, and their foals (Klingel 1967, 1968). While most of the Assateague herds were of similar size and composition, 4 of the herds (herds D, M, N, and III) contained between 6 and 10 mares, and 3 of the herds (herds E, B, and V) consisted of 10-15 mares. However, all but herds M and N live on the Virginia portion of the island where the number of stallions is limited by the removal and sale of colts.

The second type of herd did not appear to have a dominant stallion, but instead consisted of 3 young apparently co-dominant males. Such apparent co-dominance has not been reported in either New Forest ponies or in zebras (Klingel 1968, Tyler 1972).

As in zebras (Klingel 1967), bachelor herds of young males existed in the Assateague ponies. Although it is unclear why these all-male herds have formed, such herds in zebras were created when young zebra colts left their mothers at about 3 years of age. The small number of stallions in the New Forest ponies prevented the existence of bachelor herds there (Tyler 1972).

If a zebra stallion was removed from his group, the mares of that group remained together, suggesting that the mares formed a stable unit in themselves and were not kept together only by the actions of the stallion (Klingel 1967). All-mare groups also were common in the New Forest ponies, but here the number of stallions was limited by the actions of man (Tyler 1972). Stable, all-female herds also were present on

TABLE 1. Size and composition of feral pony herds on Assateague Island. Numbers represent maximum population size.

| Herd designation | Stallions | Mares | Foals | Total |
|---|---|---|---|---|
| B | 1 | 15 | 10 | 26 |
| D | 2 | 8 | 6 | 16 |
| E | 1 | 15 | 4 | 20 |
| F | 0 | 6 | 5 | 11 |
| G | 3 | 3 | 1 | 7 |
| H | 1 | 2 | 2 | 5 |
| R | 0 | 3 | 1 | 4 |
| S | 4 | 0 | 0 | 4 |
| I. | 1 | 5 | 5 | 11 |
| II. | 1 | 5 | 4 | 10 |
| III. | 1 | 7 | 5 | 13 |
| IV. | 1 | 2 | 2 | 5 |
| V. | 1 | 10 | 10 | 21 |
| M | 3 | 8 | 6 | 17 |
| N | 6 | 8 | 4 | 18 |
| T | 2 | 5 | 0 | 7 |
| K | 3 | 0 | 0 | 3 |

Herds above the line were found in the Vurginia portion of the island, herds below the line occupied the Maryland end of Assateague.

Assateague, where such groups have persisted for as long as 6 months.

Changes in the composition of many of the herds occurred during the study, but these were largely due to deaths and to the removal of foals by man. For example, 28 deaths have occurred on the island since June 1975 and 50 foals were removed and sold during the annual pennings in July 1975 and 1976.

In addition to these permanent changes in herd structure, several other kinds of changes were noted. Fusion of 2 herds took place when the stallion from herd H took over leadership of herd F, an all-mare herd. In a similar situation, fusion of two herds took place when the death of a dominant stallion allowed a younger stallion in another herd to assume herd leadership.

A number of other mares frequently left their herds to temporarily join other herds or wander independently, but these separations usually lasted for only a few days. Often these adult mares were accompanied by their offspring or by one or more adult animals. These wandering animals apparently returned to their original herds at their own volition and not as the result of any coercion by the stallion.

When attempting to remove mares from another herd, or when trying to protect his mares from a challenging stallion, the dominant stallion uses a technique called "snaking". In this posture, the ears are laid back against the head, and the neck is extended and projected frontward parallel to the ground. The stallion then runs along one side of the mare, causing her to turn in the opposite direction.

Although the dominant stallion controlled the movements of his mares in the presence of rival stallions, he did not normally control the daily activities and movements of the herd. The degree of control exerted by the stallion varied from herd to herd and may be a reflection of the age of the stallion. During grazing, movement was generally unorganized with leadership varying. When the ponies displayed long distance movements, sometimes walking over 1/2 mile without grazing to waterholes, to new grazing areas, or to evening resting sites, the leader was usually a specific mare. Often this "leader mare" directed the herd away from the stallion and he would run to catch up to the rear of the moving column or would follow at some distance behind the herd. The qualities that make a mare the leader are unknown at this time but may include age, or the number of offspring in the herd that will follow their mother.

Unlike many other animals, there was no evidence of territorial behavior observed in the Assateague ponies. As in the New Forest animals (Tyler 1972), each herd did seem to have a definite home range that was normally transversed in the pursuit of daily activities.

In conclusion, although considerable insight has been gained into the social life of the Assateague ponies, long-term observation will continue until a complete and comprehensive picture into the social organization of these feral barrier island animals has been recorded.

## LITERATURE CITED


KEIPER, R. 1976. Interactions between Cattle Egrets and Feral Ponies. Proceeding Pa. Acad. of Sci., 50:35-57.

KLINGEL, H. 1967. Soziale Organisation und Verhalten freilebender Steppenzebras. Z. Tierpsychol., 24:580-624.

KLINGEL, H. 1968. Soziale Organisation und Verhaltensweisen vom Hartmann-und-Bergzebras. *Eguus zebra hartmannae* und *E. z. zebra*. Z. Tierpsychol., 25:76-88.

TRUMLER, E. 1959. Beobachtungen an den Bohmzebras des Georg von Opel-Friegeheges fur Tierforschung II. Die Hauptflege. Saugetierk Mitt., 7:104-125.

TYLER, S. J. 1972. The Behaviour and Social Organization of the New Forest Ponies. Animal Behav. Mono., 5(2):87-196.

ZEEB, K. and KLEINSCHMIDT, A. 1963. Beobachtungen zum Paarungsverhalten von Grevyzebras in Gefangenschaft. Z. Tierpsychol., 20:207-214.

# ECOLOGICAL STUDIES OF FERAL BURROS IN DEATH VALLEY

Charles L. Douglas and Christopher Norment[1]

The feral ass (*Equus asinus*), a native of northeastern Africa is estimated to have been introduced into the Death Valley region in the 1870's by prospectors and miners (Hansen, 1973). As mining activities decreased, many animals were released to become feral, leading to the establishment of extensive herds of burros in the Death Valley area. Incremental increases in the herd through time were concomitant with environmental damage and encroachment on wildlife habitat. Numerous workers have discussed burros in Death Valley National Monument, and these animals have long been regarded as a major problem for resource management. The earliest report of burro damage was by Dixon and Sumner (1939). Welles and Welles (1961) studied bighorn sheep in Death Valley National Monument, but found no evidence of direct competition between burros and bighorn. Hansen (1973) described environmental damage caused by feral burros in the Monument. The most complete and comprehensive study of burro behavior was conducted by Patricia Moehlman from 1970 through 1973 (Moehlman, 1974). With the exception of Moehlman's study, reports on burros in Death Valley have tended to be qualitative and subjective.

Our study began in 1973 with the intent of describing seasonal movements and home ranges, population dynamics and genetics, and secondary productivity. To evaluate the impact of feral burros on vegetation, it also was necessary to study the productivity of various forage species and the seasonal changes in nutrient and energy content. It was hoped that seasonal changes in the phenology and nutrient content of forage species could be linked to behavioral characteristics of the burros, such as seasonal movements, reproduction, etc. Studies of growth and development are underway; these data are expected to be of utility in refining the model of an energy budget for the Death Valley herd. This report concerns only seasonal movements; other aspects of the study will be reported upon elsewhere.

The study area (Figure 1) is located in the Panamint Mountains of Death Valley National Monument, California, and contains approximately 600 $km^2$. It is bounded on the north by Towne Pass and California State Highway 190, on the west by Panamint Valley, on the south by Telescope Peak and Tuber Canyon, and on the east by the crest of the Panamint Mountains, except that the Trail Canyon drainage is included. The area ranges in altitude from approximately 610 m on the alluvial fans just east of Panamint Valley to 3368 m on the summit of Telescope Peak. However, the majority of the area lies at elevations between 900 m and 2100 m above sea level. Topography is varied, with open flats and wide, gently sloping valleys contrasting with steep, sharply eroded mountainous terrain and narrow, rugged canyons. There are no permanent running streams within the study area, although running water appears for short distances in Wildrose and Tuber Canyons. There are approximately 31 sources of water in the study area which are available to wildlife, with flows ranging from minimal seepage to 190 liters per minute. Distribution of these water sources is spotty, with good numbers in Emigrant, Trail, Wildrose, and Tuber Canyons and few in other parts of the area (Figure 2).

Six major plant communities, as described and classified by Munz (1959) occur within the study area: creosotebush scrub, shadscale scrub, sagebrush scrub, pinyon-juniper woodland, bristlecone pine forest, and subalpine forest. During the course of the study, burros were observed in all six of these communities.

Burros were trapped in the NPS trap in Wildrose Canyon and were then immobilized by means of an intramuscular injection of M-99 (Etorphine hydrochloride) administered either by syringe or by a dart fired from a Cap-Chur gun (Palmer Chemical Co., Georgia). Several individuals also were tranquilized in the field. All individuals were blindfolded to protect the eyes, and were restrained by means of hobbles. Measurements were taken of total length, tail, hind foot, ear, heart girth, neck, lower jaw, head, and interorbital width. Approximately 10 cc of blood was drawn from the external jugular vein for studies of physiological parameters and for a study of genetics, utilizing serum proteins. The first 40 individuals were weighed, but this procedure proved to be too time-consuming, and was discontinued. After all procedures were completed, the animal was given an I. V. injection of the antagonist M 50-50 (Diprenorphine). More than 100 individual burros were handled; some of these were later given away to residents of California who had obtained the proper permits. The remainder were tagged, and/or collared, and released. Fifty-eight individuals were equipped with ear tags; 23 of these also were equipped with color-coded collars constructed of 10 ounce vinyl cloth sewn on nylon webbing (1/4" x 4"). Collars were bolted around the necks of selected individuals by means of a metal clamp. Such collars were highly visible from the ground and from the air. Five individuals were equipped with radio telemetry collars (Telonics, Inc. of Tempe, Arizona). The transmitter and helical antenna were mounted on a 7.6 cm wide leather strap and encased in urelane plastic. Transmitters operated on 148MHz, power was supplied by a lithium battery having a 10AH capacity and a life expectancy of 18 to 24 months.

The distribution of burros was studied by means of ground and aerial surveys, which were conducted at least once each month. In the first several months of the study, movements were monitored on a bi-weekly basis. Each aerial survey was followed immediately by a ground survey.

Moehlman (1974) identified a maximum population of 237 burros in the Emigrant-Wildrose area during her study. Subsequent trapping by the NPS from 1973 to 1976, reduced the local population by 139 individuals. Selective trapping

[1]National Park Service Cooperative Resources Studies Unit, University of Nevada, Las Vegas, 89154.

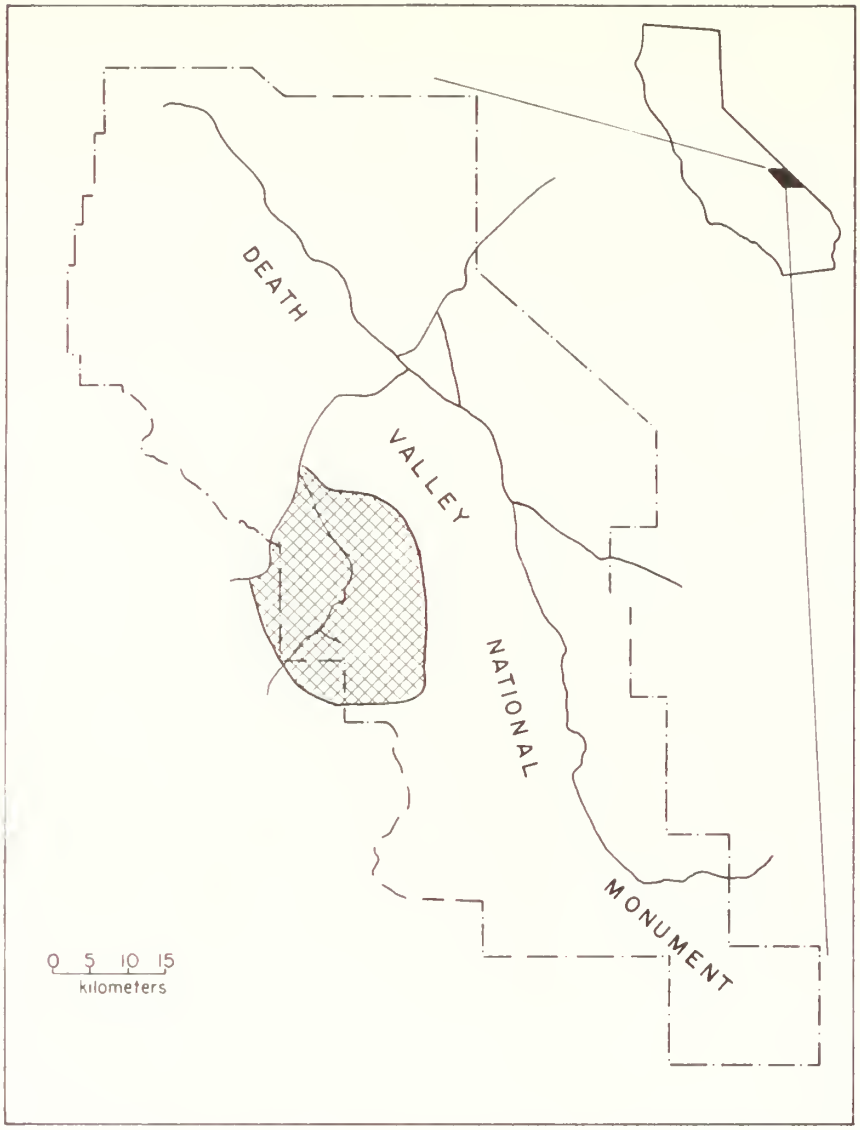



FIGURE 1. Location of study area, Death Valley National Monument, California.

for females, foals and for yearlings greatly hampered our efforts to mark young individuals for the study of movements. Our data on movement are therefore mostly for adults. The largest number of burros observed within the study area of Moehlman at any one census during our study (Figure 1) was 118 on March 15; out of a total of 23 color-collared burros, 13 were not observed during the census, for a total of 131 individuals. If this figure is subtracted from Moehlman's total of 237, a net loss of 106 animals is arrived at. The difference of 33 individuals between this figure and the 139 animals removed by trapping could be due to some immigration of adult burros into the study area in addition to new individuals born to the females remaining in the population.

Figure 3 summarizes the monthly distribution of burros in each subdivision of the study area for a period of 16 months. In spring and summer, burros were concentrated in Wildrose Canyon where their reproductive activities occur, and where there is an abundant water supply. As the temperatures moderate in the early autumn, burros move out of Wildrose Canyon into the Harrisburg, Skidoo, Nemo and Wood Canyon areas (Figure 2). In general, these are somewhat higher elevations that are poorly watered but that encompass vast amounts of acreage.

The normal circumstance is for most burros to leave Wildrose Canyon by mid-October. This was the situation in 1975, but not in 1976; in September 1976 there were extensive rains that promoted new growth of the browse species. Consequently, burros remained in Wildrose Canyon longer to take advantage of this new forage. It is important to note the long duration of time during which a large percentage of the burros remain in Wildrose Canyon. This high density of individuals in one canyon for approximately six months each year is concomitant with considerable environmental damage that will be discussed later.

Burros utilize the Arcane Meadows throughout the summer and early autumn. This part of the study area has the highest elevations and is not utilized in the winter months owing to snows and severe temperatures.

The alluvial fans are at the lowest elevation in the study area, and are utilized by burros only during the winter and spring months, while water stress is not a problem. Emigrant Canyon has some monthly fluctuations in burro numbers, but retains a small resident grouping of about 20 individuals throughout the year. Some females with foals leave Wildrose to winter in the Emigrant Canyon area.

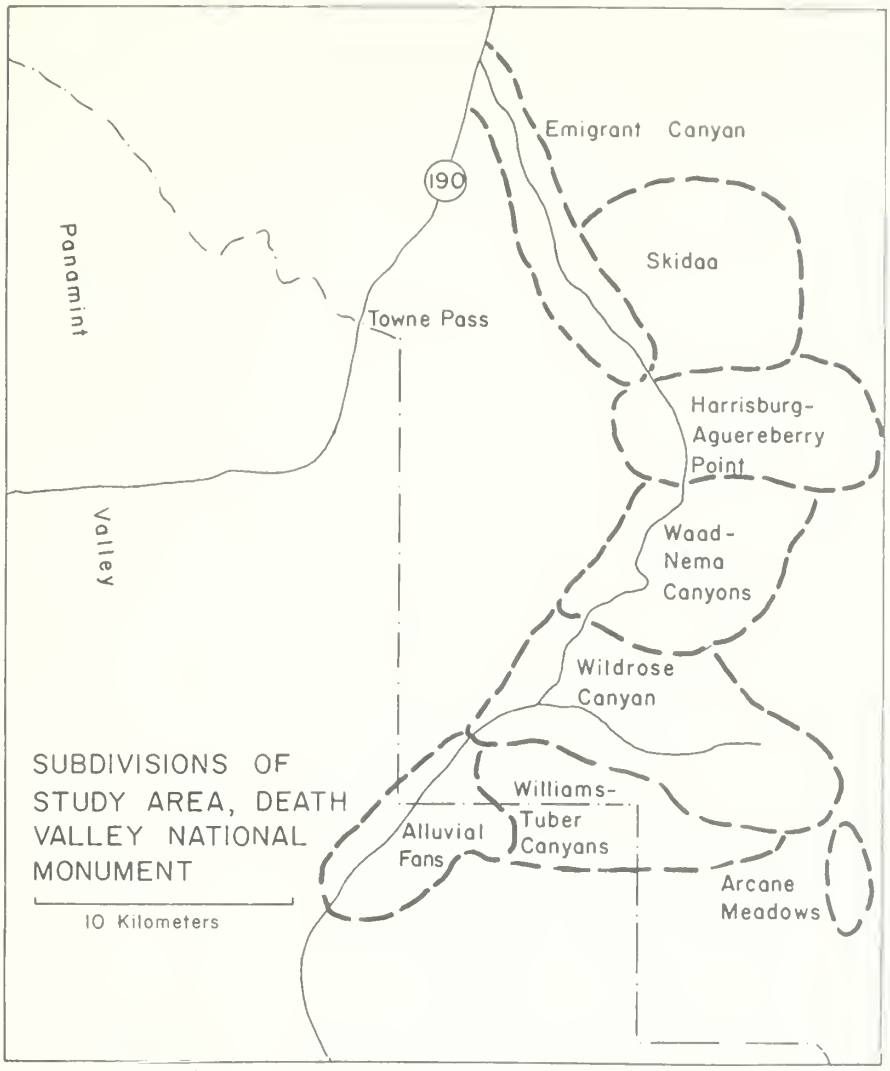



FIGURE 2. Subdivisions of the study area in Death Valley National Monument.

Monthly changes in elevational distribution of feral burros are shown in Figure 4. Our data agree with those of Moehlman (1974) insofar as changes in seasonal elevations are concerned, but differ in that we observed a significant percentage of individuals at elevations below 1200 meters during parts of the year when burros are less restricted to permanent water sources. Intermediate (1200-1500 m) and higher (1500-1800) elevations are utilized most during the hottest parts of the year. These elevations are represented by Wildrose Canyon and by Harrisburg-Skidoo-Nemo and Wood Canyons, respectively (compare with Figure 3). The majority of burros spent summer months at elevations of 1210 to 1525 meters. The highest elevations are utilized (Arcane Meadows) mostly in non-winter months, although such use is dictated in large part by the presence or absence of snows.

A major factor dictating burro movements is the availability of free water during the hot summer and early autumn months. Burros drink at least once daily in hot weather, providing water is available. Pregnant or lactating females, and young animals require more water, and may water more frequently. Figure [illegible] shows the monthly distribution of burros from water. May through September are months during which the majority of burros in the study area were within four km of water. The moderation of temperatures in September or October permits larger movements away from water, culminating in the mid-winter period during which the majority of the population are from four to more than six km from water.

The effect of burros on browse plants was evaluated by classifying browse impact on each shrub in ten, 10 x 10 m quadrats in each of four areas (Figure 6). The Vesey-Fitzgerald method (1973) of impact assessment was utilized. In this method there are the following categories: no impact; B1 - in which a slight amount of browsing such as clipped terminal ends of branches is evident; B2 - in which the browsing has altered the shape of the plant; and B3 - in which the browsing has been so severe that the plant may not recover.

Figure 6 shows that more than [illegible] percent of the plants in Wildrose Canyon have been browsed

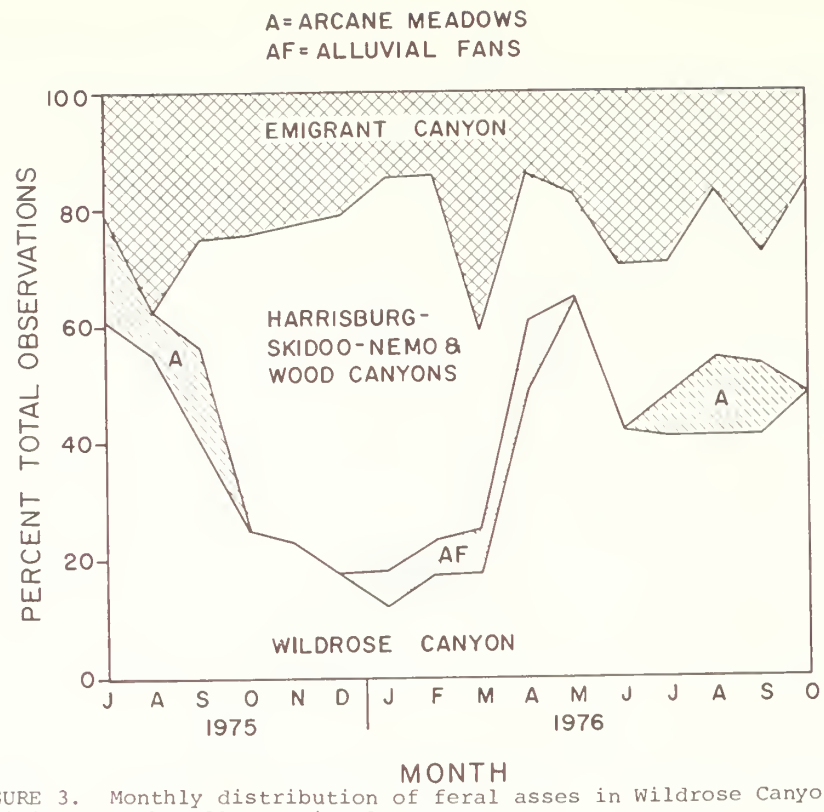



FIGURE 3. Monthly distribution of feral asses in Wildrose Canyon and vicinity, Death Valley National Monument.

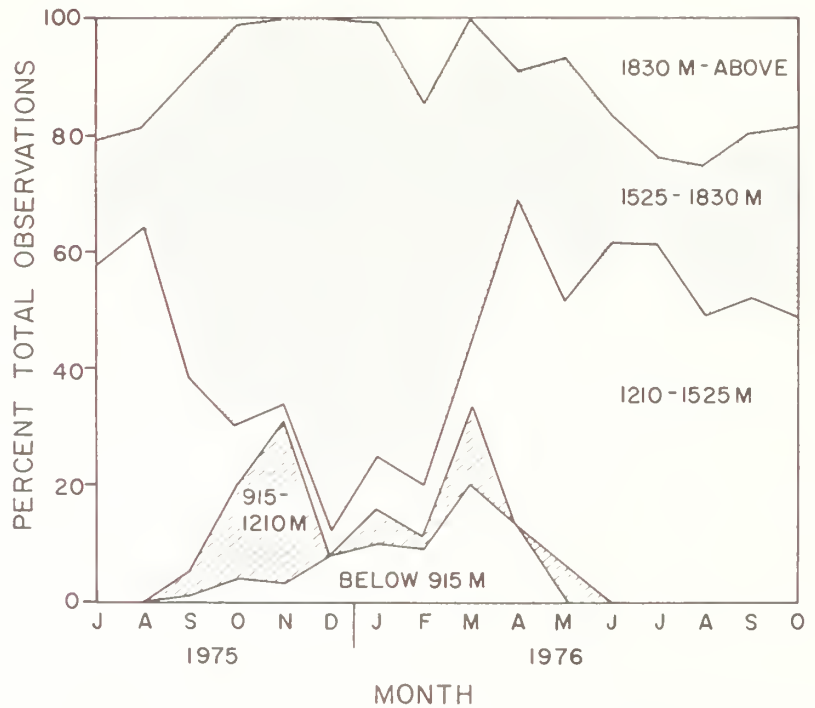



FIGURE 4. Monthly changes in elevational distribution of feral asses in Wildrose Canyon and vicinity, Death Valley National Monument.

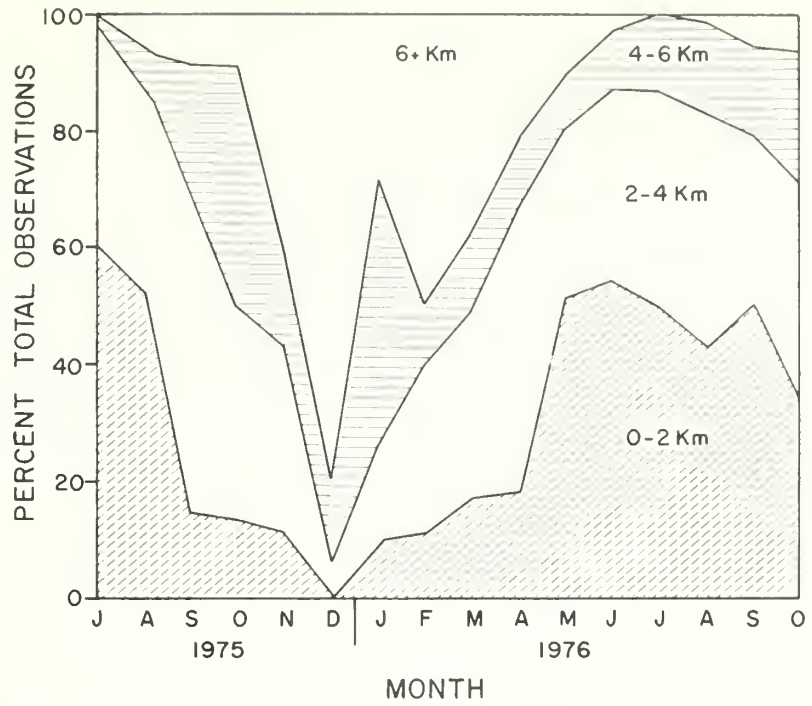



FIGURE 5. Monthly distribution of feral asses in kilometers from water, Death Valley National Monument.

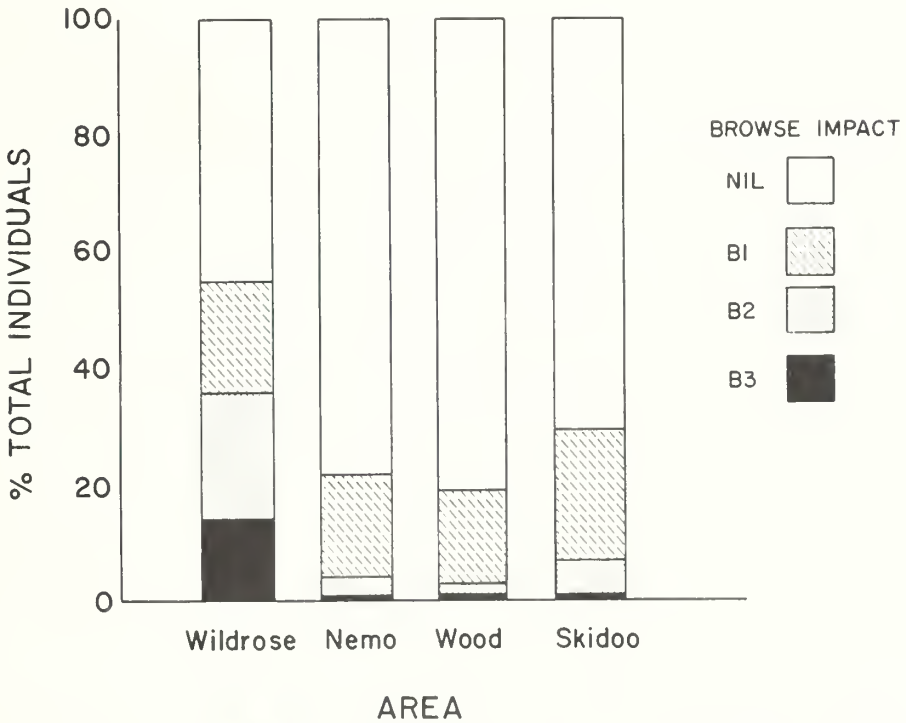



FIGURE 6. Percentages of shrubs showing browse impact in selected areas of Death Valley National Monument.

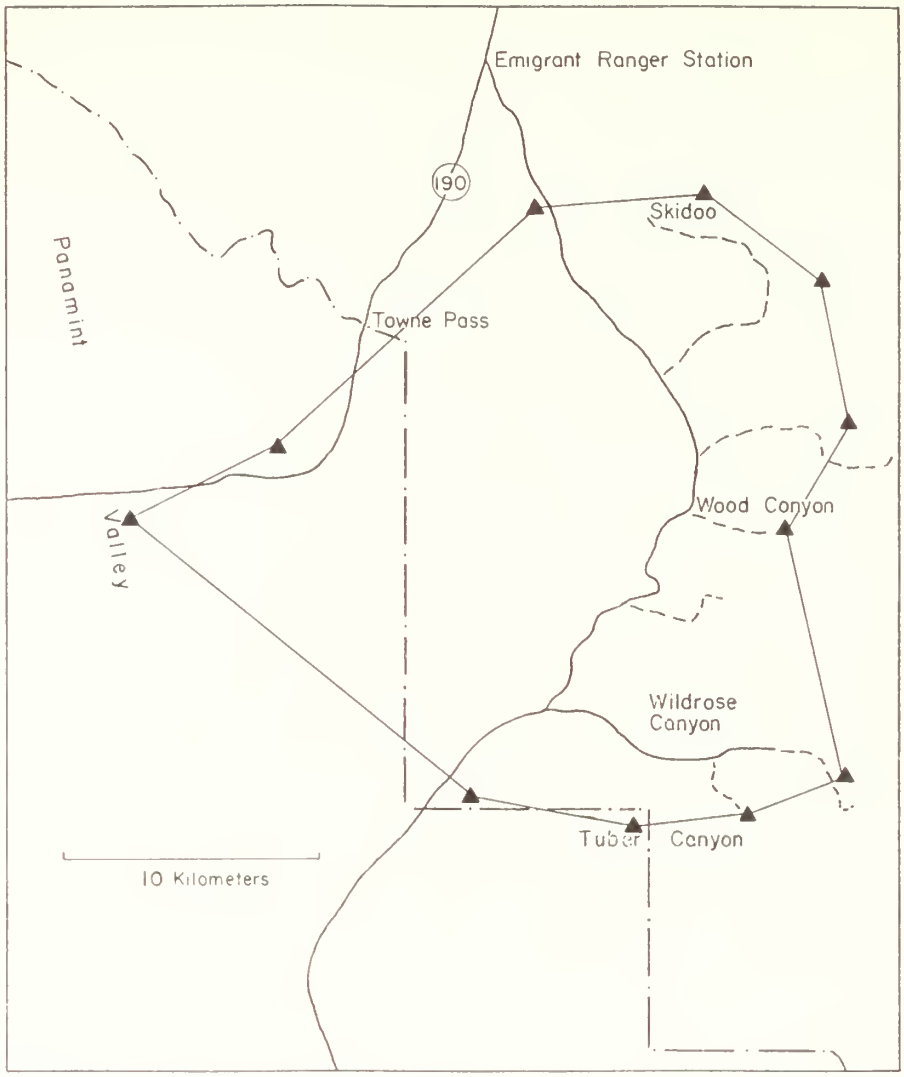



FIGURE 7. The maximum observed range of feral asses marked in Widlrose Canyon, Death Valley National Monument.

Almost 40 percent of the plants in Wildrose are in impact classes B2 and B3, indicating extensive damage to the forage species. In favored browse species such as *Acamptopapus shockleyi* approximately 50% of the total plants were in browse class B3. Other species such as *Crayia spinosa*, *Lycium andersoni*, and *Ambrosia dumosa* also received heavy use. The other three study areas show moderate to light utilization of browse species, reflecting the fact that a large percentage of the burro population remains in the Wildrose area for an extended period of time, whereas the other areas receive relatively short periods of utilization.

Seasonal movements and home ranges of individuals were determined utilizing sight records of marked individuals and records of individuals having telemetry collars. Figure 7 shows the maximum observed range, of 425 $km^2$, for all animals marked in Wildrose Canyon.

Home range was determined for all individuals sighted six or more times. The average number of sightings of marked individuals was 13.

In the following figures, home ranges for several animals are delimited. Figure 8 shows the home range of female 31, which had a spring-summer range of 15.17 $km^2$ and a total range of 41.54 $km^2$. Female 28 had overlapping spring-summer and fall-winter ranges, with an overall range of 98.06 $km^2$ (Figure 9). Figure 10 depicts the home range of male 40, which had a total home range of 97.41 $km^2$. Male 14 (Figure 11) had overlapping spring-summer and fall-winter ranges, for a total range of 90.21 $km^2$. Home ranges were overlapping and were not discrete. Some individuals occupied much of the same total area throughout the year, wherever others had discrete spring-summer and fall-winter areas of utilization. The home range of some individuals was completely contained within the home range of other burros.

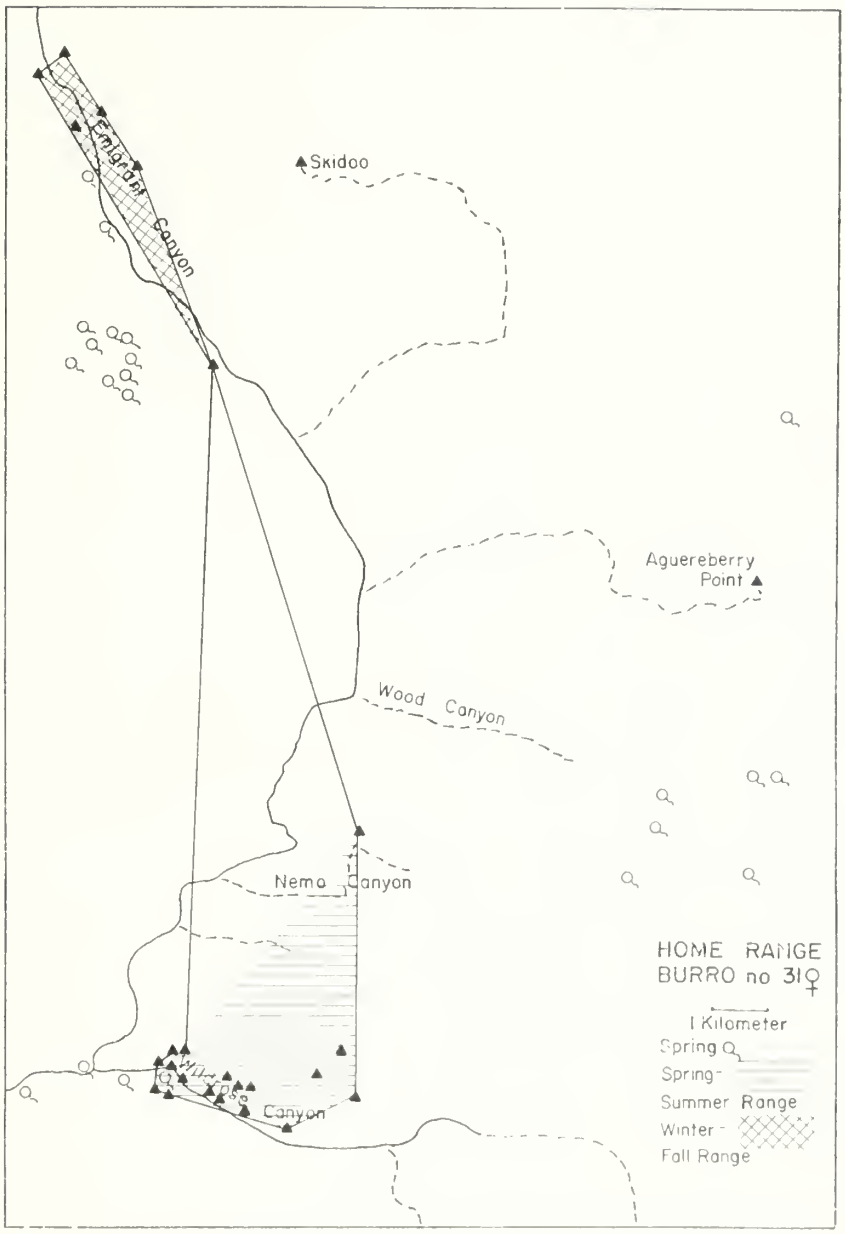



FIGURE 8. Home range of female burro 31, showing spring-summer and fall-winter areas of utilization.

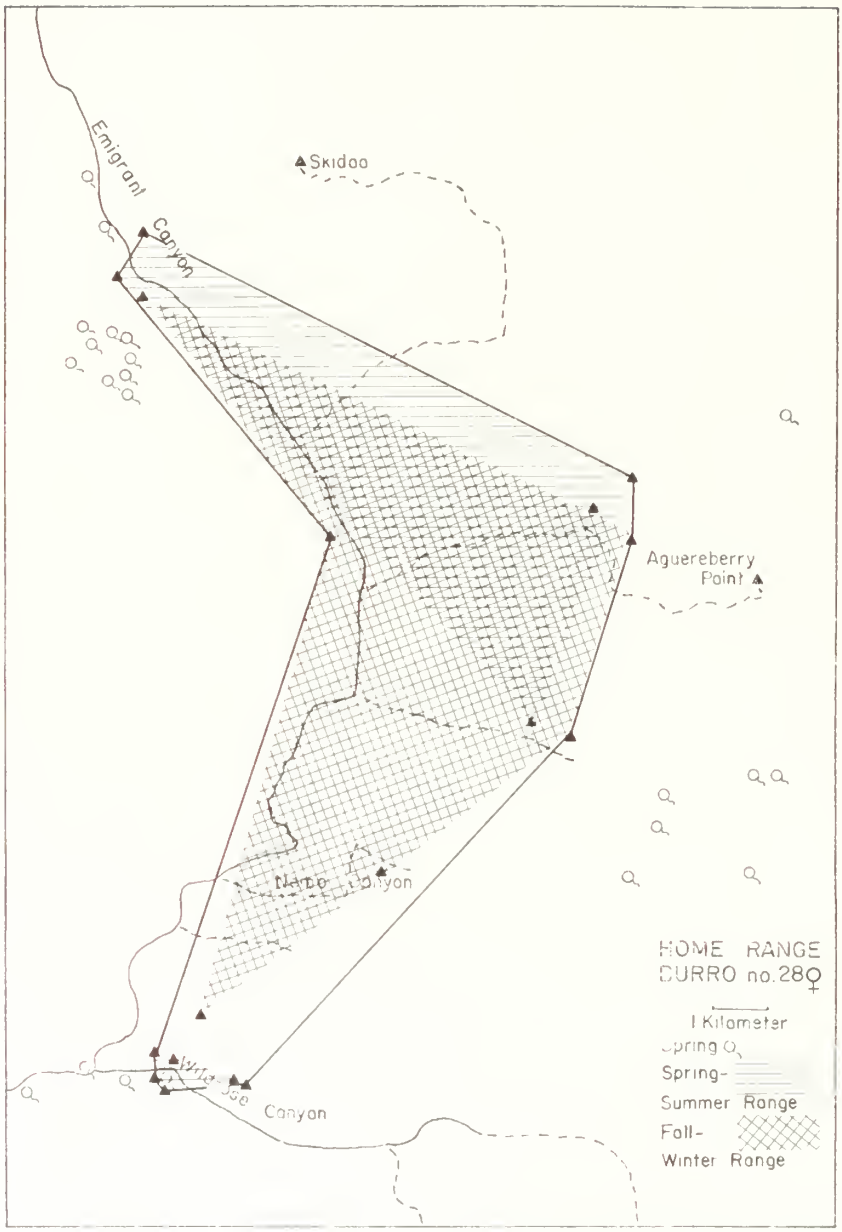



FIGURE 9. Home range of female burro 28, showing overlapping spring-summer and fall-winter areas of utilization.

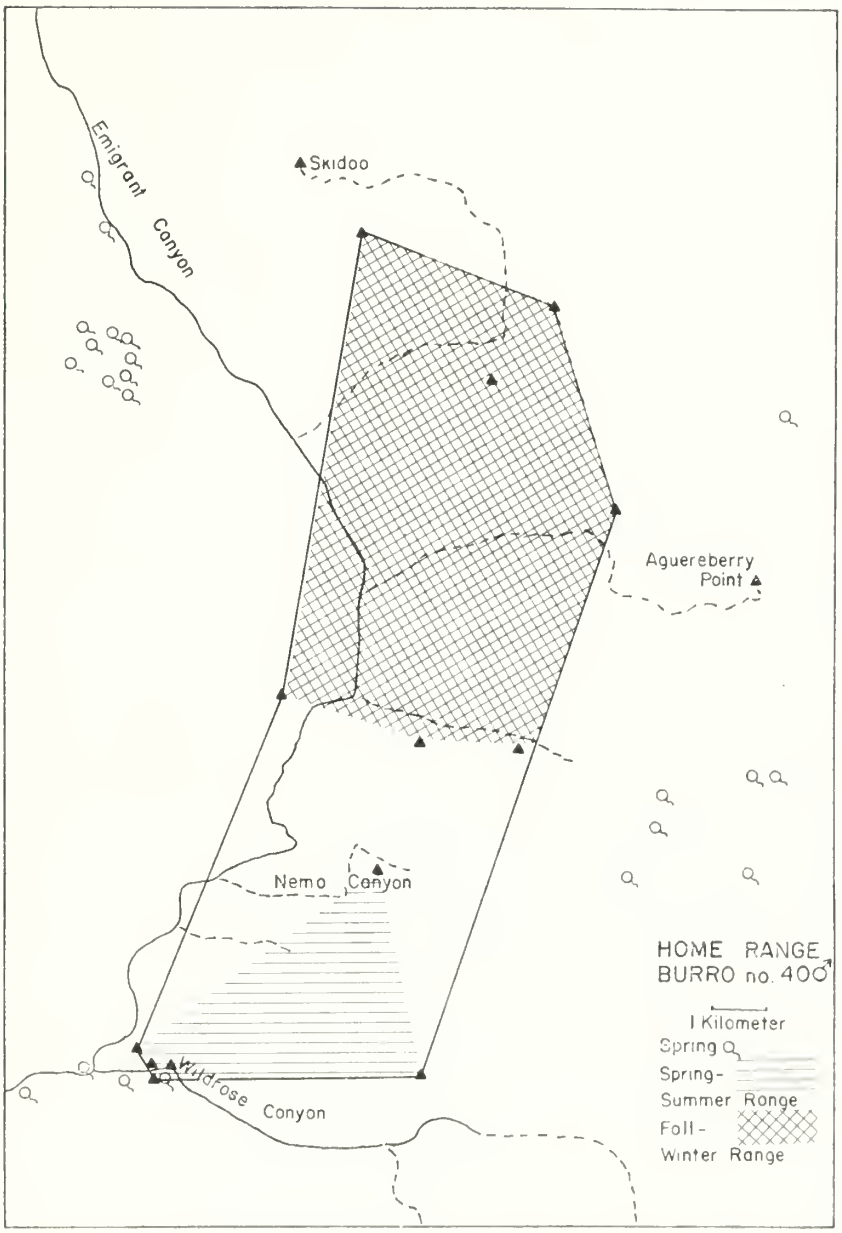



FIGURE 10. Home range of male burro 40, showing spring-summer and fall-winter areas of utilization.

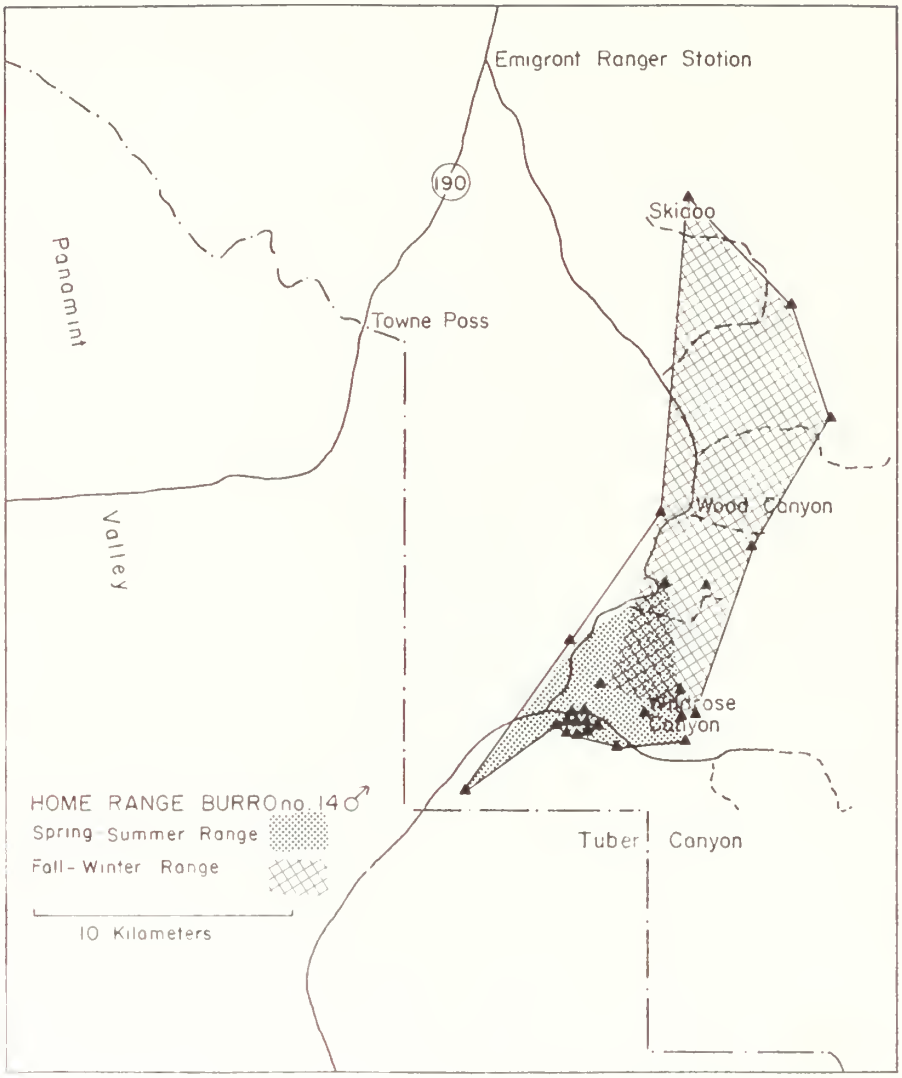



FIGURE 11. Home range of male burro 14 showing spring-summer and fall-winter areas of utilization.

The average size of home range was 68.1 ± S.D. 27.9 $km^2$. The mean home ranges of males and females did not differ significantly at the .05 level of probability, therefore, they are considered together. Fall-winter ranges had a near area of 34.2 $km^2$, whereas spring-summer ranges averaged 12.4 $km^2$. Moehlman (1974) observed a mean home range size of 10.5 $km^2$ for Wildrose individuals. It is interesting that our data show a mean home range six times as large as that determined by Moehlman. After examining many alternative explanations for this phenomenon, we have concluded that the dramatic increase in mean home range size over the past three years is a direct result of the decreased population density brought about by the NPS trapping and removal program. Thus, we believe home range size to be inversely related to density of the burro population.

Management recommendations that have resulted from this study include the following:

1. Since burros have been demonstrated to have an adverse effect upon the structure of the shadscale scrub community in Wildrose Canyon, some sort of burro control program is desirable and necessary.

2. Data gathered from studies of movements and home ranges indicate that burros can be controlled locally, since most show fidelity to a home range area and return to the locality every summer. This means that the burro population could be removed from an area such as Wildrose Canyon without causing a major influx of new animals into the area. Some immigration would undoubtedly occur, but it would be a relatively low annual rate.

3. The concentration of animals near permanent sources of water during the late spring and summer months make these seasons best suited for reduction procedures, since a large portion of the population could be located and removed without having to undertake extensive search operations.

4. Since it appears that home range size, and consequently, movement, increases as density decreases, it may be difficult to remove small remnants of the population from many areas. This effect could be compounded by selection for wary, elusive individuals occupying rough and inaccessible terrain.

5. The impact of low densities of feral burros upon vegetational communities in areas utilized only sporadically is negligible. Utilization of areas such as Skidoo, Wood Canyon, and Nemo Canyon for short periods of time during the fall, winter, and early spring did not appear to adversely affect the structure of the plant communities nor the survival of any forage species.

6. The fencing program, as outlined in the "Management Options for Natural and Cultural Resources in Death Valley National Monument" (USDI/NPS 1976), would be an expensive and inefficient method of attempting to facilitate control of the burro population. It is evident that most of the increase in the burro population is due to the production of young, rather than from immigration. The magnitude of immigration, although not quantified, appears to be insignificant. In addition, our experience has shown that burros are generally capable of overcoming barriers such as fencing if it is necessary for them to do so. They are quite adept at riding down fences or simply circumventing sections of fence in rough terrain. Burros have often been observed in extremely rugged areas that would be difficult, if not impossible to fence at a reasonable cost. Experience at Eagle Borax Spring has shown that burros have managed to penetrate an extremely sturdy and well-constructed fence designed to deny them access to water. Thus, boundary fencing, although perhaps making it more difficult for burros to enter the monument, would not prevent them from doing so.

Since it appears as though there is little exchange of individuals between populations in widely separated localities within the monument and burros exhibit fidelity to their home ranges, internal drift fencing is also not required for control operations.

7. Trapping operations in Butte Valley have demonstrated that trapping success will vary from area to area, depending upon the proximity of other water sources and the degree to which burros are accustomed to humans. In all likelihood, trapping would be extremely difficult in isolated parts of the monument where a number of water sources are available.

8. Direct reduction by shooting appears to be the cheapest, most effective and humane method available. Construction of either boundary or drift fencing is neither necessary nor advisable. It is recommended that the Park Service not attempt to eradicate every single burro from the entire monument, but rather, concentrate on systematically removing the majority of animals most easily accessible. Although residual populations may remain in certain areas, densities would be low enough to prevent significant environmental damage. Since burro populations would naturally increase over long periods of time, it would be necessary to carry out control operations on a regular basis, perhaps at five year intervals.

9. If and when the control program is initiated, an effort should be made to gather as much biological data as possible. The population of feral burros in Death Valley National Monument is one of the largest in North America, and a unique opportunity would be lost if the animals were simply shot and left to rot. A great deal of useful information on growth and development could be gathered quickly in the field.

## LITERATURE CITED


DIXON, J. S. and E. L. SUMNER, JR. 1939. A survey of desert bighorn in Death Valley National Monument. Calif. Fish and Game 25: 72-95.

HANSEN, C. G. 1973. Evaluation of burro activity in Death Valley National Monument. Unpublished report on file at the Monument.

MOEHLMAN, P. 1974. Behavior and ecology of feral asses (*Equus asinus*) Ph.D. Dissertation, U. of Wisconsin, 251 pp.

MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley, California, 1681 pp.

WELLES, R. E. and F. B. WELLES. 1961. The bighorn of Death Valley. Fauna of the National Parks of the United States. Fauna Series No. 6, 242 pp.

# FERAL BURRO MANAGEMENT AT BANDELIER NATIONAL MONUMENT, NEW MEXICO

Milford R. Fletcher[1]

Bandelier National Monument, located in north-central New Mexico, is an area of approximately 30,000 acres of which 23,267 acres were designated as wilderness on October 20, 1976, under the Wilder-Act of 1964. The area was originally set aside in 1916 to protect the more than 600 prehistoric Pueblo Indian Ruins, including pueblos of up to 400 rooms.

Sweeping vistas, solitude, and an extremely moderate climate all combine to make the back-country of Bandelier an area of great aesthetic value. Additionally, the monument has the usual complement of wildlife common to the upper Sonoran vegetative type including mule deer, elk, wild turkey, coyote, and a considerable variety of small mammals, reptiles and amphibians. One amphibian, the Jemez Mountain Salamander (*Plethodon neomexicanus*), is on the endangered species list and is endemic to the Jemez Mountains.

There is one more large mammal of considerable importance, the exotic and feral burro (*Equus asinus*) which resides on the monument. First reported in 1940, the population of burros has fluctuated in inverse proportion to National Park Service determination to rid the monument of the animals. The initial report (McDougall, 1940) indicated that there were 15 to 18 burros near the Rio Grande and he stated, "In my opinion, they should be eliminated from the monument." This opinion was prophetic, since the same sentiments have been voiced a number of times in the following years in the states of California, Arizona, New Mexico and Nevada.

In 1946, a decision was made to attempt to reduce the burro herd at Bandelier and 64 burros were destroyed in a period of approximately three months. The Superintendent of the monument estimated that about one-half of the herd was destroyed. During the next 25 years, there was only sporadic control of the herd and its numbers increased until, in 1974, the population was estimated to be about 130 animals.

Censusing of burros at Bandelier is extremely difficult owing to the very rugged terrain. In addition, burros are hard to census in pinyon-juniper areas because they frequently do not flush but hide in the vegetation.

Two particularly valuable research studies were initiated in 1974. One, a master's thesis from the University of New Mexico (Koehler, 1974) reported that 52% of the vegetation was in a downward trend. The analysis showed 47% of the range in very poor condition, 31% in fair condition, and none of the range in excellent condition. The second study, a soils study by Earth Environmental Consultants of Albuquerque, New Mexico, indicated widespread damage to both soils and vegetation on the monument (EEC, 1974). The soil erosion is apparent, but the extent of damage was surprising. The soil survey indicated that as much as 35 tons of soil per acre were being lost to erosion each year (78,000 kg/ha/yr). In an area of low precipitation and light, volcanic soils, this represents a loss that cannot be mitigated.

Armed with these facts, the National Park Service made a management decision in the fall of 1974 to substantially reduce the number of feral burros inhabiting the monument. At this time a negative declaration was passed in compliance with the National Environment Policy Act of 1969. In February 1975, marksmen of the National Park Service using high powered rifles reduced the herd by 52 animals. At the same time, radio collars were placed on seven animals and color-collars were placed on another 11 animals, in preparation for further research. The estimated population at that time was approximately 140 animals; thus, the herd was reduced by 37%. No attempt was made to salvage the carcasses but researchers from the University of Arizona and Arizona State University took a great variety of measurements, tissue samples and other data, including the heads of 25 animals for research on aging burros by tooth examination.

Further research followed. Morgart (1976) spent a full year living in the backcountry at Bandelier studying the home ranges, territory, reproductive rates, food habits and several other facets of burro ecology. He found that the territory of burros at Bandelier was quite small, averaging less than 0.2 square miled (52 ha). Home range was also small averaging 1.15 square miles (298 ha) for a sample of nine animals, with the largest home range measured being 2.3 square miles (596 ha). The herd was found to be increasing at an annual rate of 29% which indicates the population will double approximately every three years. In May 1976, 16 of the marked animals were collected by National Park Service marksmen to obtain further data on growth, reproductive cycles, growth trends, and other data germane to the ethology study.

The final major research report dealing with burros was a study to determine the competition between the feral burro and native deer. Deer are normally thought of as browsers and burros as grazers. This study (Potter, 1976) showed that the diet of deer in all vegetative associations at Bandelier is comprised of between 95% and 99% browse during the entire year. During the spring, summer, and fall, the diet of burros is primarily grasses; however, during the winter when deer move down into the pinyon-juniper and juniper associations, the burros are in direct competition for browse species. As much as 35% of the winter diet of burros is browse, particularly three species, Mountain mahogany (*Cercocarpus montanus*), Fourwing saltbrush (*Atriplex canescens*), and various oaks (*Quercus* spp.). Since the grasses on the monument are badly overgrazed, the switch from grazing to browsing by burros in the winter is not particularly surprising, especially in view of the catholic dietary habits of burros.

In May 1976, the staff at Bandelier began preparation of an Environmental Assessment on burro management at Bandelier. That assessment was sent to interested parties during mid-November and is available from the Superintendent, Bandelier National Monument, Los Alamos, New Mexico 87544.

A public meeting was held on December 15, 1976, in Santa Fe, New Mexico, to elicit public input on the management of burros at Bandelier. The public was offered alternatives ranging from "No Action" to "Removal of as many burros as is

[1]National PArk Service, Southwest Regional Office, Santa Fe, New Mexico 87501.

feasible." A workbook was provided to the public and comments were requested. By mid-January 1977, the National Park Service should have a fairly clear reading of public opinion and management actions will be planned for early 1977.

## LITERATURE CITED


EARTH ENVIRONMENTAL CONSULTANTS, INC. 1974. Survey of Range and Ecological Conditions for a Southern Part of Bandelier National Monument. (On file, Bandelier National Monument).

KOEHLER, D. A. 1974. The Ecological Impact of Feral Burros on Bandelier National Monument. Unpublished M.S. thesis, University of New Mexico.

MCDOUGALL, W. B. 1940. Special Report on Bandelier National Monument Southwest National Monument Reports, Supplement pp 332-335.

MORGART, J. R., and R. D. OHMART. 1976. Observation on the Biology of Burros (*Equus asinus*) on Bandelier National Monument, New Mexico (On file, Southwest Regional Office, National Park Service, Santa Fe, New Mexico 87501).

POTTER, L. D. 1976. Deer-Burro Utilization and Competition Study, Bandelier National Monument (Interim Report) (On file, National Park Service, Southwest Regional Office, Santa Fe, New Mexico 87501).

# INVERTEBRATE FAUNA OF THE EARTH CRACKS OF WUPATKI NATIONAL MONUMENT, ARIZONA[1]

W. Calvin Welbourn[2]

Wupatki National Monument is located about 30 miles northeast of Flagstaff, Arizona. Babenroth and Strahler (1945) described 24 small grabens in this area. Three of these were in the Monument (Citadel Graben, White Mesa Graben, and Hulls Canyon Graben, Figure 1). These three grabens and their associated earth cracks were studied by the Cave Research Foundation from September 1975 through October 1976. Bridgemon (1976) described the area and earth cracks within the Monument. The Wupatki earth cracks are tectonic in origin and to date no solutional passages have been found. Sartor and Lamar (1962) reported the possibility of an extensive, interconnected system extending from 24 to 44 miles to the south. The preliminary exploration done by the Cave Research Foundation makes it unlikely that such a system, sufficiently large for humans, exists over such a large area (Bridgemon 1976).

Five earth cracks (Dangling Flake Crack, Doney Fissure, Lomaki Fissure, Malmquist Fissure, and Supapu Cavern, Figure 1) in two grabens were examined for animal life. Four collecting trips were made to the Monument; September 1975, November 1975, January 1076, and October 1976. Each crack was visited at least twice. On each visit the walls, ceilings, floors, and organic material were carefully examined for animals. Limited samples of invertebrates were collected for identification, but no vertebrates were collected. Soil temperature and relative humidity were also measured.

The fauna associated with earth cracks consisted of one mollusk, 29 arthropods, and three invertebrates (see list). Cave animals are usually grouped according to their ecological relationship with the cave. This relationship is described by four terms: troglobite = cave dweller; troglophile - cave lover; trogloxene = cave visitor; accidentals (Vandel 1965; Mohr and Poulson 1966). Hamilton-Smith (1971) used seven groups, one of which I will use here, namely parasite. Parasite will be used to describe those species that are obligate parasites. In the list an attempt was made to describe the relationship of each organism, although as more information is obtained the actual relationship will become clear.

There were no troglobites found in the Wupatki earch cracks, although troglobitic forms are known from a cave southwest of the Monument. Troglophiles made up nine (28%) of the species. The most notable of these were the pseudoscorpions (*Archeolarca* and *Pseudogarypus*) which appear to show some adaptation to life underground. The trogloxenes comprised 12 (37%) of the animals found in the earth cracks. The most common representatives were cave crickets (*Ceuthophilus*), Harvestmen (*Liobonum*), and spiders. Eight (25%) of the animals were considered accidental. They had either fallen or were washed into the cracks. Parasites were represented by three (9%) of the species found in the Monument.

The fauna of the earth cracks was very sparse. Cave crickets, pseudoscorpions and tenebrinid beetles were the most common invertebrates encountered in the cracks. Although the spider, *Archaeraneae canionis*, was widely distributed in the earth cracks, it was not common. Other species were less common or restricted to a single locality where there was moisture and organic material.

The single most important limiting factor for the fauna in the earth cracks today is moisture. The cracks in the Monument are dry and dusty. Moisture was limited to runoff from the surface where it either evaporates or percolates through the soil. Where water collected for short periods of time, there was also a concentration of arthropods, particularly mites. The humidity ranged from 27 to 76 percent with an average of 51%. The relative humidity in caves ranges between 96 and 100 percent (Vandel 1965). In southwestern caves the relative humidity ranges between 80 and 100 percent. The relative humidity, although low for a "cave" was considerably higher than that on the surface (5-23%). The higher humidity environment of the earth cracks would attract some of the surface forms and could account for the relatively large numbers of trogloxenes found in the cracks. Temperature measurements in the cracks indicate the deeper cracks have a relatively constant temperature (11 C to 13 C) with an average of 12.5 C. This compares with the local mean annual surface temperature of 14.2 C.

An attempt was made to estimate the population of *Ceuthophilus yavapai* in Malmquist Fissure and Dangling Flake Crack using a mark-recapture census. The Lincoln-Peterson Index estimated the population of cave crickets in the two cracks to be 350-600 individuals. There was considerable difficulty in locating, marking, and counting individuals due to high ceilings, breakdown, narrow passages, and loose rocks. This may have affected the estimate.

Presently there is not sufficient data to determine the overall distribution of species found in the Wupatki earch cracks. Preliminary work in caves and earth cracks west and south of the Monument indicate there are more troglophiles and at least two troglobitic arthropod species in the area. Northwest of the Monument, Triplehorn (1975) described a troglophilic tenebrinid (*Eleodes leptoscelis*). This beetle has not been identified from the Monument. The apparent absence of some cave forms known to occur in the area could be due to the recent origin of the earth cracks.

[1]The author and Cave Research Foundation wish to thank the National Park Service at Wupatki National Monument for their help and cooperation during this project. Special thanks to John W. Wise, Superintendent of Wupatki National Monument. Rondal Bridgemon, Robert Buecher, Debbie Buecher, Leonard Jelinek, Linda Jelinek, Robert Henry, and Richard Harris assisted in the field work. For determination of species and other taxonomic assistance I am indebted to Nell Causey, millipedes; Carleton Clifford, ticks; Benjamin Foote, diptera; Willis Gertsch, spiders, Theodore Hubbell, cave crickets; William Muchmore, Pseudoscorpions; and T. J. Spilman, tenebrionids. Illustration was prepared by Susan McLean.

[2]Cave Research Foundation, 306 Sandia Road, N. W., Albuquerque, New Mexico 87107.

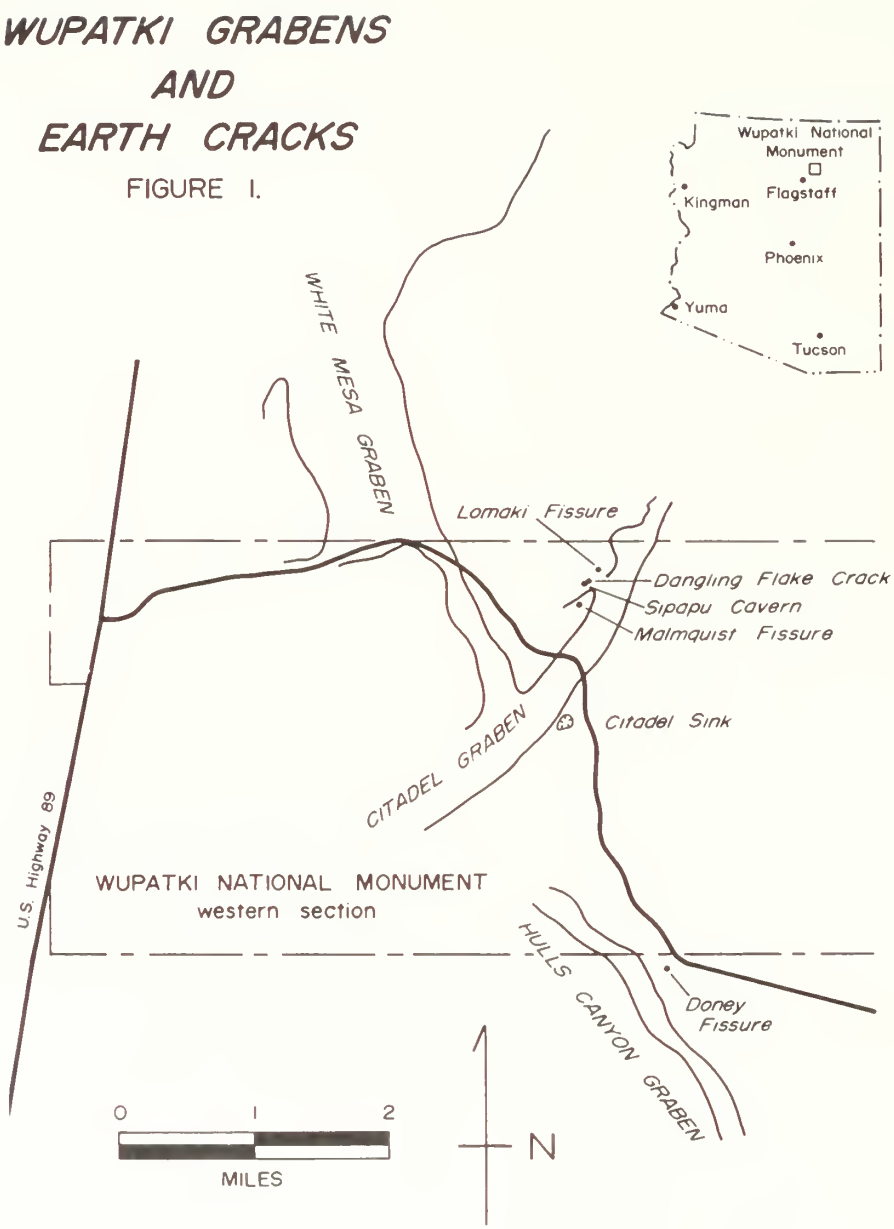

WUPATKI GRABENS
AND
EARTH CRACKS
FIGURE I.
Wupatki National Monument
Kingman
Flagstaff
Phoenix
Yuma
Tucson
WHITE MESA GRABEN
Lomaki Fissure
Dangling Flake Crack
Sipapu Cavern
Malmquist Fissure
Citadel Sink
CITADEL GRABEN
U.S. Highway 89
WUPATKI NATIONAL MONUMENT
western section
HULLS CANYON GRABEN
Doney Fissure
0
1
2
MILES
N

FIGURE 1.

Graben formation and associated faulting was probably due in part to the regional vulcanism with a late or post Tertiary origin suggested (Bridgemon 1976). A camel foot bone found in Doney Fissure by Colton (1938) indicated the crack has been open at least 20,000 years.

Further work is needed in the earth cracks and caves of northern Arizona to determine the distribution and relationships of many of the species found in Wupatki National Monument.

## FAUNA ASSOCIATED WITH THE EARTH CRACKS OF WUPATKI NATIONAL MONUMENT, ARIZONA

Listed are all invertebrates collected and vertebrates observed in the Wupatki National Monument earth cracks during the Cave Research Foundation project.

Phylum Mollusca
undetermined genus and species
Dangling Flake Crack
Trogloxene. Large number of snails were found under rocks near the entrance; probably seeking shelter.

Phylum Arthropoda
Class Diplopoda
Order Chordeumida
Family Lysiopetlidae
*Abocion* sp.
Doney Fissure
Accidental. A single specimen was found in the entrance sink.

Class Chilopoda
Order Scolopendromorph
undetermined genus and species
Sipapu Cavern
Accidental. A single, desiccated specimen was found at the bottom of Sipapu.

Class Insecta
Order Thysanura
Family Lepistatidae
undetermined genus and species
Malmquist Fissure
Trogloxene. Represented by a single specimen on the wall; can also be found on the surface under rocks.

Order Collembola
undetermined genus and species
Dangling Flake Crack
Troglophile. Several specimens collected in organic debris.

Order Orthoptera
Family Rhaphidophorinae
*Ceuthophilus yavapai* Hubbel
Dangling Flake Crack, Doney Fissure, Lomaki Fissure, Malmquist Fissure, and Sipapu Cavern.
Trogloxene. Most common organism observed in the earth cracks. Found in all the cracks examined and were usually found on the walls and ceilings, generally near the entrance.

Order Hemiptera
Family Reduviidae
Subfamily Emesinae
undetermined genus and species
Dangling Flake Crack, Malmquist Fissure
Trogloxene. Specimens found on walls near the entrance.

Order Coleoptera
undetermined genus and species
Dangling Flake Crack, Malmquist Fissure
Several coleopterans found near the entrance.
Family Carabidae
*Rhadine* sp.
Malmquist Fissure
Troglophile. A common specimen in many southwestern caves; can also be found in animal burrows, mines, and cellars.
Family Tenebrionidae
*Eleodes delicata* Blaisdell
Lomaki Fissure
*Eleodes hispilabris* Say
Malmquist Fissure
*Glyptasida sordida* LeConte
Malmquist Fissure
*Steriphanus convexulus* LeConte
Lomaki Fissure
undetermined genus and species

Sipapu Cavern
Accidental, Trogloxene or Troglophile? Many specimens were seen, although few were collected. Seem to be victims of the entrance drops. One specimen found alive at 500 foot level of Sipapu Cavern.

Order Diptera
Family Tipulidae
undetermined genus and species
Lomaki Fissure, Malmquist Fissure
Trogloxene. Specimen found in entrance area, probably uses cracks as shelter only.
Family Sciaridae
undetermined genus and species
Malmquist Fissure
Troglophile. Common fungus gnats, found in moist area after rain.

Order Siphonaptera
undetermined genus and species
Dangling Flake Crack
Parasite. Several specimens found on a bone.

Order Hymenoptera
Family Chalcidoidea
undetermined genus and species
Doney Fissure
Accidental, parasite?

Class Arachnida
Order Chelonethida (Pseudoscorpionida)
*Archeolarca* sp.
Lomaki Fissure, Malmquist Fissure.
Troglophile. Probably a new species of pseudoscorpion. Previously known only from rodent nests in Utah and New Mexico, it was found on ledges in the area of total darkness. Appears to be adapted for subterranean conditions with larger size and attenuated appendages. (Muchmore, pers. comm.)
*Pseudogarypus* sp.
Doney Fissure
Troglophile. Probably a new species of pseudoscorpion, and like previous specimens, appears to be adapted to subterranean life.
undetermined genus and species
Dangling Flake Crack, Sipapu Cavern
Troglophile. Found under rocks near the entrance in Dangling Flake Crack, those in Supapu about 40 feet down.

Order Phalangida (Opiliones)
*Liobonum townsendii* Weed
Doney Fissure
Trogloxene. These arthropods probaly are fairly common, seeking shelter in the crack by day and foraging on the surface at night. Widespread in the southwest.

Order Araneae (Araneida)
Family Araneidieae
*Araneus* sp.
Doney Fissure
Trogloxene. Found in the entrance sink.
*Archaearanea canionis* Chamberlin and Ive
Dangling Flake Crack, Doney Fissure, Malmquist Fissure, and Sipapu Cavern.
Trogloxene. Although found in four cracks, they were not common. Usually found near the entrance.
Family Uloboridae
*Uloborus diversus* Marx
Malmquist Fissure
Trogloxene. Found near entrance.

Order Acariformes
Family Eupodidae
*Linopodes sp.*
Lomaki Fissure
Troglophile. Specimens found under debris.
Family Rhagidiidae
*Rhagidia* sp.
Doney Fissure, Malmquist Fissure
Troglophile. Several specimens found in an area where water collects.
Family Trombidiidae
undetermined genus and species
Dangling Flake Crack, Malmquist Fissure, Sipapu Cavern
Troglophile, parasite. Larva of this specimen were parasitic on cave crickets (*Ceuthophilus*). Adult stages

are predacious. A single adult was found at Malmquist under debris.

Family anystidae
undetermined genus and species
Dangling Flake Crack
Troglophile. This mite was found in large numbers near the entrance where pseudoscorpions were common.

Suborder Astigmata
undetermined genus and species (Hypopus)
Lomaki Fissure
Accidental, parasite? Found in collecting bottles; probably from one of the beetles.

Order Parasitiformes
Family Argasidiae
Ornithodoros (probably concanensis)
Malmquist Fissure
Parasite. A desiccated specimen was found on a ledge. Identification tentative due to dry condition of specimen.

Phylum Chordata
Class Mammalia
Order Chiroptera
Family Vespertilionidae
*Plecotus townsendii*
Doney Fissure, Lomaki Fissure, Malmquist Fissure, and Sipapu Cavern
Trogloxene. Roosting individuals were observed in September. In January they were hibernating. None was collected.

Order Rodentia
Family Cricetidae
undetermined genus and species
Lomaki Fissure, Sipapu Cavern
Accidental. The bones and desiccated carcasses of several rodents were found, non was collected.

Order Lagomorpha
Family Leporidae
undetermined genus and species
Malmquist Fissure, Sipapu Cavern
Accidental. The remains of several rabbits were found; all were victims of entrance drops. None was collected.

LITERATURE CITED


BABENROTH, D. L., and A. N. STRAHLER, Geomorphology and structure of the East Kaibab Monocline, Arizona and Utah. Geol. Soc. Amer. Bull. Vol. 56, 1945, pp 107-150.

BRIDGEMON, R. R., The Wupatki earth cracks. in Wupatki National Monument earth cracks, May 1976. Cave Research Foundation, Yellow Springs, Ohio.

COLTON, H. S., The Exploration of limestone solution cracks, Mus. No. Ariz., Museum Notes. Vol. 10, No. 10, April 1938, pp 29-32.

HAMILTON-SMITH, E. 1971. The classification of cavernicoles, Bull. Nat. Speleol. Soc. Vol. 33 (1):63-66.

SARTOR, J. D., and D. L. LAMAR, Meteorological-geological investigations of the Wupatki blowhole system. Rand memorandum 3139-RC, June 1962.

TRIPLEHORN, C. A. 1975. A new subgenus of Eleodes with three new cave-inhabiting species (Coleoptera, Tenebrionidae). The Coleopterist Bull. 29(1):39-43.

VANDEL, A. 1975. Biospeleology. Pergamon Press, London. 524 pp.

# A YEAR IN THE LIFE OF *ORTHOPORUS ORNATUS*, A DESERT MILLIPEDE[1]

Clifford S. Crawford[2]

## INTRODUCTION

It is generally understood that millipedes are common animals in mesic, often forested environments (Blower 1955; Dowdy 1968; Kaestner 1968). There they are sometimes restricted to the soil, but are often found associated with organic debris and vegetation above the surface. In such regions they are essentially consumers of plant materials (Cloudsley-Thompson 1968), and can play a significant role in the decomposition of litter (Edwards et al. 1970).

Perhaps because of the accepted association of these animals with areas of moderate to high annual precipitation, the concept of a desert millipede has received little attention until recently. Nevertheless, millipedes have been known for some time to inhabit arid regions (Cook 1924; Chamberlain and Mulaik 1941; Kaestner 1968), and often do so in great abundance (Lowe 1968; Causey 1975). The present paper reviews work done in recent years with my students on the biology of *Orthoporus ornatus* (Girard), a very common spirostreptid millipede in parts of the Chihuahuan and Sonoran deserts of North America. The paper first considers this animal's known biology during the relatively short summer feeding season, and then indulges in a more tentative treatment of the longer dormancy season. Events occurring in both periods must be examined in order to begin to understand and appreciate a year in the life of this desert millipede.

## THE FEEDING SEASON

The onset of early summer rains occurs predictably about mid-May in the Big Bend region of southwestern Texas, and in early July in southern and central New Mexico. Within hours after these heavy thundershowers begin, enormous numbers of *O. ornatus*, ranging in length from several millimeters to over 15 cm, emerge from often localized underground chambers and swarm over the soil surface. The term "migration" has been applied to such swarms (Cloudsley-Thompson 1949), but in our experience simple dispersal appears more likely because of spot checks showing the movement to be basically random. Whatever the case, the rains appear to be a proximate signal that stimulates emergence by all mobile stages, and simultaneously wets the hard, dry soil, enabling a massive exodus by millipedes confined for many months in this subterranean habitat.

A careful observer will note that shortly after this emergence the most evident form of behavior by both wandering and stationary millipedes is that of eating, really almost incessant nibbling. Occasionally such activity is recorded from succulent cactus tissues, or from the leaves of young annuals. However, by far the most frequent feeding involves obviously dead organic material (sticks, leaves, seed husks, rodent dung) that litters the desert surface and often accumulates by the bases of shrubs and in crevices and arroyos. Less frequent, but not uncommon feeding occurs on the aerial portions of certain shrubs, where superficial tissues are systematically and noticeably scraped by the heavy mandibles.

Following rains at Big Bend National Park, a common sight is that of *O. ornatus* quietly rasping twigs of mesquite (*Prosopis glandulosa*), creosotebush (*Larrea divaricata*), acotillo (*Fouqueria splendens*), and various species of *Opuntia* cactus. In the floristically simpler desert about 30 km north of Las Cruces, New Mexico, mesquite and Mormon tea (*Ephedra* spp.) are commonly worked on, but the abundant creosotebush is ignored. A millipede population inhabiting the vicinity of a volcanic escarpment near Albuquerque, New Mexico, has a variety of shrubs at its disposal. However, it feeds only rarely on fourwing saltbush (*Atriplex canescens*) and apparently never on the locally common indigo bush (*Dalea scoparia*), although fallen flower parts of the latter species are readily ingested. Once dead, tumbleweed (*Salsola kali*) is a heavily utilized food item, but living shrubs sometimes also contain millipedes (Wooten et al. 1975).

A desert millipede must carefully regulate its horizontal and vertical activity if it is to efficiently forage on such a mixed diet. We examined behavioral thermoregulation in each population mentioned above, and found that while some feeding takes place at night, it also occurs regularly in the daytime at ambient temperatures below 35° C (Wooten et al. 1975). By mid-morning the exposed soil surface reaches temperatures corresponding to the upper thermal limit (about 40° C) of *O. ornatus*. Between that time and late afternoon, therefore, two general options are available to above-ground millipedes.

The first of these is to go underground. With a great variety of ready-made animal burrows or rocky crevices (depending on the habitat) available, it is not surprising that this course of action is often taken. How much feeding occurs in such places is not known; probably not much at all in the crevices, where quiescent aggregations of twenty or more individuals are not infrequent. Millipedes of all sizes take this option.

It is my undocumented opinion that most of the desert millipede's potential good is above the soil surface. The second option, which appears to be taken mainly by large millipedes, is that of remaining associated with such a resource. In doing so they by no means deprive themselves of shelter against the heat, a fact that can be verified by watching individuals in the aerial parts of shrubs during the morning hours. There, while either feeding or resting, they tend to align themselves so as to remain on shaded aspects of branches. By early afternoon on a hot day most aerial sites are vacated, and the millipedes move down to shrub bases and associated depressions or burrows. There they appear to cease active feeding and to remain coiled, often in aggregations, in the dense shade where temperatures rarely

[1]I owe a great deal especially to R. C. Wooten, Jr., W. A. Riddle, F. S. Nunez, L. J. Walker, S. Pugach, M. C. Matlack, and A. M. Zeitone for their help in revealing what we know about the biology of the desert millipede. I also thank officials at Big Bend National Park and W. C. Wh tford at New Mexico State University for their cooperation over the years. Partial funding for the work reviewed came from the U.S./I.B.P. Desert Biome (supported in part by NSF Grant GB-15886), and from NSF Grant BMS 74-18392.

[2]Department of Biology, The University of New Mexico, Albuquerque 87131.

exceed 35° C. By late afternoon they begin again to disperse both horizontally and vertically, and to resume feeding with their original intensity.

The physiological and metabolic adaptations of *O. ornatus* to hot, dry conditions are also highly specialized. In terms of its water relations this species is roughly an order of magnitude more resistant to desiccation than other millipedes examined (Crawford 1972). Furthermore, it imbibes water readily from a moist surface by spreading apart its anal plates and extruding rectal tissue on the substrate. While doing this it has been seen using more anterior regions for ingestion or copulation. A useful thermal adaptation of large specimens involves a reduction, between 25° C and 35° C, of respiratory $Q_{10}$ to about half the $Q_{10}$ value recorded between 25° C and 15° C for similarly acclimated animals. Rates of energy expenditure, therefore, become relatively reduced in hot weather.

The reproductive biology of the desert millipede undergoes several major changes as the summer rains begin. Copulation takes place among mature adults at this time and later in the feeding season, although the act is seldom seen. In addition, our unpublished studies indicate that the large number of tiny ova that remain undeveloped in dormant females begin to develop as the millipedes resume feeding. Within about a month many ova reach maximal size and are ready, presumably, to be oviposited.

The exact timing of oviposition remains a mystery, as does the number of times in a season or in a lifetime that a female performs such a function. Underground chambers, frequently associated with animal burrows, contain from about 100 to 500 individual pellets of maternal fecal material, each housing an egg or new larva. Since dissected females often contain over 100 mature-appearing ova, it is possible that a reproductive adult fills several chambers with egg pellets in a single season. Because the size range of gravid females is quite variable, and because we speculate on the basis of slow size increases at molt that large animals may live many years, it seems probable that they are iteroparous (breed in successive years), as are certain other millipede species (Blower 1969).

Events occurring within the egg pellets have been largely unstudied. Sometime after oviposition, a larval millipede hatches; at some future date it may undergo at least one molt. The larva is probably destined to emerge from the pellet when the next year's summer rains first wet the surrounding soil, because pellets collected shortly before the rains yield larvae within a week if placed on wet filter paper. However, we have kept larval-containing pellets from Big Bend for over two years in dry, cool conditions.

One intriguing act performed by the pellet-residing larva is to feed on the inside wall of its residence. Eventually, egg pellets become full of tiny fecal pellets produced as a result of this feeding. Two possible explanations for such a performance come to mind. One is the need by the larvae for nutrition before rains effect their release. Another is their need to acquire intestinal microorganisms enabling the digestion of complex carbohydrates later in life. The latter possibility appears plausible in view of recent findings that *O. ornatus* possesses digestive enzymes capable of hydrolyzing an assortment of carbohydrates, ranging from disaccharides to a variety of long-chain compounds (Nunez and Crawford 1976). Among such compounds are cellulose and pectin, both important components of plant cell walls. Although we have not yet attempted to culture digestion-assisting microorganisms from egg pellets or from gut contents, evidence of a transfer of these from one generation to the next is not unexpected.

During the three or four months of the year when *O. ornatus* is known to be a feeding animal, it gains an amount of dry weight equal to about one and a half times its weight at the beginning of the feeding season (Crawford 1976). Ability to feed while behaviorally thermoregulating during the day must certainly contribute to this achievement, as must the millipede's approximately 33% assimilation efficiency on natural foods, a high value among detritivores (Wooten and Crawford 1975).

The potential impact of this feeding on the flow of energy and nutrients in the desert ecosystem was examined between 1973 and 1975 at Big Bend National Park and Albuquerque. In doing this, I estimated the density of a "typical" population at Tornillo Flat in the National Park by establishing three large enclosure plots, each lined with lawn edging (Crawford 1976). It turned out that the greatest number of specimens came from the plot with the greatest plant diversity and relatively high (20%) cover. A month of millipede removals produced an estimated average density per hectare of 1302 millipedes with mid-segment widths exceeding 4.0 mm.

This density value was used together with data on size-class distribution of removed specimens to estimate feeding-season production. A value for average abundance (Petrusewicz and Macfadyen 1970) would have been more realistic than density, but no convenient way was found to make accurate and periodic censusing of above- and below-ground populations. In this study I also determined that (1) biomass production of cuticle was nearly three times that of tissue, (2) energy-production values of cuticle and of tissue were essentially the same, and (3) the Albuquerque population gained significantly more total biomass in three months than did the Big Bend population.

The potential impact of an estimated feeding-season production of 1972 kcal $ha^{-1}$ (0.85 kg $ha^{-1}$) was assessed by using a published value of net primary production (NPP) for another creosote-bush desert, in addition to an estimated consumption value of 13,712 kcal $ha^{-1}$ (Crawford 1976). The resulting estimate of seasonal consumption came to 0.24% of NPP, and compares well with similar estimates for large detritivores in other ecosystems. Nevertheless, assuming such a percentage is realistic, if conservative, it follows that other consumers of dead organic material play a more vigorous role in the movement of energy and nutrients at Big Bend. Not to be discounted, however, is the possibility that as a consumer *O. ornatus* may have other regulatory functions in the desert ecosystem.

## THE DORMANT SEASON

In late summer and fall the desert millipede gradually returns to the soil habitat where most of its life is actually spent. Until the rains of early summer come again it will remain in this subterranean environment, usually coiled and often in the immediate proximity of many others of its kind. Over the years we have excavated many dormant *O. ornatus* from the nests of *Novomessor cockerelli* harvester ants, from the soil adjacent to mammal burrows, and from beneath volcanic rocks. So situated, this millipede must conserve the finite amount of energy and water available within its body if it is to survive the dormant season.

When such an animal begins this long escape

from the rigors of the soil surface, its body cavity is invested with a conspicuous amount of fat body, a tissue known to store surplus foodstuffs in arthropods. A simultaneous examination of the large, straight gut shows it to be filled with considerable ingested material and water. Possessed of these excess supplies, *O. ornatus* experiences a drop in metabolic rate that is roughly predictable from associated changes in soil temperature, but which does not appear to be entirely under temperature control (Wooten and Crawford 1974). Meanwhile, its previous use of carbohydrate as a primary source of energy in the feeding season has also undergone a change. Measurements of respiratory quotient (RQ) in fall, winter, and spring indicate the substitution of lipids, which on a weight basis supply more water and energy than do carbohydrates.

In recent years we have concentrated on understanding some of the major trends in water balance during the dormancy of *O. ornatus*. Although our analyses are still underway as of this writing, certain trends are becoming clear and can be referred to in general terms.

First, the actual amounts of water in the gut and cuticle-tissue "compartments" appear to undergo fluctuations that were not entirely expected. Within two or three months after the feeding season terminates both water and organic material in the gut have become greatly reduced. It is not yet clear where the gut water goes, but a preliminary analysis suggests that some of it may contribute to a simultaneous increase in the hydration of cuticle-tissue.

During the remaining half year of dormancy, the small amount of water remaining in the gut compartment appears insufficient to account for further hydration of cuticle-tissue, which nonetheless seems to occur. There is no evidence at present that such hydration might come about due to some form of uptake from the surrounding soil, although inhibition from soil wetted by occasional pre-emergence spring rains is not improbable. An alternate way of hydrating the combination of tissue and cuticle could be via the production of metabolic water. Calculations of metabolic-water production are possible, based on measured oxygen uptake at winter soil temperatures and on the assumption that lipid is the main substrate in respiratory metabolism during dormancy. Initial calculations do in fact suggest that the increase in cuticle-tissue hydration during winter months is fairly close to the volume of metabolic water produced.

There are other means, too, by which appropriate levels of hydration might be maintained during the mainly dry months of dormancy. Certainly the possession of a relatively impervious cuticle is one highly adaptive trait in this regard. Another involves the osmotic regulation of internal fluids so as to minimize the potentially detrimental concentration gradient existing between animal and dry soil.

We learned from recent experiments with millipedes in the feeding season that females in particular are able to maintain a low and steady level of hemolymph ("blood") osmolality for a month of exposure to dry air (Riddle et al. in press). However, we were unprepared for an approximately 50% increase in this physiological parameter in dormant millipedes. This striking rise in the overall concentration of hemolymph particulates does not appear to be related to measured changes in seasonal levels of major inorganic ions, and may therefore be a function of some metabolic product specific to dormancy. Whatever the case, the elevation of hemolymph osmolality in dormancy would seem to modify, but not usually equalize, the gradient in "activity" (Wharton and Devine 1968) of water between hemolymph and soil (unpublished data from Albuquerque).

About a month before the summer rains arrive, the great majority of individuals in *O. ornatus* populations studied are still underground, each in a small chamber formed as the surrounding soil becomes increasingly dry. Here, before precipitation wets the soil enough to permit escape to the surface, the first immediately obvious change in the life of a dormant millipede takes place. This event is the annual molt, a rather synchronous affair, even though the soil-bound animals are seldom in actual physical contact.

Molting, or ecdysis, includes the splitting off of the old cuticle, which is sometimes shed intact. A properly timed excavation of an over-wintering site often reveals a number of coiled, premolt specimens with thin, cracking cuticles, together with many flaccid, newly molted individuals lying in or near their exuviae, and some harder postmolt animals that have eaten much of their former covering. Usually the fractured remains of many older exuviae are also present, implying not only that *O. ornatus* leaves some of the old cuticle uneaten, but also that the same site is often used in dormancy year after year.

Molting allows for expansion of the circumference of each diplosegment prior to the hardening of the newly synthesized cuticle. Judging from a series of measurements of midsegment widths taken before and after molt, there is no predictable age-specific increase in this dimension, which greatly complicates the problem of ageing these animals. Still, whatever increase in width actually does occur results in new internal space that will be progressively occupied during the oncoming months by newly produced millipede biomass. The stage is therefore set for the comparative flurry of events characteristic of the feeding season, and for another year in the life of this unusual desert animal.

## LITERATURE CITED


BLOWER, J. G. 1955. Millipedes and centipedes as soil animals, pp. 138-151. *In* D. K. McC. Kevan (ed.) Soil zoology. Academic Press, New York.

_____. 1969. Age-structure of millipede populations in relation to activity and dispersion. pp. 206-216. *In* J. G. Sheals (ed.) The soil ecosystem. Systematics Association Publication No. 8.

CAUSEY, N. B. 1975. Desert millipedes (Spirostreptidae) of the southwestern United States and adjacent Mexico. Occ. Papers Mus. Texas Tech. Univ. 35:1-12.

CHAMBERLAIN, R. V. and S. MULAIK. 1941. On a collection of millipedes from Texas and New Mexico. J. New York Entomol. Soc. 49:57-64.

CLOUDSLEY-THOMPSON, J. L. 1949. The significance of migration in myriapods. Ann. Mag. Nat. Hist. 2:947-962.

_____. 1968. Spiders, scorpions, centipedes and mites. Pergamon Press, Oxford.

COOK, O. F. 1924. Swarming of desert millipeds Science 60-294.

CRAWFORD, C. S. 1972. Water relations in a desert millipede *Orthoporus ornatus* (Girard) (Spirostreptidae). Comp. Biochem. Physiol. 42A: 521-535.

_____. 1976. Feeding-season production in the desert millipede *Orthoporus ornatus* (Girard) (Diplopoda). Oecologia 24:265-276.

DOWDY, W. W. 1968. An ecological study of some millipedes in two central Missouri communities.

Ecology 61:1059-1063.
EDWARDS, C. A., D. E. REICHLE and D. A. CROSSLEY, JR. 1970. The role of soil invertebrates in turnover of organic matter and nutrients, pp. 147-172. *In* D. E. Reichle (ed.) Analysis of temperate forest ecosystems. Springer-Verlag, New York, Heidelberg, Berlin.
KAESTNER, A. 1968. Invertebrate zoology (translated by H. W. Levi and R. L. Levi). Vol. 2. Interscience, New York.
LOWE, C. H. 1968. Appraisal of research on fauna in desert environments, pp. 569-645. *In* W. G. McGinnies, B. J. Goldman and P. Paylore (eds.) Deserts of the world, an appraisal of research into their physical and biological environments. University of Arizona Press, Tucson.
NUNEZ, F. S. and C. S. CRAWFORD. 1976. Digestive enzymes of the desert millipede *Orthoporus ornatus* Girard) (Diplopoda: Spirostreptidae). Comp. Biochem. Physiol. 55A:141-145.
PETRUSEWICZ, K. and A. MACFADYEN. 1970. Productivity of terrestrial animals, principals and methods. IBP Handbook, No. 13. F. A. Davis Company, Philadelphia.
RIDDLE, W. A., C. S. CRAWFORD and A. M. ZEITONE. Patterns of hemolymph osmo-regulation in three desert arthropods. J. Comp. Physiol. (in press).
WHARTON, G. E. and T. L. DEVINE. 1968. Exchange of water between a mite, *Laelaps echidnina*, and the surrounding air under equilibrium conditions. J. Insect Physiol. 14:1303-1318.
WOOTEN, R. C. JR. and C. S. CRAWFORD. 1974. Respiratory metabolism of the desert millipede *Orthoporus ornatus* (Girard) (Diplopoda). Oecologia 17:179-186.
_____. 1975. Food, ingestion rates, and assimilation in the desert millipede *Orthoporus ornatus* (Girard) (Diplopoda). Oecologia 20: 231-236.
WOOTEN, R. C., JR., C. S. CRAWFORD and W. A. RIDDLE, JR. 1975. Behavioural thermoregulation of *Orthoporus ornatus* (Diplopoda: Spirostreptidae) in three desert habitats. Zool. J. Linn. Soc. 57:59-74.

# REPRODUCTIVE CHARACTERISTICS AND MANAGEMENT POTENTIAL OF THE SEA TURTLE ROOKERY AT CANAVERAL NATIONAL SEASHORE, FLORIDA[1]

L. M. Ehrhart[2]

## INTRODUCTION

In the summer of 1973, studies of the population of marine turtles nesting on the beaches of the Kennedy Space Center, Florida, were begun. These studies were a part of a broader ecological baseline study being carried out by a research group from Florida Technological University and funded by NASA. Much of the Kennedy Space Center has been administered by the U.S. Fish and Wildlife Service as the Merritt Island National Wildlife Refuge, and the refuge staff became actively involved in the sea turtle research. Prior to this time, little or no information concerning this rookery was available.

The effort in that first year was limited and only 51 loggerheads (*Caretta caretta*) and one green turtle (*Chelonia mydas*) were tagged. In that year, the study was a fairly typical tagging operation, except for the fact that we devised a means for weighing our turtles on the beach, something few other investigators have been able to do. The tags were provided by Dr. Archie Carr of the University of Florida through his grant (NO. 2162 B71) from the National Science Foundation.

The research effort was expanded somewhat in the summers of 1974 and 1975 as we began to understand the importance of this rookery. In 1974, we handled 111 loggerheads and two green turtles; in 1975, 121 loggerheads and two green turtles. These records of green turtle nesting are the most northerly records for this species in the western hemisphere. Details relating to these nestings have been presented elsewhere (Ehrhart, 1975).

The data produced in these studies, together with information recently developed independently by Carr (personal communication), affirm that this area is an integral part of the most important loggerhead rookery on the coast of North America, which is one of only three or four reservoirs for loggerheads remaining in the world. During 1975, approximately 40 km. of this nesting beach at the Kennedy Space Center were incorporated into the newly created Canaveral National Seashore. It is clear that one of the truly important and unique attributes of this seashore is the sea turtle rookery on its beaches.

Unfortunately, marine turtle eggs are very susceptible to predation by raccoons and the problem is especially serious at Canaveral. Almost 100% of all eggs deposited there are destroyed on the first or second night. In response to this, the joint FTU-FWS team embarked on what has become a second major phase of the operation, a sea turtle hatchery. In 1974, we began to gather freshly laid eggs, pack them in sand, and transport them to refuge headquarters and our laboratory for secure incubation there. We realized that the eggs and hatchlings were an excellent source of data relating to the reproductive condition of the population. During 1975, the entire hatchery operation was moved to our laboratory and we began to take increased advantage of the availability of the eggs and hatchlings to gather basic morphometric fertility, and hatchability data. It is the information derived from this hatchery, primarily 1975, that will be presented here.

## RESULTS AND DISCUSSION

*Clutch size.* The numbers of eggs in six loggerhead clutches processed in 1974 and 43 clutches processed in 1975 are given in Table 1. Mean clutch size for the larger body of data in 1975 (110 eggs) seems somewhat smaller than the 126 reported by Caldwell (1959) for Jekyll Island loggerheads but is exactly the same as that reported by LeBuff (1969) for Sanibel Island.

Caldwell (1959) and LeBuff and Beatty (1971) reported a decrease in clutch size as the season progressed. The period over which we gathered eggs was too short (about five weeks) for proper investigation of this phenomenon, but a regression analysis of these preliminary data shows no relationship between clutch size and point in season.

The single green turtle clutch secured in 1974 contained 167 eggs. In 1975, the only *Chelonia* clutch collected contained 62 eggs.

*Egg diameter and weight.* Mean diameters of samples of 20 eggs from six clutches in 1974 and 43 clutches in 1975 are given in Table 1. There is some variation in egg shape, but they are essentially round. Nevertheless, the mean diameters observed here are greater than those given by Ernst and Barbour (1973) for "greatest diameter" of loggerhead eggs.

Weights of the same samples of eggs mentioned above are given in Table 1. Average weights were very similar in the two years (41.7 g. in 1974 a and 42.0 g. in 1975).but substantially greater than the mean of 35.0 g. reported by Caldwell (1959).

We only have data for one clutch of green turtle eggs, but the mean weight (60.1 g.) and the range (55.8-63.8 g.) exceed those of loggerheads by a considerable amount. The diameter of green turtle eggs (mean: 47.5 mm.) is correspondingly larger than that of loggerheads.

*Incubation period.* In the wild, the average incubation period for loggerhead eggs is 55 days and the range is 49 to 62 days (Caldwell, 1959). Inasmuch as all of our eggs were kept inside an unairconditioned building, temperatures undoubtedly were not as high as they would have been on the beach. Incubation periods were lengthened correspondingly. The mean (69 days) is a week longer than the observed maximum period in the wild. The minimum incubation period observed was 63 days; the maximum, 75 days.

The green turtle clutches collected in 1974 and 1975 began to hatch in 69 and 66 days. Not surprisingly, these also exceeded the normal maximum incubation period in the wild, reported by Ernst and Barbour (1972) as 45 to 60 days.

[1]Contribution No. 6, Merritt Island Ecosystems Studies. This research was supported by NASA grant NGR 10-019-004.

[2]Florida Technological University, P.O. Box 25000, Orlando, Florida 32816.

TABLE 1. Number and size of eggs deposited by loggerhead turtles (*Caretta caretta*) at Canaveral National Seashore, 1974 and 1975.

| | | Clutch Size | | Diameter (cm) | | Weight (g) | |
|---|---|---|---|---|---|---|---|
| Year | N | $\bar{x}$ | (Range) | $\bar{x}$ | (Range) | $\bar{x}$ | (Range) |
| 1974 | 6 | 117 | (81-149) | 4.23 | (4.02-4.48) | 41.7 | (36.5-46.0) |
| 1975 | 44 | 110 | (43-154) | 4.22 | (3.70-5.52) | 42.0 | (28.2-52.9) |

TABLE 2. Summary of hatch rates, fertility rates and other data generated in the protective program at Canaveral National Seashore, Summer 1975. (*Caretta caretta*)

| | N | $(\bar{x})$ | |
|---|---|---|---|
| Eggs Secured: | 4703 | 109.4 | (43-154) |
| Eggs Hatched: | 3470 | 80.7 | ( 73% ) |
| Pipped but Dead: | 39 | 0.9 | ( 0.8% ) |
| Hatchlings Released: | 3431 | 79.8 | ( 72% ) |
| Fertile but Unhatched: | 508 | 11.8 | ( 10% ) |
| Infertile: | 599 | 13.9 | ( 12% ) |
| Unaccounted For: | 126 | 2.9 | ( 2% ) |
| Minimum Fertility Rate: | 85.1% | | |
| Maximum Fertility Rate: | 87.7% | | |

TABLE 3. Morphological characteristics of loggerhead turtle hatchlings at Canaveral National Seashore, 1974 and 1975.

| | | Weight (g) | | Carapace Length (mm) | | Carapace Width (mm) | |
|---|---|---|---|---|---|---|---|
| Year | N | $\bar{x}$ | (Range) | $\bar{x}$ | (Range) | $\bar{x}$ | (Range) |
| 1974 | 6 | 21.7 | (16.1-25.8) | 46.1 | (39.2-49.9) | 34.7 | (30.2-38.0) |
| 1975 | 42 | 20.8 | (12.2-27.6) | 45.5 | (33.5-49.5) | 34.0 | (29.0-38.4) |

*Fertility rate.* At the end of the 1975 season, all unhatched eggs were cut open and examined. We followed Hughes, Bass and Mentis (1967) and regarded any egg in which there was no discernible signs of embryonic development as infertile. Fertility rates of eggs from 43 loggerhead clutches deposited in 1975 are listed in Table 2. In almost every clutch, some discrepancy arose between the number of eggs reported and the number accounted for. There were multiple causes for this but probably the most important were human error in counting on the beach and the fact that infertile eggs were torn apart and obliterated in the sand by the mass of scratching, climbing hatchlings on the day of hatching. Because of this discrepancy, minimum fertility rates (assuming all unaccounted for eggs were infertile) and maximum rates (assuming all unaccounted for eggs were fertile) are reported. The difference between the overall mean minumum (85.1% and maximum (87.7%)rates is not large and it seems certain that the true fertility rate was approximately 87%. Hughes, Bass and Mentis (1967) reported a fertility rate of 88.3% for Tongaland loggerheads.

Minimum and maximum fertility rates for the clutch of 62 green turtle eggs collected on 13 July 1975 were 79% and 85.5%.

Fertility rate may well prove to be a sensitive indicator of the reproductive health of a sea turtle population. With some improvement in technique, annual assessments of fertility rates might serve as invaluable indicators of environmental influences on loggerhead reproduction.

*Hatching success.* During 1974, a total of 5117 loggerhead eggs and 167 green turtle eggs were protected. Over 85% (4352) of the loggerhead eggs and 74.2% (124) of the green turtle eggs hatched and the young turtles were released into

the Atlantic Ocean. Hatchlings were released on the day of emergence at the sand surface.

An account of the total loggerhead eggs hatched, eggs pipped but with hatchlings dead, and hatchlings released, for 1975, is given in Table 2. Hatching success in 1975 was poorer than in 1974 but still relatively good. Of a potential of 4703 eggs, 3431 hatchlings (72%) were actually released. The causes of this variation are obscure. Caldwell (1959) reported that in the wild hatch success varies from 16 to 98%.

Of the 62 green turtle eggs secured in 1975, 40 (64.5%) hatched and the young were released.

*Morphology of hatchlings.* Means and ranges of the weight, carapace length and carapace width for loggerhead hatchlings in 1974 and 1975 are given in Table 3. Mean carapace length of these Canaveral Seashore hatchlings (45.5 mm. and 46.1 mm.) closely resembles the 45 mm. mean reported by Caldwell (1959) and Hughes and Mentis (1967). Carapace widths also were similar.

Caldwell (1959) stated the mean weight of 104 hatchlings was 21.2 g., which is very comparable to the 21.7 g. and 20.8 g. observed here.

Although steadfast conclusions should not be drawn from the single clutch of green turtle hatchlings in 1975, it is interesting to note that the mean weight of *Chelonia* hatchlings reported by Ernst and Barbour (1972) was 25 g., whereas our observed mean was 31.1 g. with a range of 26.1 to 34.1 g. Linear measurements of these Canaveral hatchlings were, however, similar to those given by Ernst and Barbour.

*Management potential.* It seems clear that the 40 km. stretch of nesting beach at the Canaveral National Seashore is of critical importance to the Atlantic population of *Caretta caretta* and also to that nearly extirpated population of *Chelonia mydas*, the vestiges of which nest on these beaches. The management potential here is excellent because the entire area is well controlled by the National Park Service, the Fish and Wildlife Service, NASA, the U.S. Air Force and the Florida Marine Patrol. The problem for management is the raccoons. What follows is a brief acoount of measures that might be considered, should a committment to egg and hatchling protection ever be made.

1. Removal of raccoons by trapping, shooting, poisoning, or the introduction of disease.

a. The use of kill-traps and poisons, we believe, is unacceptable because of the large populations of spotted skunks (*Spilogale putorius*), opossums (*Dedelphis virginianus*), bobcats (*Felis rufus*) and otters (*Lutra canadensis*) that are also present but not implicated in any way in turtle egg destruction. Our live-trapping studies of these intermediate-size mammals (March 1973 to February 1974) at Canaveral indicate that hundreds of these non-target mammals would be killed. In addition, live-trapping and removal is not practical; it is too labor intensive and not compatible with use of the area by the public.

b. Hunting raccoons by authorized government agents, with the aid of trained dogs, may seem out of order on a refuge or seashore but may well be one of the more viable alternatives.

c. Apparently raccoon populations in Florida's coastal areas are occasionally decimated by canine distemper. Intentional introduction of this disease into the population in this isolated area may be an alternative worth considering, if it can be shown that harmful side effects are negligible.

2. Repellents.

a. Efforts to apply raccoon repellents (if suitable ones could be found) or to train raccoons to avoid turtle eggs by application of lithium chloride of other distasteful substance would be extremely labor-intensive, would have to continue indefinitely and would probably be ineffective.

3. Construction of enclosures over nests.

a. This, too, would be a very time-consuming operation and would have to be continued indefinitely.

4. Continuation and expansion of hatchery.

a. The current hatchery operation is scheduled to continue through 1978, under the present NASA funding structure. The hatchery serves the dual function of egg preservation and provision of good information about clutch size, egg diameter and weight, and fertility rates. These data can be thought of as parameters of the reproductive health of the population, and constitute an annual monitoring of that reproductive health. This may well be the most useful function of the hatchery and adequate justification for its continuation. Although there is no apparent way to assess the survival rate of released hatchlings, it is undoubtedly very small.

b. Considering the suspected low survival rate, it may be worthwhile, at some later date, to consider tank-rearing of hatchlings to yearling size, when they are apparently better able to avoid predators. If studies now being carried out on green turtles by the Florida Department of Natural Resources show that such turtles eventually return as breeding adults, it may be worth considering.

## LITERATURE CITED


CALDWELL, D. K. 1959. The loggerhead turtles of Cape Romain, South Carolina. Bull. Florida St. Mus. 4:319-348.

EHRHART, L. M. 1975. *Chelonia mydas* nesting on Merritt Island, Florida. Florida Scientist 38(1):5 (abstract).

ERNST, C. H., and R. W. BARBOUR. 1972. Turtles of the United States. Univ. Press Kentucky, Lexington. 347 pp.

HUGHES, G. R., A. J. BASS, and M. T. MENTIS. 1967. Further studies on marine turtles in Tongaland. I. Lammergeyer 3:5-54.

HUGHES, G. R., and M. T. MENTIS. 1967. Further studies on marine turtles in Tongaland. II. Lammergeyer 3:55-72.

LEBUFF, C. R., JR. 1969. The marine turtles of Sanibel and Captiva Islands, Florida. Spec. Publ. Sanibel-Captiva Conserv. Found. 1:1-13.

LEBUFF, C. R., JR., and R. W. BEATTY. 1971. Some aspects of nesting of the loggerhead turtle, *Caretta caretta caretta* (linne), on the Gulf coast of Florida. Herpetologica 27(2): 153-156.

# HERPETOLOGICAL RESEARCH IN THE NATIONAL PARK SYSTEM[1]

David J. Morafka[2]

## INTRODUCTION

For too long the National Park Service has served as cordial but passive host to herpetological investigators operating on its lands.

As a major national administrator of the North American wilderness, the Park Service should take a more active role in upholding professional standards and in coordinating future research.

I have prepared this critique with the benefit of some recently acquired humility. My words of advice are not quite the first ever addressed to the Park Service, not even by herpetologists. It seems that Edward Drinker Cope has me scooped by about 90 years, his similarly titled article appearing in 1884. In reviewing policy statements of individual park administrations, I have also discovered some of my best and most "original" suggestions have already been part of park practice for years. Finally, my survey of titles in the 1974 yearbook of the Chief Scientist, revealed the sad fact that no more than two percent of current National Park (and Monument) research was herpetological.

Nonetheless, herpetological investigations offer unusual opportunities and challenges in research, management, and education. I suspect few in the Park Service realize how much herpetological research has to offer. Equally few herpetologists now recognize how well their knowledge and activities could serve our parks and monuments.

I would like to develop three major themes: 1) the current status of herpetological research within the National Park System, 2) quality controls that will ensure the value and purposefulness of future endeavors, and 3) the special insights that may be gained through herpetological research. On the basis of these three points, I would establish a fourth, the value of active dialogue between the park service and the herpetological community. This dialogue should focus the long-term and national goals of both communities as well as their more immediate needs and aspirations. The specific suggestions that I offer here are designed to initial this dialogue, to get people thinking. I do not pretend to be a spokesman for the entire herpetological community nor would I want my suggestions institutionalized into inflexible policies. I only hope they will be considered as possible guidelines and provoke further discussion.

## THE PAST AND PRESENT STATE OF HERPETOLOGICAL RESEARCH

### *Past Research*

In our national park system, most early herpetological works were subsections of park fauna and flora inventories. The first 75 years of park-based research consisted largely of these check-lists of species, often constructed with an inordinately strong respect for park boundaries, as defining study limits. Most other herpetological research was taxonomic. Often these took the form of meristic studies describing new local subspecies (e.g. based on scale counts, superficial pigmentation, etc.). The remainder included a scattering of reports on diet, habitat preferences, and the autecology of a few conspicuous species (es. turtles and crocodilians).

Often the results of these early surveys and other investigations were synthesized into popular field guides, some of which were very well illustrated and included effective local taxonomic keys.

As the general sophistication of field biology increased, so too did the number of parks with completed faunal surveys. As a net result, recent park based research has progressed considerably. Recent ecological, evolutionary, physiological, and behavioral studies focus much more on causal processes than did descriptive surveys and taxonomic reports of the past.

### *Park Criteria for Research Approval*

Changes in criteria for permitting park-based research have largely paralleled the advances in field biology. In most parks, permission is now granted only when an explicit set of standard requirements have been met. Regional NPS Directors, in the act of replacing old application (and permit) forms in 1973-74, have generally tightened criteria for permitting scientific collecting. Applications for collecting (Form PSN-101) require the collecting period, the type and quantity of specimens to be collected, other permits (state and federal), reason for collecting within the Park or Monument, and place of specimen deposition. In addition, the investigator requesting permission to collect vertebrates must offer a proposal including the following: 1) the purpose of the study within the Park, 2) objectives of the study, 3) study methds, 4) literature review, and 5) personnel data.

The proposals are reviewed by the Management Biologist, Chief Park Naturalist or other NPS official designated by the Superintendent. Final approval is granted only by the Superintendent of the Park or Monument. Guidelines for the review process include consideration of:

[1]I would particularly like to thank the NPS staff serving in Pinnacles National Monument, California, during 1964 through 1968 for the patience, tolerance, instruction, and support that they extended to a young (undergraduate) fanatic herpetologist who invaded the Monument for extended periods of time. I would also like to thank Kheryn Klubnikin, Carl Lief, Robert Murphy, and Laurie Vitt for their insights, suggestions, and criticisms. David J. Parsons, NPS Research Scientist for Sequoia-Kings Canton National Parks, Roland Wauer, Chief, Division of Natural Resources of the NPS Southwestern Region, and Milton C. Kolipinski, Research Scientist in the Western Regional Office all provided substantial background information, existing policies, and guidelines regarding collecting permits.

[2]Department of Biological Sciences, California State College-Dominguez Hills. Dominquez Hills 90747.

reasons for collecting within the park, deposition of specimens, the number of specimens, as well as the species involved. Some species are to be considered "restricted," either because they are designated "endangered" by the U.S. Fish and Wildlife Service, or because they are locally rare or endangered. Collection of these restricted species would normally be prohibited. A collection "due date" must also be designated. On that date, a complete report and specimen inventory must be supplied.

*Analysis of Current Research*

The 1974 Yearbook (see Lit. Cit.) provides a convenient survey of current and approved herpetological research. Quantitatively, herpetology's percentage of total scientific research for 1974 is as follows:

| | |
|---|---|
| Total number of scientific investigations: | 1021 |
| Exclusively herpetological investigations: | 2% |
| Biological Surveys (including herpetofauna): | 1%+ |
| Paleontological Surveys (including herpetofauna): | 0.2% |

The 20 specific titles that make up the purely herpetological research produces the following information:

| General Category | No. | % |
|---|---|---|
| Ecology | 9 | 45 |
| Evolution and Taxonomy | 5 | 25 |
| Faunal Survey (herpetofauna) | 4 | 20 |
| Physiology and Anatomy | 1 | 5 |
| Behavior | 1 | 5 |

Since these breakdowns represent only a single year, I don't wish to overemphasize their significance. Yet, the relatively small number of ongoing surveys and the predominance of ecological projects is striking.

*Assessment of Current Research Trends*

At this point, I would like to make a brief assessment of the current state of park-based research in herpetology. It is a reflection of more general trends in field biology, with perhaps some lags in physiology and behavior. Generally, the historical progression has involved both topics and techniques. A more mechanistic ecology is now replacing the descriptive inventories and taxonomy of the past. I think this trend will enhance the utility of many current and future projects relative to park needs in the fields of management decisions and public education. I state this without wishing to imply that the surveys were without value. My intent is only to encourage more sophisticated research beyond that preliminary state. A glance at current topics indicates that many of the problems recently undertaken deal with major biological phenomena and/or with species of broad ecological importance.

However, I do offer two major criticism based on this survey of 1974 titles. Firstly, too few species are being studied. North America has rich and diverse herpetofauna with many localized or endemic forms. The inadequacy of the situation is aggravated by a concentration of the active research in Appalachian and Gulf Coast parks. Seventy percent of the titles referred to projects based in these two regions. Biologically there is really no justification for this bias.

Secondly, a glance at the titles shows no continuity between them. Even within a major field, such as ecology, it is apparent no system-wide standardization of projects or approaches exists. The value of many of the projects would be greatly enhanced if parallel studies were being undertaken in other parks and monuments. Instead of system-wide coordination and standardization, we find a collection of totally independent projects, all headed in different directions with no relationship to one another. The passive nature of Park Service involvement in herpetological research is, at least, in part to blame.

*Criteria for the Approval of Future Research*

Well chosen criteria for the approval of research projects might serve well the dual functions of upholding research quality and focusing its direction. It might also encourage the standardization that is so completely absent from the current efforts. As already noted, many parks presently enforce well-developed criteria for deciding approval. Still, it would be reassuring to see uniform minimal standards established system-wide. Even where well chosen qualifications have been established, refinement of explicit details would be desirable. In particular, most criteria could be improved by adding more specific "teeth" to them, "teeth" that force the definition of objectives, sample sizes, schedules, etc.

I am proposing here three major criteria, in the form of questions, which should make enforcement of standards more practical and at the same time ensure the quality and usefulness of the proposed research. The questions are posed in a progession from more general to more specific.

*Adverse Effect*

(1) *Will the proposed research have an adverse effect on Park or Monument ecosystems and their herpetofaunas?* If so, (a) *why must the investigator disturb a protected (Park) population?* and (b) *has every effort been made to minimize the negative impact of the proposed research without seriously impairing the accuracy of the project?*

Obviously, many investigators may be unable to give explicit answers to the questions in the initial phases of their proposal. Probable consequences of their research might be established through a literature search for similar experimental designs undertaken in similar environmental conditions. Unfortunately, the diet, behavior, and productive capacities of many amphibians and reptiles are poorly known. As a result, a search of previous literature may not provide adequate answers. In these cases, and especially involving projects of major proportions, pilot studies may be necessary. These small scale trials should be run outside the park lands, if at all possible. Their results should provide an accurate basis for appraisal of potential impact.

*Relative Importance*

(2) *Is the importance of the project's objectives sufficient to justify anticipated burdens imposed upon park resources and/or staff?* Two subordinate questions might help resolve the one just posed. These two are: (a) Is the proposed work redundant with studies already in the literature or those being undertaken elsewhere in the park system? (b) How will the study

results benefit the scientific community in general and the managerial and educational needs of the park in particular?

As noted in the first criterion, a good literature search is valuable. In this instance, it not only reduces the probability of redundance, but also demonstrates how the proposed study will build on pre-existing knowledge. Evidence that a particular proposal parallels work done or in process in other parks should be viewed with particular favor. Standardized sets of comparable data are the mainstay of science. Comparative studies are crucial to ecology and evolution, subjects in which responsible extrapolation and prediction are always difficult.

*Experimental Design*

Once the general appropriateness of a proposal has been established, the Park administration may focus on the quality of the research design. I have suggested a third question for this purpose, something on the lines of the following: (3) *Is the experimental design, sample size, field site, funding, equipment, and schedule of the proposal realistic, relative to the objective?* Here again both a thorough literature search and, possibly, a pilot study would be invaluable. Ideally, a good bibliography should accompany any proposal. The NPS administration should not assume that experimental design, statistical treatment of data, units of measure, or controls are adequate. It should be unrestrained in offering constructive criticism and in drawing upon the knowledge that only a local permanent staff could acquire.

A formal contract between the administration and the investigator would make explicit timetables, quotas, techniques, locations, and any mutual responsibilities.

Nature has no respect for "the best laid plans of mice and men"--permit renewal should not be made contingent exclusively on the fulfillment of some tentative or ideal timetable. Rather the contract would serve as a well calibrated yardstick with which to measure the effectiveness of a particular project. Such a relative measure would prove educational to both the administration and the investigator.

Special care should be devoted to the determination of sample sizes. As noted earlier, amphibian and reptilian life histories are little known, with regard to salamanders and snakes. In addition, they often have populations of unknown size, stability, biotic potential, or intrinsic rate of growth. Without these sources of information, it is virtually impossible to estimate the impact or recovery time incurred by the culling of even a few individuals. Simple numbers, out of context biologically do not mean much. For example, the removal of 10 western toads (*Bufo boreas*) from Yosemite Valley might easily have a negligible impact. The toad has a wide range both ecologically and geographically, high population densities and very high biotic potential. In contrast, the removal of ten rare Mte. Lyell salamanders, *Hydromantes platycephalus* from Half Dome might decimate the isolated small deme (local population) beyond hope of recovery. The latter species is ecologically restricted, and geographically confined to the Sierra Nevadas. Its biotic potential and population densities are low. Perhaps a direct population count, or Lincoln Index estimate, should be undertaken before a number is set for permitted collections, at least in critical cases.

It should also be noted that in many cases, taxonomic collection quotas (especially for snakes) could be met by the preservation of highway road kills (DORs)--thus obviating the need for removing living animals.

The NPS should also have the investigation proposal, including the specific contract, reviewed by a professional herpetologist. Each proposal should suggest a professional reviewer not associated with the project. In lieu of a suggested reviewer, the NPS could submit the proposal to the conservation committees of any of the three herpetological societies. Such a review would relieve the NPS of extraordinary efforts to research the validity of proposal claims. Thus, professional reviews would add no expense or workload to the park service, yet it would not usurp the NPS as the final authority regarding collecting or investigative proposals.

These suggestions pertain to all proposed herpetological research - not just collecting requests. Poorly planned mark and recapture projects, for example, could have appreciable negative impact, even though no "collection" was being made.

For the sake of balance, I would suggest also that collection numbers not be set so low that statistically significant results are made unattainable. If a population could sustain the loss, a herpetologist might justifiably request a sample size of 25 or 50 individuals or more, especially in a systematic or ecological study where intrapopulation variation was great. Token collections are no more meaningful than are manifestations of tokenism in any other context.

## SUBJECTS AND STRATEGIES FOR ENDURING SYSTEM-WIDE RESEARCH

The NPS is a potentially powerful instrument for scientific research. It administers some of North America's best protected and distinctive wilderness, including representatives of most of the continent's major ecosystems. Moreover, the NPS commands a small army of personnel coupled with an impressive network of field stations, laboratories, museums, equipment, vehicles, publications, and the service now adds to this inventory its own computer system, The Ecological and Environmental Management Informational System, or EEMIS. This resource, still in the initial stages of development (see Douglas 1975) should serve admirably the dual functions of information retrieval and predictive model simulation. Such an array of resources should engender vigorous research - even without much further funding. An institution with so many resources at its command should be more than a passive, if gracious, host to "piece-meal" research, even in such a "peripheral" field as herpetology.

I am recommending three broad areas - evolution, ecology, and conservation - in which a system-wide effort at herpetological research would be especially productive. I do not suggest these to the exclusion of others, nor do I advocate the rejection of individual investigations conceived outside the system. I make these suggestions for the purpose of generating interest in programs of coordinated, standardized herpetological research. At the same time, I do hope my discussion of these three will highlight the insights that herpetological studies could bring to bear on basic environmental phenomena.

I will focus on the potential contributions

afforded by the recognition of amphibians and reptiles as: 1) evolutionary indicators, 2) ecological indicators, and 3) conservation, especially of endangered species.

### *Evolutionary Indicators*

By use of the term evolutionary indicator, I am referring to species or races of organism whose morphology, behavior, and/or distribution reflect specific evolutionary pathways or the evolutionary impact of events in geological history. The antiquity of amphibian and reptilian lineages, coupled with their responsiveness to physical environmental limits make members of these classes excellent indicators of evolutionary processes. I will confine my discussion to living forms and their antecedents, though many of my observations apply in varying degrees, to extinct fossil faunas as well.

Amphibians and reptiles have been on earth a very long time. This holds true not only for the classes with their 350-400 million years of history but also for the subordinate orders, families, and even genera. The dusky salamanders, genus *Desmognathus*, the soft-shelled turtles, genus *Trionyx*, and perhaps the alligator lizards, genus *Gerrhonotus* may all date back at least 70 million years to the Cretaceous Period in Wyoming (Estes 1964). The living genera of alligators (*Alligator*), the gopher tortoises (*Gopherus*), the Gila Monster (*Heloderma*) and the spade-foot toads (*Scaphiopus*) all may be traced through the fossil record to Miocene-Oligocene Epochs, some 20-30 million years ago.

Most modern species probably have recognizable conspecific ancestors dating back 5 to 10 million years into the Pliocene Epoch if I may extrapolate from a limited fossil record (Milsted, 1965). The same cannot be said for many other faunal groups, either because their record is too feeble (insects) or their modern speciation more recent (rodents).

Amphibians and reptiles are tied as closely to the conditions of climate and landscape as they are to past geological history. Their powers of dispersal are limited (marine and 'waifing' forms excepted). Limited also are their capacities to regulate against physical environmental stress. As a result, amphibian distributions are defined by terrestrial wilting points, substrates, ground cover, slopes and drainage as well as physical parameters of the aquatic environment such as dissolved oxygen pressure, salinity, and universal factors, temperature being an example of the latter. Reptiles conform to many of the same environmental parameters and within similar ranges, but exercise more physiological regulation and ecological independence relative to water-based factors (since they are often excellent osmoregulators). Furthermore iguanid lizards and certain other groups effectively reduce temperature constraints by behavioral thermoregulation.

Both antiquity and physiologically responsiveness (or dependence) on the immediate physical environment, couple to make amphibians and reptiles superb links between events of geological and biological history. They present Park interpretation programs with an outstanding opportunity to integrate geological and biological education programs. The synthesis of historical geology, evolutionary history, and the present distributions and adaptations of organisms is the discipline of historical biogeography. Simplified biogeographical accounts, especially if clear and well illustrated, make exciting lecture and reading material. These accounts could integrate diverse scientific knowledge into concise presentations and give park visitors a perspective of geological time that would be difficult to convey in any other way. Historical biogeography establishes the revelance of the past to the present by use of examples available to the public for immediate observation. Amphibians and reptilian examples are abundant. As an example, Morafka and Banta (1972) correlated the distribution of endemic species and races in the Gabilan range (Pinnacles National Monument) to the shore lines of Pliocene Islands in coastal central California. Such studies could easily be adapted for popular presentations.

### *Ecological Indicators*

The intimate relationships between amphibians and reptiles to the fine grain perturbations and alterations of their physical environment makes them as valuable an analytical tool for the ecologist as they are for the biogeographer. The taxonomy of U.S. forms is well worked further enhancing their utility. Many 'herptiles' serve admirably as index or indicator species, defining or identifying both temporal units (such as successional stages) and spatial units ranging from elevational zones (life zones) to major biotic provinces. In addition, herpetofaunas are sufficiently diverse (in species) at least in the southern half of the United States that they may be utilized in the quantitative analysis of zone, community, or province affinities (with other like units) through the calculation of resemblance coefficients. Finally, these faunas are available tools for physiological bioassays of environmental quality (through their use in toxicity studies, biological magnification, diversity indices, etc.).

### *Use as Indicators of Temporal Units*

Successional stages are generally recognized by the presence or predominance of key index species. These are traditionally drawn from dominant vascular plants, mammals, and occasionally, insects. In some situations, amphibians and reptiles, particularly lizards, would also serve admirably as indicators of transitional stages or unstable disclimax conditions. Unisexual hybrid clones, often identifiable as "species" in the lizard genus *Cnemidophorus* are strongly associated with transitional circumstances such as early successional stages, disclimax, and ecotones between communities. Lowe and Wright (1968) have discussed the significance and associations of these "weed species" of lizards in the southwestern United States and Mexico.

## USES AS INDICATORS OF SPATIAL UNITS

Plants, birds, and mammals are as established as *indicator* species for spatial units (zones, communities, provinces) as they are for temporal (successional) (see Shelford, 1964) units. Most investigators have considered amphibians and reptiles so inconspicuous or secretive that they would be of little practical value as indicators. I take strong exception to this view. In particular, I find that ecologists have long overlooked the abundant and diurnal lizards which are such a conspicuous part of Western North America's fauna. The sun-basking lizards of the predominately Western family Iguanidae are more easily approached and identified than are most birds and mammals. Furthermore, these lizards often segregate according to major communities and elevational zones (species of the genus *Sceloporus* demonstrate this tendency particularly well, relative to one another). Species of horned

lizards (genus *Phrynosoma*) often have ranges conforming to major biotic provinces. American lizard taxonomy is generally in good condition. Most species are easily identified through the use of popular field guides for the eastern and western United States (Conant, 1975, and Stebbins, 1966, respectively). Size, color, posture, profile, characteristic movements and perch site may be used to diagnose lizards just as effectively as they are employed for bird identification. True, lizards don't trill and warble, but then you don't need binoculars just to see one.

## USES AS INDICATORS OF ENVIRONMENTAL QUALITY

We are capable of discriminating a deterioration in environmental quality from a number of perspectives. In some of these perspectives, toxicity, biological magnification, and community stability, herpetofaunal studies may make valuable contributions.

While we still know little about the effects of toxins on amphibians and reptiles, it is certain that some species have high sensitivities to both physical environmental traumas and chemical toxins. Some cold stream salamanders, such as the Olympic salamander (*Rhyacotriton olympicus*) are visibly stressed by even a very low thermal load. Many amphibians respond negatively to salts and other potential toxins added to an aquatic substrate. By way of illustration: Frogs and tadpoles are among the most abundant and sensitive experimental animals available for the bioassaying of freshwater quality. They should demonstrate superior toxin sensitivity (even manifest behaviorally) relative to many older standards, such as the fish, *Gambusia* and *Fundulus*. The work of Cooke (1972), Ferguson and Gilbert (1967), Herald (1949), and Kaplan and Overpect (1964) all document anuran toxin sensitivities, especially in regard to chlorinated hydrocarbons like DDT.

Species of both classes occupy niches situated at virtually every trophic level above that of primary producer. Thus, these species could serve as effective monitors of the biological magnification of environmental toxins (the progressive concentration of toxins passing up a food chain). Many turtles and some lizards are primary consumers. Most lizards and amphibians are secondary consumers. Snakes, carnivores all, operate at still higher trophic levels. Many amphibians and reptiles are more abundant than their avian and mammalian counterparts at the same trophic levels (since they convert more indigested food into their own biomass and less into body heat). They are often more easily captured as well.

Environmental quality may be assayed by the survival and/or physiological condition of individuals of a particular species. But it may also be assessed by calculations of the diversity and frequency distribution within and between whole sets of species. Ordinarily community species diversity varies directly with community stability. The well being of the community in turn, generally correlates with high community stability. As previously noted, amphibian and reptiles species are well defined taxonomically in the United States and sufficiently diverse, at least in the southern half, to be used in indices of diversity. Such indices, particularly those comparing areas of intensive public use with those ecologically similar areas of pristine wilderness could serve as calibrating measurements of the degrees of human impact.

Physiological responsiveness, a wide range of trophic positions, physical accessibility of samples, and well defined species diversity all recommend the use of amphibians and reptiles as indicators of environmental quality. In none of the attributes just listed are these two classes unique, but they are available and valuable tools to the ecologist and the park administrator. They are tools that too often are ignored or rejected without reason.

## THE CONSERVATION OF RARE AND ENDANGERED SPECIES

In a philosophical sense, I am still pursuing the ecological relationships of amphibians and reptiles. Perhaps with added evolutionary biproduct, extinction, thrown in. However, the issue of conservation at any level is so immediate in its importance that it makes little practical sense to subordinate it to another title. I will approach the general topic from three consecutively expanded perspectives: autecology, conservations problems intrinsic at the taxonomic class level (especially public prejudice), and ultimately, conservation at the ecosystem level.

### *Autecology*

Autecology, or ecology from the perspective of a single species, has been the historical vehicle by which herpetologists (and most biologists) investigated distinctive or endangered species. The approach is sometimes overly narrow, an investigator literally not seeing the forst for the trees. Yet this approach does have redeeming features, especially for the conservationist and/or park administrator searching for specific facts pertinent to the survival of a waning population. Autecological studies often hone in on such facts, considering and illucidating the fine details of biotic potential, life cycles, diet, disease, predation, dispersal and microhabitat preferences. These details may escape the surveys of broader studies, yet they may make the difference between success and failure in wildlife management. Autecological studies are particularly desirable for endangered forms, but other species that contribute to environmental resistance, provide peculiar microhabitats, present health hazards, and those of striking aesthetic value should also be investigated throughout the park system.

Several amphibians and reptiles are recognized as endangered and are so listed by the U.S. Fish and Wildlife Service. Many more are threatened with local extirpation. Species in both categories occur within National Parks and Monuments. Roland Wauer, Chief Scientist for the NPS southwestern Region noted the present general situation (1976:176): "I would hate to think of the bind that we could find ourselves in if we were required to develop a plan for all the endangered species that occur on Park Service administered lands within a few months." The U.S. Bureau of Sport Fisheries and Wildlife has recently coordinated a continental program of autecological studies of endangered North American turtles and tortoises. It might serve as a useful model for future coordinated studies on a continental or national level.

Such investigations should not be restricted to forms on the brink of extinction. Many others are crucial to ecosystem stability because of key niches they occupy. Many amphibians and reptiles are major components in the density-dependent environmental resistance to disturbing population booms of opportunistic primary consumers such as insects and rodents. Illustrative of this role

are horned lizards (genus *Phrynosoma*). As intensive and selective predators (Stebbins 1966), horned lizards perform the role of thermostats repressing ant population booms that might otherwise devastate seed crops in years of high productivity. Ants may radically affect seed crop distribution and survival and thereby govern the structure and stability of many arid southwestern ecosystems (Tevis 1958 and Rogers 1974).

Other species generate microhabitats that would otherwise not exist. The mud wallows of alligators in the Everglades during times of drought and the burrows of the North American gopher tortoises (genus *Gopherus* ) serve as classical examples. The microhabitats and associated microclimates provide refuge for whole faunas which could not otherwise survive the climatic extremes of the environment.

Unfortunately, amphibians and reptiles are also important in reducing ecosystem diversity and stability. These forms are exotics, introduced by design or accident through the actions of human agents. The introduction of the Bullfrog (*Rana catesbeiana*) to western U.S. rivers and ponds may well be reducing the diversity of native amphibians. In the Hawaiian Islands, the entire terrestrial herpetofauna is introduced. Such recent and unstable exotics deserve detailed individual studies wherever they occur in the park system.

Noxious species, especially the three pit viper genera, *Agkistrodon, Crotalus,* and *Sistrurus,* the coral snakes (*Micruroides* and *Micrurus*) and the one U.S. poisonous lizard (*Heloderma suspectum*) need intense study for two reasons: First, they are legitimate health hazards to park visitors; secondly, to dispel the grotesque distortions about the degree of real danger they present. Since 1950 annual deaths from poisonous reptiles have run about 15 to 25 in the United States (U.S. Dept. Navy, 1966). More Americans die of golf balls or lightning. In Arizona, a state endowed with a coral snake, the Gila Monster, and no less than ten species of rattlesnakes, the total deaths from venomous animal bites from the years 1929 to 1951 (excluding 1937) was broken down into the following sources: Scorpions 69, rattlesnakes 18, insects 6, spiders 7, Gila Monsters 1, centipede (secondary infection) 1 (Klauber 1972). Reptile bites made up less than 20% of the total. Interestingly, the small secretive coral snake failed to account for a single death. Its fangs may have real difficulty piercing human skin. It has no propensity for biting when captured. The snake is an exquisite and virtually harmless endemic of the Sonoran Desert. Autecological work could confirm its true nature. Such enlightenment would benefit not only the fauna but the visitor as well. Bites are far more likely when visitors attack snakes than when they simply avoid them. It is both biased and unnecessary to treat rogue bears (Moment 1968) with kid gloves and at the same time destroy or tolerate the destruction of venomous reptiles simply because they are near campsites or trails.

Autecological studies of amphibians and reptiles may often serve the needs of NPS interpretation programs, as well as they do the needs of management. Detailed life histories could pinpoint abundant local and diurnal predators, such as frogs and lizards. These organisms, carefully observed from a distance, would introduce the park visitor to a phenomenon such as a prey-predator relationship, territoriality, and sexual selection. Their abundance, relative to classical birds and mammal examples, often gives the visitor a much greater chance of seeing nature in action. A live lizard chasing an ant illustrates predation far more effectively than a taxidermist's mount in the Park Museum of a bobcat holding a mouse. How many park visitors ever see a bobcat in the wild, let alone witness its predatory behavior?

## CONSERVATION ISSUES INVOLVING MAJOR TAXONOMIC GROUPS

The issue of prejudiced treatment of amphibians and reptiles both by the public and NPS is not confined to poisonous snakes and Gila monsters. Both classes are generally viewed with disgust by the public. The NPS and much of the biological community tend to ignore amphibians and reptiles as leftovers of another age, straggling survivors of the "lower" vertebrates. I reject both attitudes. Reptile species alone outnumber mammals worldwide. Amphibians and reptiles are no less evolved than so-called higher vertebrates. In fact, one reptilian family, the pit viper, is specifically adapted by its heat sensitive pits to hunt homeothermic prey. They all deserve the same concern and protection.

The slaughter of snakes on NPS administered highways every spring and summer highlights the need for system-wide investigations that would benefit a neglected taxonomic group, in this case the suborder Serpentes. Snakes often assume high positions on food chains. As a result, the local densities of these large carnivores are often low. Thus the loss of even a few hundred individuals to traffic kills could deplete local populations severely, even irreversibly. At the same time, prey rodents and lizards might respond with increasing populations disturbing to whole ecosystem. The snakes are drawn to the paved roads at night by the heat differential maintained by the pavement relative to the cooling night air. Traffic runs over thousands of individuals (within the parks) every year, as they lie basking on the warm surface. Warning signs, cattle guards, and speed limits are invoked to reduce road kills of big game. Snakes have often been diverted by drift fences, even a few centimeters in height. Surely, a short ridge (with accommodation for drainage) paralleling the road along its edges would reduce the losses. Yet, I know of no effort either to appraise or remedy the snake kills on park and monument highways.

### *Ecosystem Conservation: Applications of Island Equilibrium Theory*

At least as early as the "Leopold Report" (Leopold, et al., 1963), there has been a growing recognition of potential status of our park reserves and monuments as ecological islands surrounded by seas of pollution, disclimax, agriculture, and urban development. Diamond (1975), Kolata (1976), Simberloff and Abele (1976) and Terborgh (1974) have all explored the possible utility of employing the predictive mathematics of McArthur's Island Equilibrium Theory. Using McArthur predictive models, strategies may be developed to maintain maximum biotic diversity within existing individual park ecosystems. Specific suggestions derived from the model include the development of protective buffer zones and/or corridors that would interconnect parks and other refuges, thereby allowing continued immigration or recolonization between tracts of protected land.

Other plans based on Equilibrium theory suggest that park refuge boundaries be set at minimal areas to protect the subset of the natur

ecosystem of full diversity or within 1% of that species diversity. Such plans take into account the effects of island-like isolation that will progressively follow the differentiation of a park from the surrounding unprotected landscape. Most authors urge that parks be designed in the future or expanded in the present so that their boundaries reflect the minimal areas required by equilibrium theory to maintain diversity. At present park boundaries are often the result of political and economic compromise with protected areas designed to contain a specific landscape feature (geysers, caves, canyons), not an intact ecosystem.

Here, too, herpetology could make a contribution. As the taxonomy, distribution, and general ecosystem affinities of most U.S. species are well known, herpetofaunas lend themselves well to biogeographical analyses that could help define more effective park boundaries.

## CONCLUSION

As I review the substance of what has just been presented, I find that I am ultimately arguing for the validity of herpetology as biological discipline. The herpetological perspective could offer unique and valuable insights to very broad problems in biology and park management. Too often also amphibians and reptiles have been viewed as irrelevant, peripheral, and possibly dangerous survivors of another age.

My response to these attitudes is simple. Amphibians and reptiles are vigorous and important taxia. They should not be ignored or taken for granted either by the theory oriented biologist or the applied ecologist of NPS. Many species are of immense and unmeasured value, both intrinsic to their being and relative to the ecosystems in which we all must live.

And what I say of herpetofauna I will say of herpetologists as well. Do not take us for granted. Whether the issue is an interpretation program that integrates evolution and geology, or bioassaying for toxins, or redesigning park roads or park boundaries, take advantage of the herpetological perspective. And more specifically take the initiative of developing system-wide investigations that coordinate herpetological investigations and maximize their value.

We, as a herpetological community, have something to offer. The NPS has much to offer in return: Some of North America's best managed and most beautiful pristine landscape, field stations, museum collections, local expertise, equipment and computer facilities, even publication outlets. These resources alone, even without massive financial aid for new research, would attract many professional volunteers. What we need most is more dialogue in order to integrate the talents and resources that could so improve the professional effectiveness of us all.

## REFERENCES


CONANT, R. 1975. A field guide to the reptiles and amphibians of the eastern and central North America. Houghton-Mifflin, Cambridge, Mass.

COOKE, A. S. 1972. The effects of DDT, dieldrin, and 2, 4-D on amphibian spawn and tadpoles, Environ. Pollut. 3:51-68.

COPE, E. D. 1884. Zoology in the National Parks. American Naturalist, 18:708-9.

DIAMOND, J. A. (1975). The Island Dilemma: Lessons of Modern Biogeographic Studies for the Design of Natural Reserves Viol. Consp. (7) 129-146.

DOUGLAS, C. 1975. NPS Information - A Look at Future Proceedings of the 2nd Resources Management Conference, Southwest Region, National Park Service, U.S. Dept. of the Interior, pp. 130-135.

ESTES, R. 1964. Fossil vertebrates from the late Cretaceous Formation of Eastern Wyoming. Univ. Calif. Pub. Geogl. Sci., 49:1-180.

FERGUSON, D. E. and C. C. GILBERT. 1967. Tolerance of three species of anuran amphibians to five chlorinated hydrocarbon insecticides. J. Mississippi Acad. Sci. 13:135-138.

GEHLBACH, F. R. 1965. Amphibians and reptiles from the Pliocene and Pleistocene of North America: a chronological summary and selected bibliography. Texas J. Sci., 17(1):56-70.

HERALD, E. S. 1949. Effects of DDT - oil solutions upon amphibians and reptiles. Herpetologica 5:117-120.

KAPLAN, A. M. and J. G. OVERPECT. 1964. Toxicity of halogenated hydrocarbon insecticides for the frog *Rana* pipiens.

KOLATA, G. B. 1976. Theoretical Ecology - Beginnings of a Predictive Science; Science (183) p. 400-401, 450.

KLAUBER, L. M. 1972. Rattlesnakes. Their Habits, Life Histories and Influence on Mankind (Vol. II) University of California Press. Berkeley.

LOWE, C. H. and J. W. WRIGHT. 1968. Weeds, polyploids, parthenogenesis and the geographical distribution and ecological distribution of all femal species of *Cnemidophorus* Copeia (1):128-139.

LEOPOLD, A. S., S. A. CAIN, C. M. COTTAM, I. N. GABRIELSON, and T. L. KIMBALL. 1963. Wildlife Management in the National Parks. U.S. Dept. of Interior.

MORAFKA, D. J. and B. H. BANTA. 1972. The Herpetozoogeography of the Gabilan Range, San Benito and Monterey Counties, California. The Wasmann J. of Biology 30(1-2):197-240.

MOMENT, G. B. 1968. Bears: The Need for a New Sanity in Wildlife Conservation Bio Science Vol. 18(12):1105-1108.

ROGERS, L. E. 1974. Foraging activity of the western harvester ant in the short grass plains ecosystem. Environ. Ent. 3:420-424.

SHELFORD, V. E. 1963. The Ecology of North America. Univ. of Illinois Press. Urbana.

SIMBERLOFF, D. S. and L. G. ABELE. 1976. Island Biogeography Theory and Conservation Practice. Science (191):285-286.

STEBBINS, R. C. 1966. A field guide to western reptiles and amphibians. Houghton-Mifflin Co., Cambridge, Mass.

TERBORGH, J. 1974. Preservation of Natural Diversity: The Problem of Extinction Prone Species. Bio Science 24(12):715-722.

TEVIS, L. 1958. Interrelations between the Harvester Ant *Veromessox pergandei* (Mayr) and some desert ephemerals. Ecology 39:695-704.

U.S. DEPT. OF THE NAVY. 1966. Poisonous Snakes of the World. Bureau of Medicine and Surgery. NAVMED P-5099. U.S. Gov. Printing Office, Washington, D.C.

U.S. NATIONAL PARK SERVICE. 1974. Chief Scientist. 1974 Yearbook, Washington, D.C.

WAUER, R. H. (Coordinator). 1976. Proceedings of the 3rd Resources Management Conference Southwest Region Superintendent's Conference. U.S. Dept. of the Interior.

WILSON, E. O. and E. O. WILLIS. 1976. Applied Biogeography in Ecological Structure of Species Communities, ed. by M. L. Cody and J. M. Diamond. Cambridge, Mass. Harvard University Press.

# SPECIES-ORIENTED MATRIX STUDIES TO INVESTIGATE ECOSYSTEMS IN A CANADIAN NATIONAL PARK[1]

L. N. Carbyn[2]

## INTRODUCTION

Research within Canadian National Parks can be broadly classified as either mission oriented or pure research. The conceptual approach in this paper attempts to combine the two in a manner significant for the long-term management of large mammals in parks.

The orientation is based on studying the biology of a predator and assessing its role in the ecosystem. A conspicuous predator population is chosen and we ask ourselves: "Why is it there? On what species does it depend? How does it affect its environment? What will happen to it in time?" Such questions led to a study of the major species that are directly or indirectly implicated in the food chain of the primary predator. Rather than initiating studies at the base of trophic pyramid and timing the initiation of the studies in sequential order upward, the present proposal involves studies carried on simultaneously, with specific reference to the top of the food chain. This results in a matrix of species oriented studies.

In a general sense, the approach is based on the analogy between populations of species as the building blocks of communities and ecosystems, and the cells and organs of organisms. Looking at levels of organization leads to the concept of integrative levels as discussed by Fiebleman (1954). He proposed several laws stating that complexity in any organization increases in higher levels and that higher levels depend on lower ones. The functioning of the system, therefore, cannot be explained entirely in terms of lower or higher levels. A holistic approach is needed to broaden the scope of investigation and thereby increase our understanding of the mechanisms that regulate any system with a structural organization. Such an understanding increases our predictive capabilities and, therefore, is of practical value.

The first phase is an investigation of predator-prey interactions. Identification of a key predator species is important. Concurrently, or phased-in at suitable intervals, research is directed at population dynamics and food requirements of other species that would affect the predator-prey interactions (Figure 1). Studies proceed "down" to such important entities as habitat requirements, range ecology, plant succession and fire ecology. The latter are ultimately most important in long-term management programs. The approach suggested here is relevant in national parks, where objectives must be clarified before management schemes are implemented.

## RELEVANCE OF THE CONCEPT

In Canada there has been considerable discussion on what kind of research is relevant to park requirements. Impact oriented and inventory work generally focus on current management problems. These must take high priority wherever the problems have been clearly defined. Studies of the type outlined in this paper will provide some information of immediate use but in addition to short-range problem solving, integrated studies provide data which are essential for long-range management programs.

For example, plant ecologists generally can identify successional stages of a plant community and predict climax conditions. On the other hand, animal ecologists rarely predict what will happen over time to an animal community that is subjected to the same evolutionary processes. If management proposals are implemented (for example, prescribed burning) or, alternatively, no management is employed, it becomes necessary to direct research in a manner that will identify the status of species and animal communities. The status of populations can best be determined if their functional interactions with each other and the environment are assessed. Inventories, such as biophysical programs in national parks, focus on the static or structural aspects of ecosystems. Although often necessary as precursors to functional studies, inventories do not describe the mechanisms operating within particular ecosystems. Knowledge of some interactions among populations in ecosystems is not synonymous with the ability to predict all the changes within the systems. Long-term climatic changes and other perturbations, such as fires and disease, drastically alter systems within short time spans. Once such occurrences take place, given a broad information base, short-term predictions on the outcome of certain trends can be made.

## SPECIFIC EXAMPLE--RIDING MOUNTAIN NATIONAL PARK

### *Study Area and Present Status of Research*

Because research involving the suggested approach of species oriented matrix studies was initiated in 1975 in Riding Mountain National Park, Manitoba, this area will be used as a specific example to demonstrate the applicability of the proposed model.

The park covers an area of 2944 km$^2$. Aspen parkland and coniferous forest form the main vegetation cover. The western section of the park also has extensive remnants of fescue prairie, and in the east there are elements of eastern hardwood forests. The satellite photograph (Figure 2) shows the park essentially as a wilderness "island" surrounded by agricultural land (Figure 3). A large percentage of its human visitors come from the urban centers of Winnipeg, Brandon and Regina. Total visitors in 1975 numbered around 830,000.

The wolf (*Canis lupus*), being the summit or top predator in the large mammal food chain of the park, was chosen as the key species for the matrix study proposal. The species is vulnerable to human activities outside the park and is a resource that can be effectively utilized in the park interpretive programs (Carbyn 1975). The wolf/prey interaction is the highest trophic level within the large mammal food chain and to increase predictive capabilities, results obtained in the

[1]I would like to thank Dr. D. Hocking, Mr. Angus Maclean, Dr. G. Scotter and Mr. D. Karasiuk for review and comments on the manuscript.

[2]Canadian Wildlife Service, 1110, 10025 Jasper Avenue, Edmonton, Alberts, Canada T5J IS6.

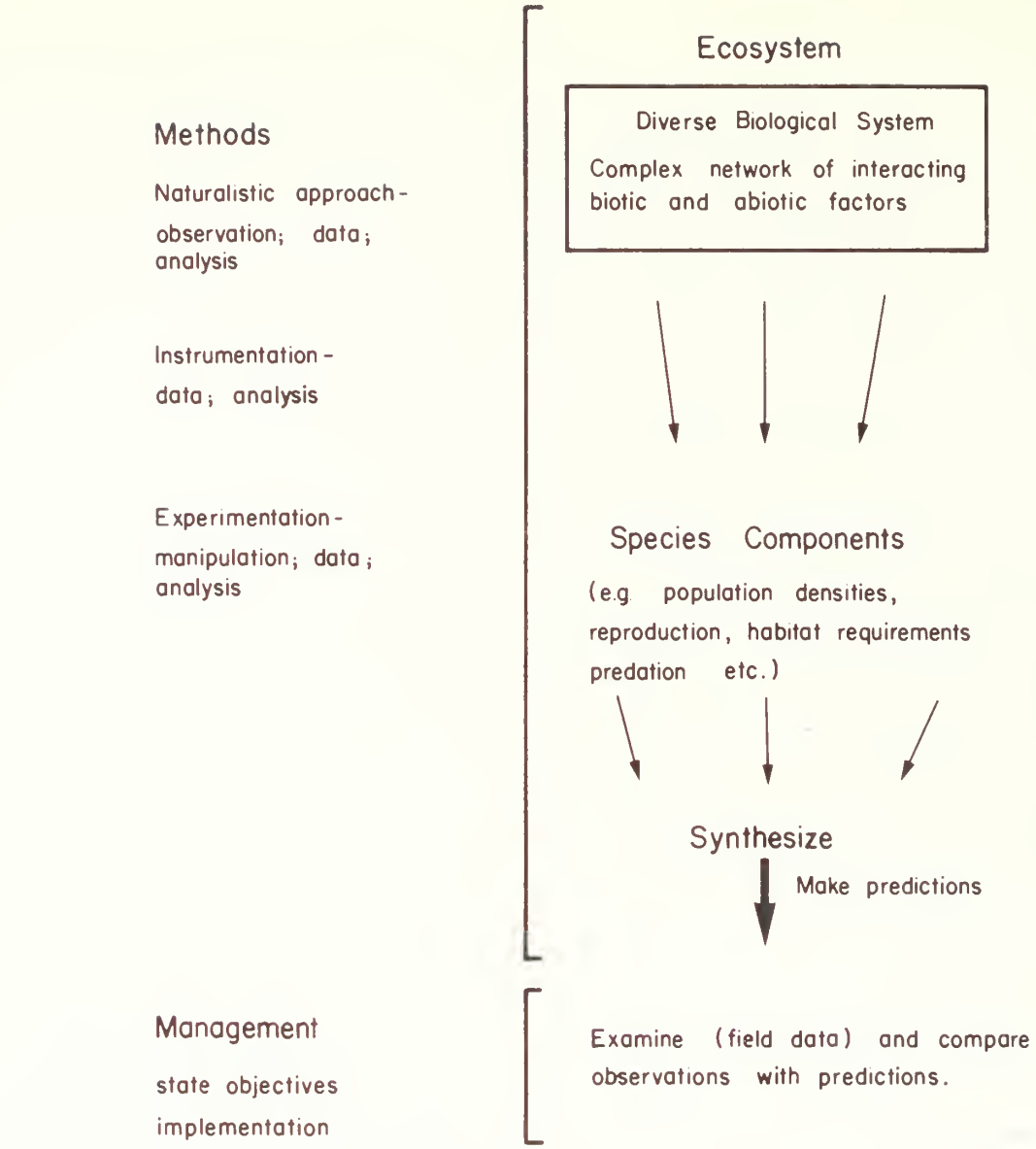



FIGURE 1. Conceptual approach to large mammal systems studies in national parks.

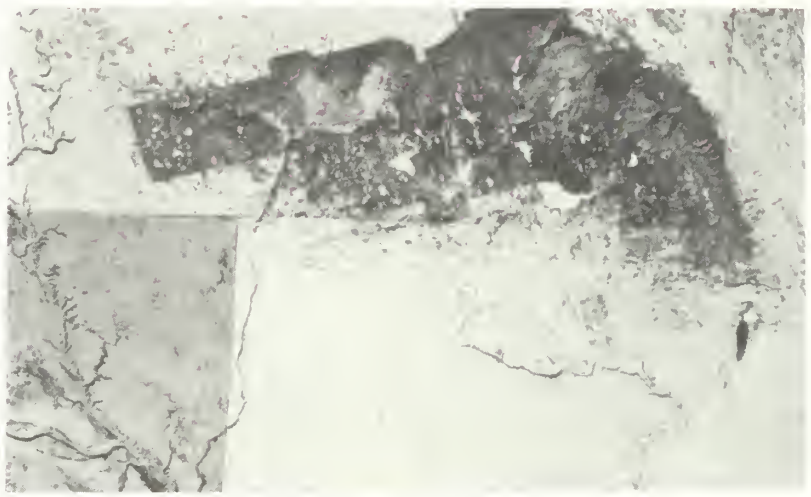


FIGURE 2. A satellite view of Riding Mountain National Park, illustrating how the park forms a wilderness island within a "sea" of agricultural land.



FIGURE 3. The boundary between Riding Mountain National Park and agricultural areas is generally distinct.

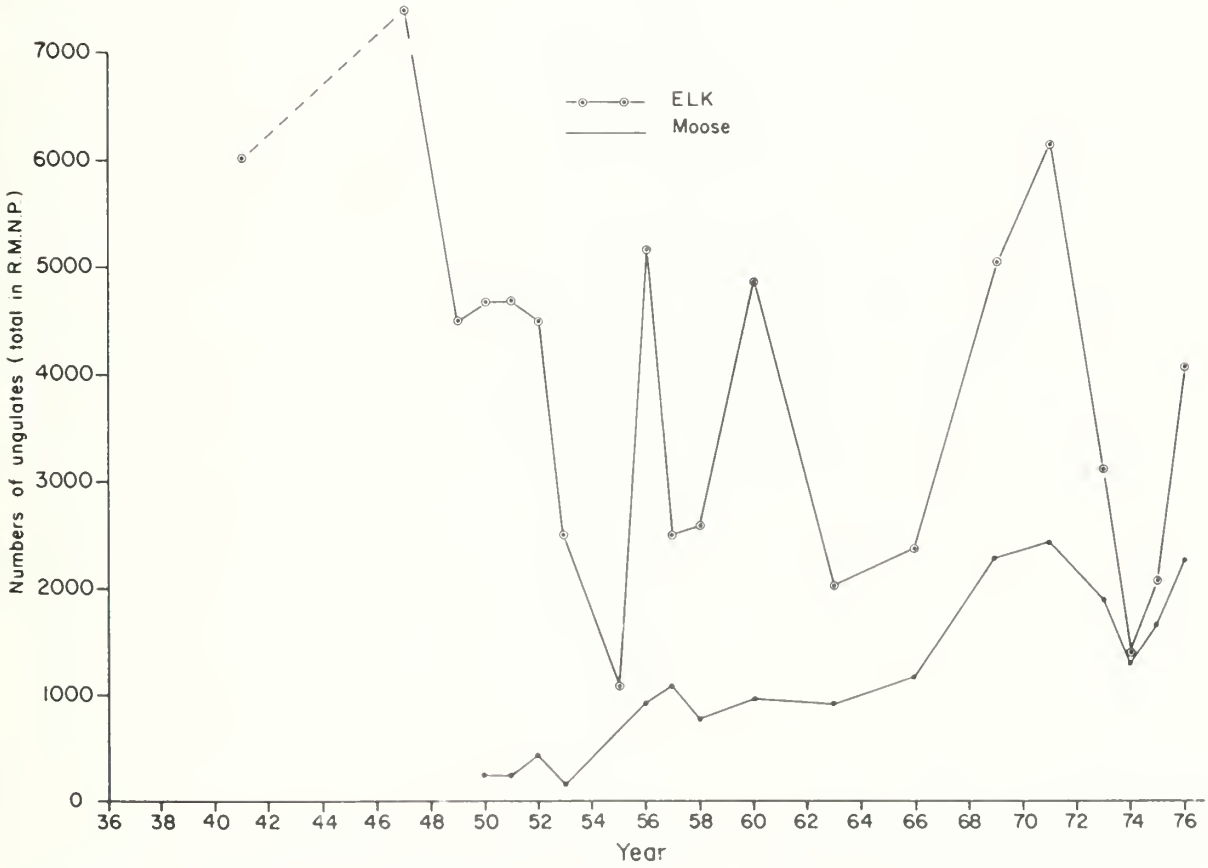



FIGURE 4. Population fluctuations of elk and moose in Riding Mountain National Park within the last 30 years (from Rounds 1976).

study will be subjected to modelling. Parameters isolated for study in the first year were:

1. Population densities, territoriality and movements of wolves (using radiotelemetry).
2. Population densities and distribution of ungulate prey species (using aerial surveys).
3 Interaction of wolves with prey (using ground checks and radio tracking).
4. Interaction of wolves with coyotes (using nocturnal howling surveys for abundance indices, and radio tracking).
5. Loss of wolves from the park system due to external human activities.

Radiotelemetry, involving capturing and marking of canids, is a contentious issue within the context of national parks policy. This technique has been used for coyotes in Jasper National Park, Alberta, and Grand Teton National Park, Wyoming. Unlike Isle Royale, with its restricted area, reliable information on population densities and movements of wolves cannot be obtained in Riding Mountain National Park without resorting to this technique.

Elk (*Cervus canadensis*), moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) are the ungulate species that constitute the main prey base for wolves. Ongoing population censuses, using fixed-wing aircraft and flying transects at specific altitudes and specific widths, have been conducted for ungulate populations since 1949. These surveys are believed to be fairly accurate for moose and elk (Rounds 1976). The population trends are shown in Figure 4. Information available prior to 1949 has been summarized by Banfield (1949), and is based on ground counts and general population estimates.

Within the first year of study, some information with short-term management implications was obtained. Data were gathered on illegal poisoning of the wolves along the park boundary, as well as data regarding the crippling and killing of these predators with traps. The long-range management implications will have to be assessed within the framework of parks policy.

Population studies of the large mammals will be extended to studies of plant communities and habitat requirements, thereby including the lower trophic levels of the food chain. Range studies will focus on stand origin and history, forage production and seasonal use by sex and age classes of ungulates and foraging patterns as related to cover, snow cover and range conditions (G. Trottier, pers. comm.). This is the first suggested direction of research. The second direction of investigation is toward other species directly or indirectly linked to the principal predator/prey study.

*Second Level Investigations*

One could extend the number of substudies indefinitely. The model presented here does not take into account the cycling of microelements within different trophic levels as described by Ovington (1962). Such studies may ultimately be desirable; however, in the context of this concept, species studies are chosen that more directly affect the wolf to prey relationship.

Snowshoe hare (*Lepus americanus*) can be readily singled out as a key species both in the context of the wolf-prey relationship and the other components that are more directly affected. In Riding Mountain National Park snowshoe hare studies may be incorporated into existing and planned studies on wolves, coyotes, ungulates, and ungulate range. Snowshoe hare are an important cyclical herbivore in boreal ecosystems. In peak years they are a significant food item for many mammalian and avian predators. The population size may be 60 or more times larger at a peak than at a low. This could affect the wolf/ungulate relationship in different ways at different times.

Changing hare densities could affect wolf densities directly through an increase in available food supply. However, there is little evidence that snowshoe hare are an important food item of wolves, and it is more likely that the effects are indirect.

Changing hare densities may affect wolves through competition for the same resources in the herbivore trophic level; that is, the effects are indirect by reducing food available to the prey. Competition has been documented between moose and hares, (Dodds 1960; Telfer 1974) and between deer and hares (Bookhout 1965; Telfer 1972) for winter browse. Work by Rounds (pers. comm.) suggests that competition for food may also be occurring between hares and certain segments of the elk population. Keith (1974) suggests that hares, during a peak, can be effective in reducing the browse to a point when it takes several years to recover.

There is another manner in which the population size of the snowshoe hare could be affecting wolves Hare increases may affect other medium-sized predators such as lynx (*Lynx canadensis*), coyotes (*Canis latrans*) and possibly black bear (*Euarctos americanus*). On the decline of the hare cycle there could be additional predation pressures on the ungulates, particularly the young of the year. Various authors (Saunders 1963; Moran and Ozoga 1965; Ozoga and Harger 1966) have shown that lynx and coyotes will kill ungulates; similarly, observations in the park have shown that black bear will kill elk calves.

Snowshoe hare numbers also affect avian predators. This is clearly illustrated by the study of McInvaille and Keith (1974). They have found that great horned owls (*Bubo virginianus*) exhibit functional and numerical responses to changing snowshoe hare densities, while red-tailed hawks only show a functional response. The percentage of biomass of hare in the diet of great horned owls increased from 23% during the low to 81% at a high. Red-tailed hawks utilized the hare as prey at 8% during the low to 52% during a high of the cycle. With an increase in hare the number of owl breeding pairs and fledging survival increased, whereas the number of hawk breeding pairs remained stable throughout the hare cycle.

An absence of an increase in population size of the hawks could be explained because they migrate out of the park. Owls, in contrast, are year-round residents, subject to food shortages in winter, this would explain their adaptive mechanisms to adjust their population densities to their fluctuating food supply. These few examples suggest that there are complex interrelationships between predator-prey populations, affected in various ways by changing densities of snowshoe hare.

Another relevant species to study would be porcupine (*Erethizon dorsatum*) because reintroduction attempts have been made for fisher, a mustelid which preys on snowshoe hare and porcupine. Data on numbers and distribution of porcupine are routinely gathered during nocturnal canid surveys. Coyotes occasionally prey on porcupines (direct observations) and in turn, are affected by the wolf population (either directly or indirectly), so that linkages between these species exist. Habitat changes predictably will occur through plant succession and fire suppression.

Having information on the biology and habitat requirements of the species allows one to predict what effects such changes would have on some of the vertebrate species.

*Implications of the Island Effect on Large Mammals in Riding Mountain National Park*

National parks are increasingly becoming ecological islands within a "sea" of development. Riding Mountain National Park is a good example of an ecological island (Figure 2). How does the island effect influence species diversity and what can be expected in the future? Species-oriented matrix studies will establish the current status of the various populations implicated in the specifically defined food chains, and, furthermore describe its functional relationships within the system. The more we know about a species the better we can predict its role within the park in the future; and, subsequently, management programs can be designed to maintain specific faunal conditions.

The biogeographical isolation of the park is a relatively recent phenomenon. Settlers began clearing the land in the 19th century and the process in now complete. Prior to geographical isolation mammals movements probably were less restricted than is the case today; furthermore, fires were not suppressed. Both of these factors will probably have an effect on the species diversity in the future.

Fifty-six species of mammals are known to occur in the park. Eight species have become extinct, or nearly so, since the arrival of Europeans in western Canada. Mule deer (*Odocoileus hemionus*) were present until the 1960's (park files) and have probably recently become extinct. Bison (*Bison bison*), though present historically, are today extinct (this is excluding a display herd of bison). In addition, caribou (*Rangifer tarandus*), fisher (*Martes pennanti*), otter (*Lutra canadensis*) marten (*Martes americana*) and grizzly bear (*Ursus arctos*) are no longer found in the park. Reintroduction plans for some of these species are now in progress.

The wide fluctuations of elk (Figure 4) are of interest. Prior to settlement large herds summered in the Riding Mountain area (Green 1933). By 1890 elk numbers were diminishing and the population seemed to have reached a low point by 1914 when it was estimated at 500 animals (Banfield 1949). Banfield recorded the highest population figure in 1946 when the total was about 17,000 animals. Winter severity, hunting adjacent to the park and wolf predation are the factors which probably are responsible for these wide fluctuations. Hunter kill amounted to as much as 1,700 animals (Rounds 1976). Wolves reinvaded the park around the mid-1930's.

Moose existed at low population levels prior to the mid-1930's (Green 1933). As can be seen in Figure 4 this species has shown a gradual increase. Speculation concerning the reason for this is premature; however, several factors such as wolf predation, plant succession, cessation of logging and fire protection should be examined more closely.

Recent papers by Ayala (1971), Diamond et al. (1976) and May (1975) discuss the various problems related to island biogeography and conservation. For example, is in-breeding a problem, ard if so, at what population level to the negative effects become negligible? Can the area, isolated as it is, maintain a genetically sound population without introduction of new gene pools? Field ecologist, geneticist and bio-mathematician will have to address themselves to these problems in the future. Species-oriented population studies and habitat studies, could lay the foundation for such future work.

## CONCLUSION

Experience has shown that it is difficult, if not impossible, to predict all the changes occurring within ecosystems, particularly when research is restricted to individual components within the system. Research to date in Canada is largely directed toward practical management problems (mission-oriented research) or basic resource inventory (biophysical surveys). The latter is currently in vogue. Management directed toward protecting, preserving or restoring natural or pristine ecological relationships and interpreting resources requires a functional approach, not disregarding the importance of the former approaches. Species-oriented matrix studies, beginning with top carnivores, is one way in which a more holistic approach can be realized. We ask ourselves, "What does it take to have a carnivore population and how can we keep it there?" The matrix approach of species-oriented population and habitat studies. if properly designed, can provide a better understanding of the interrelationships between mammals and their environment needed for park planning. Ultimately, the results of these and other studies could be incorporated into a resource management plan. Two fundamental considerations in such a plan should be the concepts of biological originality[3] and biological diversity (Pimlott 1969). The thoughts presented in this paper are an extension of the ecosystem concept in national parks as discussed by Reid (1968), Cole (1971), and Houston (1971).

[3]Biological originality here is defined as a condition that existed during the pre-European settlement periods in Canada, or those conditions that would have prevailed without man's influence.

## LITERATURE CITED


AYALA, F. 1971. Competition between species: frequency dependence. Science 171:820-824.

BANFIELD, A. W. F. 1949. An irruption of elk in Riding Mountain National Park, Manitoba. J. Wildl. Manage. 31:127-134.

BOOKHOUT, T. A. 1965. Feeding conditions between showshoe hares and white-tailed deer in Northern Michigan. Trans. N. Am. Wildl. Nat. Res. Conf. 30:321-334.

CARBYN, L. N. 1975. Wolf howling as a technique to ecosystem interpretation in National Parks. *In* Symposium on the Behavior and Ecology of wolves. Anim. Soc. Meetings. Wilmington, North Carolina. (In Press).

COLE, G. 1971. An ecological rationale for the natural or artificial regulation of native ungulates in parks. Trans. N. Am. Wildl. Nat. Res. Conf. 36:417-425.

DIAMOND, J. M., J. TERBORGH, R. F. WHITCOMB, J. F. LYNCH, P. A. OPLER, and C. S. ROBBINS. 1976. Island biogeography and conservation: strategy and limitations. Science 193:1027-1032.

DODDS, D. G. 1960. Food competition and range relationships of moose and snowshoe hare in Newfoundland. J. Wildl. Manage. 24:52-60.

FIEBLEMAN, G. K. 1954. Theory of integrative levels. Brit. J. Phil. Sci. 5:59-66.

GREEN, H. W. 1933. The wapiti of the Riding Mountain, Manitoba. Can. Field.-Nat. 47:105-111, 122-132, 150-157, 172-174.

HOUSTON, D. 1971. Ecosystems of National Parks. Science 172:648-651.

KEITH, L. B. 1974. Some features of population dynamics in mammals. XI Int. Congr. Game Biol. :17-58.

MAY, R. M. 1975. Island biogeography and the design of wildlife preserves. Nature 254:177-178.

MCINVAILLE, W. B. and L. B. KEITH. 1974. Predator-prey relations and breeding biology of the great horned owl and red-tailed hawk in Central Alberta. Can. Field.-Nat. 88:1-20.
MORAN, R. J. and J. J. OZOGA. 1965. Elk calf pursued by coyotes in Michigan. J. Mamm. 46:498.
OVINGTON, J. D. 1962. Quantitative Ecology and the Woodland Ecosystem Concept. *In* Cragg, J. B. (ed.), Advances in Ecological Research. 1:103-203.
OZOGA, J. J. and E. M. HARGER. 1966. Winter activities and feeding habits of Northern Michigan Coyotes. J. Wildl. Manage. 30:809-818.
PIMLOTT, D. H. 1969. The value of diversity. Trans. N. Am. Wildl. Nat. Res. Conf. 30:321-334.
REID, N. J. 1968. Ecosystem management in the National Parks. Trans. N. Am. Wildl. Nat. Res. Conf. 33:160-169.
ROUNDS, R. 1976. Selected Ecological Aspects of the Wapiti and Moose of Riding Mountain National Park, Manitoba. Unpub. Rep., Parks Canada, Winnipeg, Manitoba. 278 pp.
SAUNDERS, J. K. 1963. Food habits of the lynx in Newfoundland. J. Wildl. Manage. 27:384-390.
TELFER, E. S. 1972. Browse selection by deer and hares. J. Wild. Manage. 36:1344-1349.
TELFER, E. S. 1974. Vertical distribution of cervid and snowshoe hare browsing. J. Wildl. Manage. 38:944-946.

# DEPLOYMENT, DISPERSAL, AND ADAPTIVE STRATEGIES OF LAND VERTEBRATES ON ATLANTIC AND GULF BARRIER ISLANDS[1]

James D. Lazell[2]

Island biogeography, from the Darwinian simplicity of descriptive natural history to all its convoluted, contrived, and abstruse formulations of higher mathematics, is the most important and most controversial focal point for research in ecology and conservation today. As a class, barrier islands stand apart for many obvious reasons: they are closely adjacent or adherent to mainlands; they are nowhere broad enough or high enough to escape the profound effects of salinity; they are underlain by sea water on which fresh water, from precipitation, floats and therefore are apt to show marked seasonal variations in deep ground temperatures; and they are made of sand.

As attested by the proverbial truism of human culture and the facts of history, land made of sand is ephemeral, shifting, deceiving, and treacherous. The shapes, positions, and occupying features of barrier islands along our coasts have changed dramatically and frequently since Europeans first documented the continental margins. Yet the presence of barrier islands is a major, omnipresent feature of our Atlantic and Gulf coasts. As one of my students once said years ago to an Army Engineer in North Carolina: "The Coastal Plain will come and go, but there will always be Outer Banks."

The Harvard herpetologist Thomas Barbour (in Barbour and Engels 1942) puzzled three and a half decades over the fact that the slim slip of barrier beach called the Outer Banks of North Carolina had its own, endemic kingsnake, while the entire Atlantic Coastal population from New Jersey to Florida was essentially uniform in characteristics. He just had not imagined how our coastline would look at the height of an interglacial.

In terms of the generation times of vertebrate animals, the constant shiftings of barrier islands are of little consequence; similar habitats and similar ecological problems faced the raccoons of a thousand years ago as face those living today, even if the land they live on has moved a hundred miles. In terms of real estate agents, land developers, and property owners, the shifting of barrier islands are an intolerable affront to tidy, if artificial, preconceptions of how the world should be. Sooner or later, of course, we will have to learn to enjoy barrier islands the way raccoons do, just as we will have to learn to give up the Coastal Plain. I can only hope that the wonderful and unique animals of the barrier islands--many of them now entrusted to National Park Service care--will survive the inevitable transition in our attitudes.

As a Park Service collaborator, I have been able to study three widely separated barrier island complexes largely within National Seashore limits: Cape Cod in Massachusetts, Cape Hatteras-Cape Lookout in North Carolina, and Gulf Islands in Mississippi. While I will concentrate on these, it is worth noting that I have also been able to visit and study barrier islands in New Jersey, Virginia, Georgia, Florida, Texas, and Alabama. My views and opinions are thus based on a broadly comparative examination.

Cape Cod, itself an island, is subtended by a virtual archipelago of other islands of glacial morainal or outwash origins; these are variably fringed with tombolos, barrier beaches, and major barrier islands (Figure 1). The Geology, ecology, and herpetology of this complex is the subject of my recent book on the area, *This Broken Archipelago* (Lazell 1976a).

Several ecological factors are of note here: the sea insulates these lands and makes the climate equable, relatively cool in summer, warm in winter. This fact favors land animals that might be excluded by either temperature extreme. On the other hand, both ocean and precipitation temperatures directly affect the ground temperature within the land, causing summer warming and winter cooling far more extreme than on the mainland. These extremes can be limiting for ectothermic organisms and all those that hibernate or aestivate. Barriers and tombolos constantly form and fragment, so no island remains long disjunct from sources of overland propagules. Thus, for speciation to progress, evolutionary rates must be extremely rapid (see Lazell 1972, for formula and theories).

Our most spectacular Atlantic barrier islands are, of course, the North Carolina Outer Banks. Beginning in the late sixties, Dr. Paul Godfrey and others elucidated geological and ecological processes of this complex that make it today perhaps the best known set of barrier islands in the world (see Godfrey 1970; Godfrey and Godfrey 1975), and works cited therein. At the same time, fresh from my island adventures in the Caribbean, I began a study of reptiles on the Outer Banks, and picked up the long-forgotten threads Barbour and Engels had dropped. Soon, with my students, this study branched out to include amphibians, mammals, and even invertebrates and plants. Here I began to perceive that the processes shaping evolution on the coastal islands and peninsulas were quite different in emphasis and degree from those seen on the oceanic islands I had studied so long. To quote David Stick (1958): "Stretching along the North Carolina coast for more than 175 miles . . . is a string of low, narrow, sandy islands. . . . They are separated from the mainland by broad, shallow sounds, sometimes as much as thirty miles in breadth, and are breached periodically by narrow inlets which are forever opening and closing."

Isolation, with its attendant founder effects and generic drift, cannot be the major feature of evolution here. The islands are attached to the mainland at either end; the inlets are forever opening and closing; longshore current moves sand perpetually along--and with the sand go the animals adapted to the barrier islands. The selection pressures here will be primarily ecological, and they will be severe.

For the first time since childhood, I returned to the Gulf Islands of Mississippi in the fall of

[1]I am indebted to Dr. Donald Bradburn, Dr. Martin C. Michener, Jonathan Coddington, and Jeremy Jackson for photographic documentation, and to the staffs of the various National Seashores for their time and assistance in the field.

[2]Massachusetts Audubon Society, Lincoln, Massachusetts 01773.

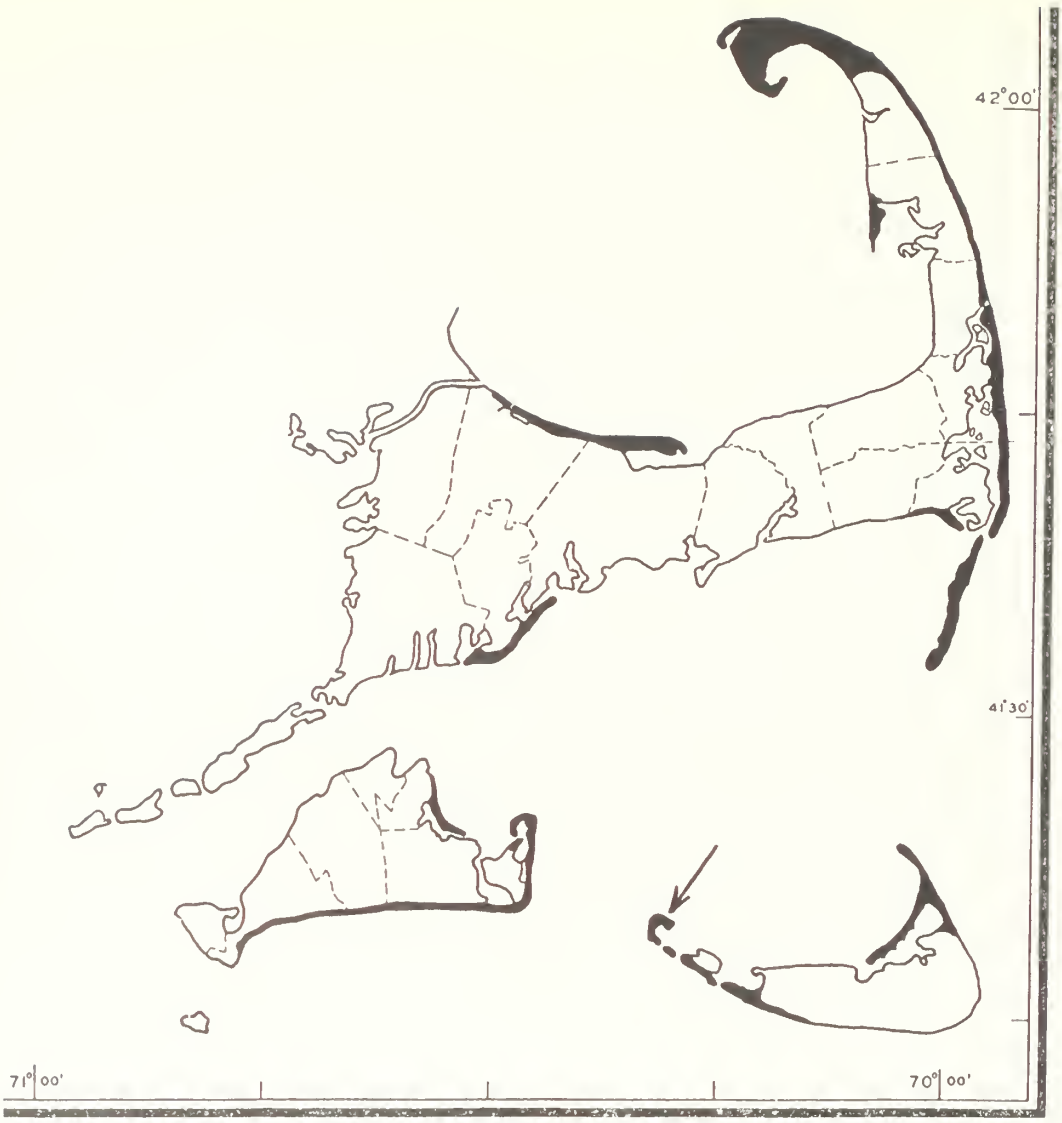



FIGURE 1. Cape Cod and associated coastal islands of Massachsuetts; the barrier beaches, drift sand islands, and tombolos are indicated in black. The arrow points to Muskeget.

1974. I was appalled to find a beleaguered--but not small--group of conservationists and local politicians engaged in battle against--seemingly--all the entrenched forces of the mighty federal government, which wanted to build a marina, permanent buildings, and surfaced roads along this last Gulf Coast wilderness. Paul Godfrey may as well have never lived, or spoken, or written; or he might as well have worked for the National Park Service of China. Battles won and points proven in North Carolina had never even been heard of in Mississippi. These Gulf Islands, especially Horn, Round, and Petite Bois, were (and largely remain) a *terra incognito* despite the efforts of Richmond (1962, 1968) to catalog their species. Among land mammals, Richmond knew only of rabbits, raccoons, introduced European rats, house mice, and domestic hogs, and the exotic nutria (*Myocastor coypus*). He recorded no rice rats (*Oryzomys*), no native mice (*Peromyscus, Sigmodon, Reithrodontomys,* etc.), and no mustelid carnivores (*Mustela, Lutra, Mephitis,* etc.). The effect of feral hogs on Horn Island may become catastrophic for reptiles and rodents rooted up; the pigs should be removed.

Because barrier islands have a number of major features of physical and chemical ecology in common, it is not surprising that they also share various land animals. In Table 1, I have listed eight ubiquitous forms.

In Table 2 I have listed other widespread and characteristic barrier island forms.

I have left out a number of forms. Shrews of the genus *Blarina* have diverged into at least two endemic races on Massachusetts islands. However, the islands are morainal, not sand, and the shrews are rare or absent on proximate tombolos or barrier islands. The only *Blarina* known from the Outer Banks is a single specimen I collected in 1974; it has not even been identified to species. No shrews are known from the Gulf Islands. Rattlesnakes are present in Buxton Woods on the Outer Banks, and would there qualify as a rare and local, parenthetical form; their status on the Gulf Islands is controversial and badly in need of documentation.

I have also omitted introduced exotics and feral domestics, even though some of these--like nutria (*Myocastor soypus*) murid rodents (*Rattus* and *Mus*), and feral hogs (*Sus scrofa*) may be of profound ecological importance.

Among the ubiquitous species of our barrier islands, two deserve special comment. The diamond-

TABLE 1. Ubiquitous barrier island mammals and reptiles. In some areas evolutionary adaptation is highly visible; these are indicated as follows: C = Cape Cod region. B = Outer Banks of North Carolina. G = Gulf Islands between Florida and Louisiana.

| | |
|---|---|
| Raccoon, *Procyon Lotor* (G) | Racer, *Coluber constrictor* (B) |
| Cottontails, *Sylvilagus* ssp. | Water snake, *Natrix sipedon fasciata* complex (C,B,G) |
| Native mice, *Peromyscus* ssp. (C,B,G) | Terrapis, *Malaclemys terrapin* |
| Hognose snake, *Heterodon platyrhinos* | Snapping turtle, *Chelydra serpentina* |

TABLE 2. Mammals and reptiles of Cape Cod region, North Carolins Banks, and Gulf Island barriers. Asterisks indicate forms showing marked evolutionary departures at species, subspecies, or ecotypic levels. Parentheses are for rare or very local populations.

| Cape | Banks | Gulf |
|---|---|---|
| Vole* | - | - |
| Muskrat | Muskrat | ? |
| - | Rice rat | Rice rat |
| Mink | mink | ? |
| Otter | Otter | ? |
| Harbor seal | - | - |
| Gray seal | - | - |
| - | (Alligator) | Alligator |
| - | Mud turtle | Mud turtle |
| - | Slider | Slider |
| Garper snake* | - | - |
| Ribbon snake | (Ribbon snake) | ? |
| Smooth green | Keeled green | ? |
| - | Longsnake* | Kingsnake |
| - | (Ratsnake) | Ratsnake* |
| - | - | Whipsnake |
| - | Cottonmouth | Cottonmouth |
| - | Glass lizard | ? |
| - | Racerunner | Racerunner |
| - | SE snake | SE snake |
| - | (Anole) | Anole |

back terrapin (*Malaclemmys terrapin*) and the hognose snake (*Heterodon platyrhinos*) are species widespread in the south that reach their northern limits in coastal New England. The details of terrapin distribution support the view that it is closely tied to land and does not cross large saltwater expanses. Like other southern forms at their northern limits on Cape Cod, it does not occur on the islands that were separated by rising sea level after the Wurm glaciation. Just like the hognose snake, the terrapin is a common resident of Cape Cod barriers and quite absent from those of the Vineyard, or Nantucket, or even Monomoy. This distribution pattern, typical for southern forms that do not cross sea water readily, is puzzling in the light of late winter low ground temperatures on the barrier spits and tombolos that must provide hibernation sites. Superficially, it seems easy to explain why warm climate species are present on Cape Cod: they got there recently over land, but are not on the islands; they did not cross interglacial-level seas. The fact that they can withstand low ground temperatures, however, makes it puzzling that they have not extended their ranges farther north along the mainland, where warmer summer temperatures prevail. They could extend hundreds of miles before they hit hibernation temperatures as low as those they must endure, for example, at Sandy Neck.

Several trends in my summary of deployment are apparent: mammals are a large proportion of the total diversity in the north, lizards become increasingly numerous in the south. Water snakes (*Natrix sipedon* complex) and mice (*Peromyscus*) are prone to rapid adaptive alterations everywhere. The Gulf Islands are very poorly known. The last of these, pure artifact, needs immediate remedy.

An analysis of origins of barrier island faunas indicates that they usually come from the direction of prevailing longshore current and, therefore, seem to have dispersed along the barriers concordant with sand transport. Because Clay Gifford, at Cape Hatteras 10 years ago, first pointed this out to me, I call it "Giffordian" or "Dry Rabbit" dispersal. A rabbit, for example, can get on the Banks in Virginia and (given time) travel all the way to Onslow, below the Banks in North Carolina, without ever getting his feet wet. A species pushing southward, as longshore current builds the land, may have its proximal populations separated by new inlet formation, but it need never cross an inlet. Traveling up the barrier, against the predominant longshore current, is harder (Lazell and Musick 1973), and only the glass lizard (*Ophisaurus ventralis*) seems to have done this in North Carolina.

Over-water, waif dispersal apparently so important in initially populating oceanic islands, is of little consequence on barriers. Even major storms, that litter the land with propagules, seem to result in few or no survivors (Conant and Lazell 1973).

Human introductions, especially of rodents like *Rattus* and *Mus*, seem to be short-lived after human habitation terminates. Thus *Mus musculus* and *Rattus rattus* are known from literally piles of mummified bodies in attics and buildings at Portsmouth, Core Banks, but are rare or extinct there today. Livestock, such as pigs, seem better able to survive. Horn Island pigs are said by local people to have been set back by hurricane Camille, but they are believed to now be increasing. From October 1974 to November 1976, I believe I could detect a definite increase. These feral swine root up extensive areas in search of plant rhizomes for food; they are also quite carnivorous, and root up long stretches of wrack line ostensibly in search of snakes and lizards or the nests and young of rodents. They are well known to dig out and consume eggs of all sorts, especially those of turtles. Resilient as barrier island faunas are to natural disruption, man and his introduced livestock can extirpate endemic species. This has not yet happened, I hope, on islands here considered, but feral pigs are presumably the exterminators of the rodent, *Geomys cumberlandicus*, in Georgia.

Any discussion of barrier island adaptive strategies must begin with Muskeget, most bizarre islet of Atlantic America. The Muskeget vole, *Microtus breweri*, is strikingly pale and often shows a white frontal blaze (Tamarin and Kunz 1974). This pallor is presumably adaptive on Muskeget, an island made entirely of drift sand and completely lacking the ericaceous plants that carpet other New England sand lands (Wetherbee et al. 1972). *M. breweri* is also very large. Size conveys two obvious advantages: (1) it brings the surface:volume ratio down and thus mitigates heat loss in this fossorial creature exposed to very low winter ground temperatures; and (2) it makes *M. breweri* a difficult prey for the snake *Natrix sirtalis*, so well adapted to warm-blooded prey elsewhere in the Cape-Islands region (Lazell and Nisbet 1972; Lazell 1976a).

The protozoan blood parasite *Babesia microti* is found in 100% of *Microtus pennsylvanicus* from

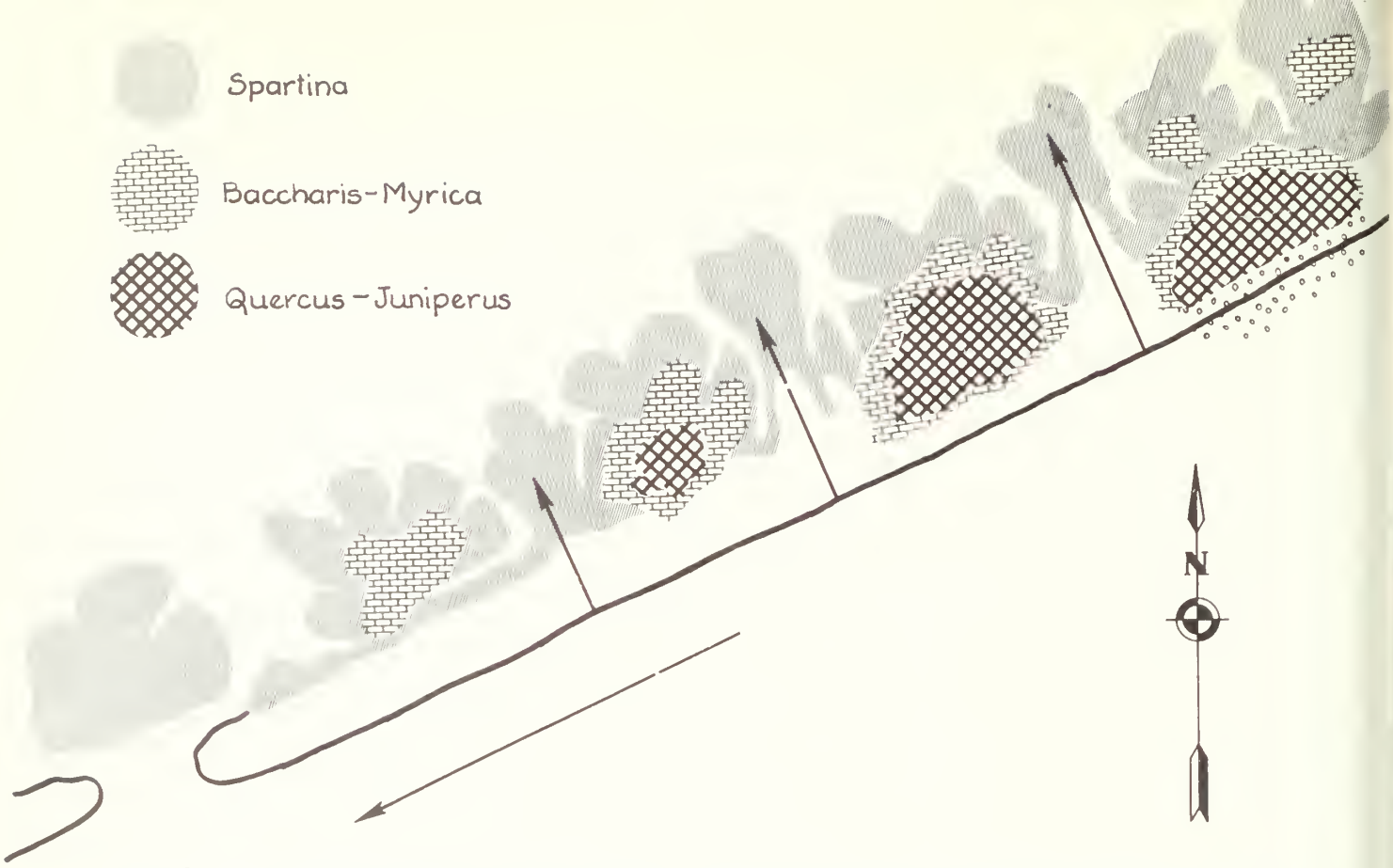



FIGURE 2. As longshore current closes inlets in North Carolina's Inter-Capes Zone, old flood-tide deltas succeed to hammocks. The rice rat, kingsnake, and wax myrtle live in the *Baccharis-Myrica* association. Overwash fills land between hammocks, and rising sea level erodes old Sound-side habitats.

islands neighboring Muskeget. It does not occur in *Microtus breweri* (Healy et al. 1976). Can this remarkable fact, of major importance in human pathology, derive from high summer ground temperatures directly or indirectly affecting the parasite?

The largest carnivore of the eastern United States, the gray seal or horsehead *Halichoerus grypus* weighs in at 800 or more pounds. The only U.S. population, and the southernmost in the world, is at Muskeget. These huge seals pup in midwinter (Andrews and Mott 1967; Rough 1968). There is excellent evidence that gray seals were a staple in the diet of aboriginal man following the Wurm glaciation (Waters 1967). Midwinter pupping makes the most vulnerable time in the lives of the seals coincident with the most dangerous and difficult time for man to hunt them. Today, however, feral descendents of a hybrid hodge-podge of species and races of geese raised as live decoys decades ago are increasing all over New England. These birds do not migrate and are present at Muskeget in midwinter; they are ecologically destructive and the hunting season on them has been extended further and further into gray seal pupping time (Lazell 1976b). A catastrophe could result if the gray seals are overly harassed on the Muskeget Shoals.

In the Inter-Capes Zone of the Outer Banks, between Cape Hatteras and Cape Lookout, a remarkable trilogy has been discovered, primarily by N. C. Spitzer (1973, and unpubl.). Here the rice rat (*Oryzomys palustris*), the only native small rodent present, the wax myrtle (*Myrica cerifera*), and the endemic kingsnake (*Lampropeltis getulus sticticeps*) coexist interdependently. Rice rats live primarily under rush (*Juncus*) wrack and are the basic staple in the diet of the peculiar kingsnake. The rice rats and kingsnake together would drown when the Banks overwash in winter storms: the rush marshes and frequently even the high hammocks are flooded. In Figure 2 I have diagrammed the situation in the Inter-Capes Zone. Rice rats excavate storm refugia under the domed, multi-trunked root masses of the wax myrtle. These refugia, or chambers, have a solid wood roof and thus provide air pockets during the several hours of predictable annual flooding. Spitzer monitored the chambers with maximum-registering thermometers. Under normal circumstances the temperatures never varied from average ground temperatures; in major storm-flooding the temperatures shot up much higher than ground, air, or water temperatures around them. Spitzer learned to spot chambered *Myrica* trees from a distance and predict the presence of kingsnakes close to them with uncanny accuracy. The kingsnakes apparently use the rice rats' storm refugia beneath the wax myrtle as hibernacula, and thus survive the storms of winter themselves.

I have located chambered *Myrica* and rice rats on the Gulf Islands, where endemic *Peromyscus* mice occu. Do they (and other mammals and reptiles) use these as storm refugia and hibernacula as well? We do not yet know. However, a program initiated by the Park Service on the Gulf Islands to exterminate nutria with zinc phosphide could have spelled disaster. It was believed no native aquatic rodent was present (none had ever been looked for), so poisoned carrots on floating platforms were believed "specific" for nutria. Fortunately, the program was quickly stopped and both rice rats and nutrias survived.

The biogeography of our barrier islands fails utterly to fit the theory and mathematical models presented by MacArthur and Wilson (1967). The theory has been cogently attacked by Simberloff and Abele (1976) and Simberloff (1976). David Lack (1976) also smelled a rat. If Simberloff

and Abele eviscerated the theory with the scalpel and forceps of precise methematics, and Lack obliterated it with brush strokes of tropical ornithology, I had already bludgeoned it with the sledge of logic and dismembered it with the axe of satire (Lazell 1972, 1976a).

Barrier island faunas are tenacious and resilient and highly evolved. Under natural conditions there is no turnover of species and no "equilibrium" of extinction and colonization. The number of species on any given island has to do with a plethora of factors beyond mere size and separation distance; mostly it has to do with the specific and unique and unpredictable attributes of each individual and the autecology of each individual animal species. The number of species on an island, or anywhere else, can only be empirically determined.

Only man, with his dredges, bulldozers, jetties, groins, and livestock can so alter barrier islands as to exterminate their native faunas. It is the mission of the National Park Service to prevent that.

LITERATURE CITED


ANDREWS, J. C., and P. R. MOTT. 1967. Gray seals at Nantucket, Massachusetts. J. Mamm. 48(4): 657-658.

BARBOUR, T. R., and W. L. ENGELS. 1942. Two interesting new snakes. Proc. New England Zool. Club 20:101-104.

CONANT, R., and J. D. LAZELL. 1973. The Carolina salt marsh snake: a distinct form of *Natrix sipedon*. Breviora, Mus. Comp. Zool. 400: 13 pp.

GODFREY, P. J. 1970. Oceanic overwash and its ecological implications on the Outer Banks of North Carolina. Office of Nat. Sci. Studies, Nat. Park Service, U.S.D.I., Washington: 37 pp.

_____ and M. M. GODFREY. 1975. Some estuarine consequences of barrier island stabilization. Estuarine Research II: Geology and Engineering, Academic Press, New York: 485-516.

HEALY, G. R., A. SPIELMAN, and N. GLEASON. 1976. Human babesiosis: reservoir of infection on Nantucket Island. Science 192(4238):479-480.

LACK, D. 1976. Island biology illustrated by the land birds of Jamaica. Univ. California Press, Berkeley.

LAZELL, J. D. 1972. The anoles (Sauria: Iguanidae) of the Lesser Antilles. Bull. Mus. Comp. Zool. 143(1):115 pp.

_____. 1976a. This broken archipelago. Quadrangle Press, New York.

_____. 1976b. Of geese and gray seals. Soundings, The Cape Codder, 1 Jan. Sect. 2:6.

_____, and I. C. T. NISBET. 1972. The tern-eating garter snakes of Nomans Land. Man and Nature, June: 27-29.

MACARTHUR, R. H., and E. O. WILSON. 1967. The theory of island biogeography. Princeton Univ. Press, New Jersey.

RICHMOND, E. A. 1962. The fauna and flora of Horn Island, Mississippi. Gulf Research Reports 1(2): 57-106.

_____. 1968. A supplement to the fauna and flora of Horn Island, Mississippi. Gulf Research Reports 2(3):213-254.

ROUGH, V. 1968. Gray seals in New England. Massachusetts Audubon 52(3):20-27.

SIMBERLOFF, D. 1976. Species turnover and equilibrium island biogeography. Science 194(4265): 572-578.

_____, and L. G. ABELE. 1976. Island biogeography theory and conservation practice. Science 191 (4224):287-288.

SPITZER, N. C. 1973. Rice rat's world. Man and Nature, March:24-26.

STICK, D. 1958. The Outer Banks of North Carolina. Univ. North Carolina Press, Chapel Hill.

TAMARIN, R. H., and T. H. KUNZ. 1974. *Microtus breweri*. Mamm. Species 45:1-3.

WATERS, J. H. 1967. Gray seal remains from southern New England archeological sites. J. Mamm. 48(1):139-141.

WETHERBEE, D. K., R. P. COPPINGER, and R. E. WALSH. 1972. Time lapse ecology, Muskeget Island, Nantucket, Massachusetts. MSS Educational Publ. Co., New York.

# ECOLOGY OF ELK ON ALPINE TUNDRA IN ROCKY MOUNTAIN NATIONAL PARK

David R. Stevens[1]

## INTRODUCTION

The alpine tundra is one of the most unique resources in Rocky Mountain National Park. About one-third of the park's area is above 11,000 feet elevation, with 33,000 acres considered to be alpine tundra vegetation. Parts of the tundra are easily accessible to the park visitor via Trail Ridge Road in the summer. The annual increase in visitor use is causing obvious deterioration near parking areas but may be causing more subtle changes over the entire accessible area. The affects of human activities have been well documented by Willard and Marr (1970) and Willard and Marr (1971).

In recent years, elk (*Cervus canadensis nelsoni*) wintering on the alpine tundra appear to have increased. Marr (1964) considered this behavior to be of rather recent origin as a result of human population pressures at lower elevations. Much of the alpine area, including Trail Ridge, is considered to be elk range at some time of year. Some of these areas are also important habitat for other species, such as bighorn sheep and ptarmigan. Capp (1967) attempted to analyze competition between elk, deer and bighorn sheep. It was believed that since elk can have a major ecological influence on their habitat under certain circumstances, their affect on the alpine needed to be assessed. Management of the alpine tundra resources requires a complete knowledge of all influences so that the human impact can be isolated and, if possible, eliminated.

The objective of this paper is to examine the relationships of elk and the alpine tundra and assess natural effects. The data were gathered in conjunction with an elk ecology study of 1968 to 1976.

## THE STUDY AREA

Rocky Mountain National Park, 412 square miles, lies along the Continental Divide in north-central Colorado. Elevations range from 7,600 feet to 14,256 feet, with about one-third of the total area over 11,000 feet above sea level. The mountains are formed by a series of granitic batholiths, intruded into precambrian micaschists and pegmatite. The physiography of the East Slope is characterized by steep cliffs and U-shaped valleys, as altered by local Pleistocene glaciation. The generally more level, rolling alpine tundra areas were apparently not glaciated. On the west, the mountains fall off less steeply to the Colorado River valley at about 9,000 feet elevation.

The vegetation is characterized by three zones, well described by Marr (1961). The upper montane zone occupies from 7,600 to about 9,000 feet elevation and is characterized by a ponderosa pine (*Pinus ponderosa*) savannah with various shrub and grassland understories. Big sagebrush is common on some of the larger openings. The valley bottoms show indications of past disturbance of grazing and cultivation. Willow (*Salix* spp.) and meadow types dominate the vegetation.

From 9,000 to about 11,000 feet is the subalpine forest zone. The primary forest formation is Engelmann spruce (*Picea engelmanni*)/ subalpine fir (*Abies lasiocarpa*) community. Numerous open parks are present, with willow, grasses, forbs and sedges.

Above the subalpine zone is the alpine tundra. Several studies have been made describing the vegetation of the alpine tundra in the park. These include Kiner (1939), Griggs (1956), and Willard (1963). The tundra vegetation is characterized by a complex mosaic of vegetation communities related to physiography, snow accumulation, moisture availability, exposure, temperature, and substrate. For the purposes of this discussion, five vegetation types were considered. Fellfields were on exposed sites and characterized by cushion plants such as moss campion (*Silene acaulis*), nail wort (*Paronychia sessiliflora*), alpine sandwort (*Arenaria obtusiloba*), and dwarf clover (*Trifolium nanum*). Alpine turf type was characterized by kobresia (*Kobresia myosuroides*), alpine avens (*Geum rossii*), sedge (*Carex rupestris*), bistort (*Polygonum bistortoides*), and Rocky Mountain sage (*Artemisia scopulorum*). The snowbed types were characterized by hairgrass (*Deschampsia caespitosa*), rush (*Juncus drummondii*), sibbaldia (*Sibbaldia procumbens*), and arctic mountain sage (*Artemisia arctica*). Alpine marsh type was characterized by sedge (*Carex scopulorum*), marsh marigold (*Caltha leptosepla*) and Parry primrose (*Primula parryii*). The willow type was characterized by several willow species (*Salix planifolia*, *Salix brachycarpa*, and *Salix glauca*). Understory was hairgrass, sedges (*Carex* spp.), and narcissus anemone (*Anemone narcissiflora*).

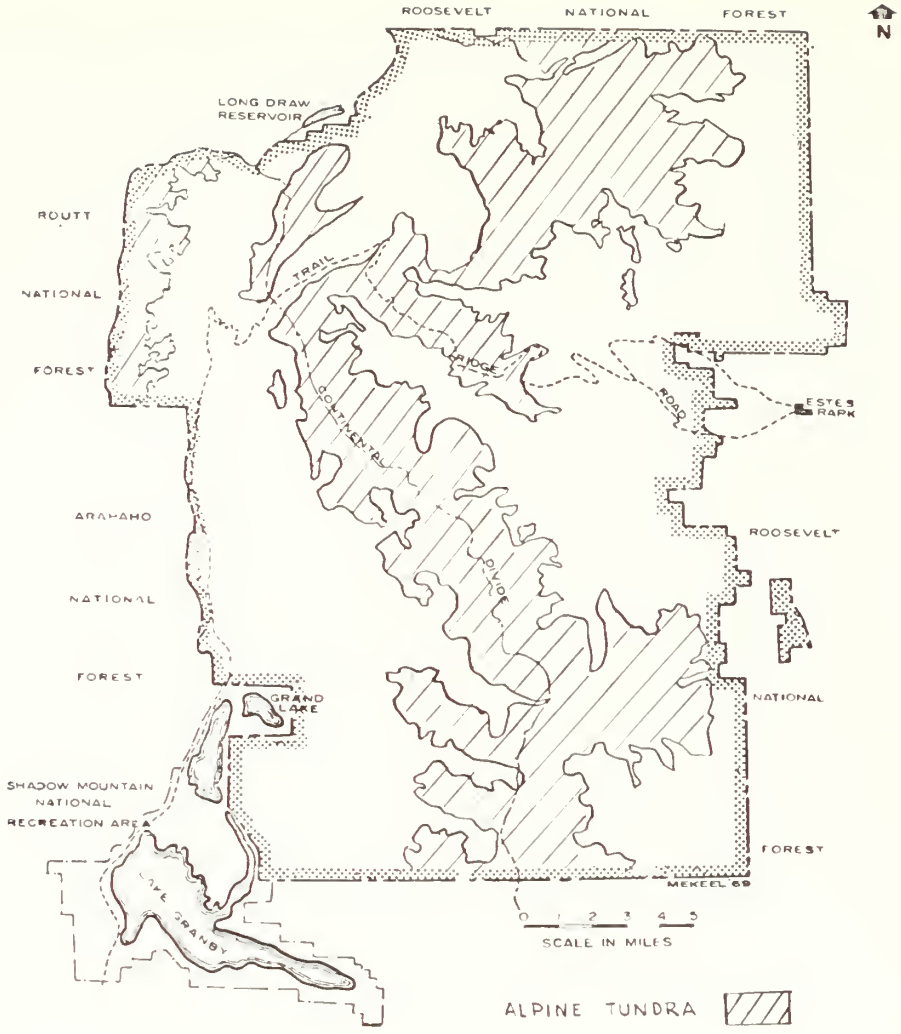
It is recognized that this is a very simplified classification of the vegetation present.

The climate of the alpine has been described by several authors, including Marr (1961), Willard (1960), and Bell (1974). The summers are short and cool with frequent thunderstorms. Fall days are clear, dry and cold. The winters are long, cold, and very windy. Glidden (1974) measured wind speeds of greater than 74 mph on 44 per cent of the days from January to May 1974. The spring is cool and wet. Annual precipitation is 25-35 inches, with mean annual temperatures of 25-28°F. The climate can be characterized as severe, when compared to the lower elevations of the park.

Elk in the Estes Park area were extirpated by 1880 through market hunting and competition with domestic livestock for winter range. In 1913 and 1914, 49 elk were reintroduced from Yellowstone Park. Records show that by 1930, 430 elk were counted on the winter range. Migration routes over the alpine tundra were reestablished. The first elk wintering on the alpine tundra were recorded in 1933 (Annual Wildlife Report). At that time, 23 elk were observed on Trail Ridge and 6 bull elk above Lost Lake.

Summer range areas were noted in the head of Forest Canyon and in the North Fork of the Big Thompson River. By 1943 the herd was considered too large for the low elevation winter range, and a reduction program was initiated. These reduc-

[1]Rocky Mountain National Park, Estes Park, Colorado.




ROCKY MOUNTAIN NATIONAL PARK

TABLE 1. Winter elk distribution by vegetation zones as determined by aerial observation.

| Year | Upper montane | | Subalpine | | Tundra | |
|---|---|---|---|---|---|---|
| 1968 | 174 | (36)[a] | 136 | (28) | 178 | (36) |
| 1969 | 447 | (69) | 9 | ( 1) | 193 | (30) |
| 1970 | 306 | (73) | 10 | ( 2) | 103 | (25) |
| 1971 | 396 | (79) | 0 | | 105 | (21) |
| 1972 | 484 | (80) | 10 | ( 2) | 115 | (18) |
| 1973 | 286 | (74) | 1 | (tr) | 101 | (26) |
| 1974 | 413 | (80) | 0 | | 103 | (20) |
| 1976 | 547 | (63) | 0 | | 316 | (37) |
| Mean | 381 | (69) | 21 | ( 4) | 152 | (27) |

[a]Percentage is in ( ).

tions were held periodically until 1968. The herd has been allowed to increase the last few years.

Other ungulates important to the park are mule deer (*Odocoileus hemionus*) and bighorn sheep (*Ovis canadensis*). No major predator on elk is present. The gray wolf (*Canis lupis*) and the grizzly bear (*Ursus arctos*) were expirpated, probably before the turn of the century.

## METHODS

Both ground and aerial observation trips were conducted during the study period. All observed elk were noted as to sex, age, activity, vegetation type, elevation and location. Where possible, feeding sites were examined to determine plants eaten and relative frequency.

Eight agronomy cages (4' x 4' square wire mesh) were established on Trail Ridge on representative vegetation types. They were originally designed for the vegetation to be clipped annually, but the use was so light that it was only described subjectively and photographed.

At each study site, transects using a 20 x 50 cm plot frame (Daubenmire, 1959) were established in 1971 to show long-term trends. Twenty-one plots were mechanically distributed along a 100-foot line so that plots could be duplicated exactly on subsequent measurements. These were sampled the second time in 1976 for a 5-year period.

Pellet group counts were made in the spring on the Trail Ridge sites to determine relative use by ungulates at these sites.

## RESULTS--DISTRIBUTION AND RANGE USE

Tundra use data were tabulated on 2391 elk in 135 groups observed by ground observation. In addition, on 19 helicopter flights, 1291 elk were observed on the alpine tundra. As determined by aerial observation over the past nine winters, between 18 per cent and 37 percent of the elk population (Table 1) remaining within the park boundaries utilize the alpine tundra. Most of the remainder migrate to the lower elevation ranges on the East Slope of the park. The most heavily used alpine ranges are all in the north half of the park on Trail Ridge, Mount Ida Ridge, Mummy Mountain, and Mount Dickinson. Trail Ridge was most heavily used, averaging 38 per cent of the total observations for the alpine. The total number of elk using the alpine was high in 1968 and 1969--178 and 193 respectively, then remained fairly constant, averaging 105 until 1976. This past winter, the highest number ever recorded--316 elk--were counted on the alpine tundra in March. This increase, however, was not reflected by the pellet group counts of Trail Ridge.

The mean sex and age composition of these elk for the 8-year period was 20 percent adult males, 6 per cent yearling males, 59 per cent females, and 13 per cent calves. In 1974, the composition of elk parkwide was 9 per cent males, 6 per cent yearlings, 61 per cent females, and 24 per cent calves (Stevens, 1974).

Vegetation types on which elk were observed in the winter reflect the importance of areas blown free of snow by wind. Of the 1714 elk classified as to vegetation used, 65 per cent were on tundra turf and 32 per cent were on fellfield. Both willow and marsh areas were used, but because of the relative size of these sites, the observed use was less. The actual degree of use was indicated by pellet group counts. An average of six elk days use per acre was recorded on the tundra turf sites, but 21 elk days use per acre was found on the willow sites.

Elk used all elevations from treeline at about 11,200 feet to the tops of the mountains in winter. On the 22 March 1969, elk were observed on Mummy Mountain at 13,000 feet elevation.

In winter, elk use the alpine sites primarily for feeding but, during good weather, will also bed there. Of 243 elk observed undisturbed from the ground, 38 percent, or 93, were bedded. During inclement weather, elk move down into the tree cover of the krumholz to rest.

As vegetation begins to green up in the low country and snow begins to crust in the subalpine forest, the elk appear to move down to lower elevations. In 1968, a flight April 30 showed only 63 elk on the alpine, while in February, 177 elk had been observed. They probably do not return to the alpine until mid-May, when the annual migration back to the summer range begins (Gill, 1967). Capp (1967) reported that elk were on the alpine ranges in mid-June. Much of the elk use of alpine areas in June is while en route to summering areas. Trail Ridge receives most use during this period. The vegetation type most used was tundra turf, where 73 per cent of the observations, or 661 elk, were made.

Use of alpine as summer range is related to major summering areas. (Gill, 1967) noted five major summer concentration areas: Mirror Lake-Mummy Pass area, Flatiron Mountain-Mount Chapin area, Specimen Mountain, Forest Canyon Pass-Gorge Lakes, and the Snowdrift Peak-Nakai Peak area. Other areas where large summer elk populations have been noted were the head of West Creek, Fairchild Mountain, and the Cony Creek drainage in Wild Basin. Observations in July, August, and September indicated the most important habitat types for feeding elk were right at treeline, in what is called the "krumholz" area. An average of 52 percent of the elk were observed in this type from 1968 to 1975. Only 23 percent of the observations were made on the alpine tundra, and this was in close association with the krumholz. Of 930 elk recorded on the alpine, 64 percent were on tundra turf and 22 percent on alpine marsh sites. Moist areas with lush vegetation appeared to be preferred. This was also noted by Capp (1967). The only area where it was believed that the tundra was key vegetation type for summering elk was on the southeast ridge of Mount Fairchild.

Generally, the elk will bed in the spruce fir forest and move into the more open types to feed. Feeding elk were observed at almost all times of the day on the alpine, but the most common time was early morning and evening. During mid-day, most of the elk would bed near the feeding sites, often using solifluction terraces unless disturbed. Calves would be bedded in groups as the females fed. The solifluction terraces were often so heavily used that concentration of urine killed the vegetation in bedding sites. Observations by Capp (1967) indicated similar use.

During the breeding season, in early September, some of the elk begin to move to lower elevations. A reduction of elk on the alpine was clearly evident at that time. However, many elk were still observed in the alpine, especially on Trail Ridge, as they began to migrate back to the winter range. The alpine tundra was believed to

TABLE 2. Food habits of elk on alpine tundra as determined by feeding site examination.

| Taxa[1] | Winter | Summer |
|---|---|---|
| Browse | | |
| Salix spp. | 3/18[2] | 4/8 |
| Forbs | | |
| Arenaria obtusiloba | 3/36 | 2/16 |
| Anemone narcissiflora | - | 3/25 |
| Artemisia spp. | tr/9 | 7/42 |
| Caltha leptosepla | - | 7/25 |
| Polygonum spp. | - | 4/33 |
| Trifolium spp. | 6/18 | 46/83 |
| Other forbs | 5/82 | 18/83 |
| Total | 14/82 | 87/100 |
| Grass and Grass-like Plants | | |
| Carex rupestris | 29/54 | - |
| Carex spp. | 12/71 | 5/75 |
| Kobresia myosuroides | 19/36 | 1/8 |
| Poa spp. | 16/64 | tr/16 |
| Other grasses | 7/14 | 3/16 |
| Total grasses and grass-like | 83/100 | 9/100 |

[1] Only Taxa amounting to at least 2% during one season are listed.

[2] Percent/frequency of sites

TABLE 3. Changes in cover and frequency of key taxa on three sites.

| | Trail Ridge Tundra Turf | | Mt. Fairchild Tundra Turf | | Trail Ridge Willow | |
|---|---|---|---|---|---|---|
| No. Transects | 4 | | 1 | | 3 | |
| Taxa[1] | 1971 | 1976 | 1971 | 1976 | 1971 | 1976 |
| Salix brachycarpa | - | - | - | - | 24/43[2] | 21/43 |
| Salix planifolia | - | - | - | - | 25/51 | 16/52 |
| Geum rossii | 31/99 | 25/96 | 1/24 | 1/24 | 25/86 | 21/93 |
| Polygonum bistortoides | 8/82 | 7/80 | - | - | 3/49 | 2/51 |
| Sedum rosea | - | - | - | - | 4/46 | 3/47 |
| Trifolium spp. | 8/36 | 6/36 | 32/90 | 34/100 | - | - |
| Trifolium parryi | 4/23 | 4/23 | - | - | - | - |
| Artemisia scopulorum | 11/81 | 7/64 | - | - | 12/68 | 9/67 |
| Arenaria obtusiloba | 4/34 | 2/27 | 18/95 | 11/95 | - | - |
| Anemone narcissiflora | - | - | - | - | 6/21 | 5/35 |
| Caltha leptosepla | - | - | - | - | 9/33 | 7/44 |
| Deschampsia caespitosa | 4/20 | 5/17 | - | - | 27/90 | 18/83 |
| Kobresia myosuroides | 20/64 | 19/49 | 18/90 | 20/100 | - | - |
| Carex rupestris | 14/61 | 16/67 | 5/57 | 2/24 | - | - |
| Carex scopulorum | - | - | - | - | 2/35 | 5/39 |
| Poa spp. | 2/37 | 2/30 | 7/76 | 4/81 | - | - |
| Bare ground | 4/42 | 1/21 | 3/33 | 3/43 | 1/10 | 1/10 |

[1] Taxa listed amount to at least 2% total cover.

[2] Per cent cover/frequency in 20x50 cm plots.

be very important to migrating elk, since it represented the most easily traveled routes in many cases.

Most of the elk that were to winter in the low elevations had arrived on these areas by mid-October.

Wintering areas did change during the season, as indicated by the tracking of 62 elk which had spent early winter in the willow bottoms of the Kawuneeche Valley on the west side, but moved to the alpine tundra of Mt. Ida Ridge on February 1, 1972.

## FOOD HABITS

To determine food habits, 11 feeding sites, recording 1,162 instances of use, were examined during the winter period (Table 3). All were from Trail Ridge. These data indicated that grasses and sedges, including kobresia, make up the major portion of the winter diet (83%). They were used on all the sites examined. Forbs, primarily represented by cushion plants, *Arenaria obtusiloba* and *Trifolium* spp., made up 14 percent of the use. The only shrub to appear on the feeding sites was willow, with 3 percent. No other studies of winter foods for elk on the alpine are known.

Summer food habits on the alpine sites were determined by examining 12 feeding sites and recording 1,325 instances of use. During this time, forbs formed 87 percent of the use. Clover (*Trifolium* spp.) represented by three different species, formed the major portion of this with 46 percent of the total. Other important items were marsh marigold and sages (*Artemisia* spp.), both with 7 percent. Grasses and other grass-like plants made up only 9 percent of the use. Again, willow was the only shrub, with 4 percent.

On one feeding site examined by Capp (1976), 72 per cent of the use was forbs, of which 49 percnet was clover (*Trifolium dasphyllum*) and 28 percent were grasses or sedges. Nichols (1957) studied elk on an 11,000-ft-elevation park in the White River Area. He found the most important items in the elk summer diet to be hairgrass, miscellaneous forbs, marsh marigold and Baltic rush (*Juncus balticus*).

## VEGETATION REACTION

On Trail Ridge, eight agronomy cages were established in 1968. Instead of clipping and weighing the vegetation annually, these cages were used as a protected site to estimate plant utilization. Of the four tundra turf sites, the elk use generally was very light and almost not discernible. Various species of *Poa* on one site did show fairly heavy use. After eight years of protection, an increase in plant litter inside the cages was noticeable.

On the three willow sites, the use of willow was quite obvious each year. On all sites, the willow inside the cages after eight years was considerably taller and almost one-third taller in most cases. This degree of use was also indicated by the pellet group counts, which averaged 23 elk days use per acre.

Quantitative data on the trend of the vegetation were obtained on eight transects, established in 1971. Four transects were established on tundra turf vegetation of Trail Ridge. The data collected (Table 4) indicated a probable trend toward less groundcover. All major cover species except *Carex rupestris* lost cover, and most also lost in frequency. The reduction in bare ground could indicate a shift in vegetation composition and not just a loss of groundcover. This was also indicated by the increase in *Arenaria fendleri*, *Carex scopulorum*, *Deschampsia caespitosa*, and *Carex rupestris*. These changes were not considered statistically significant.

Only one transect was established on the southeast slope of Mount Fairchild on a tundra turf site. Some loss was noted in *Arenaria obtusiloba*, but the two major cover species, alpine clover and kobresia, increased in cover. This area was considered a primary summer range, as no elk was observed on this site in winter.

On the willow types of Trail Ridge, cover loss by the major cover species (Table 3) was also noted. This corresponds with the indication of heavy use by annual observation and pellet group count. These species, being willow, both lost in cover but not frequency. Hairgrass also lost in both percent cover and frequency. This, however, was somewhat compensated for by an increase in *Carex scopulorum*. These changes are not considered statistically significant.

## SUMMARY AND DISCUSSION

The use of alpine tundra as winter range has been reported in other areas by Schwan and Costello (1951) and Houston (1976). In Rocky Mountain National Park, elk were first reported wintering in the alpine in 1933, and probably they have used these areas historically. It would appear that, as the elk population in the park increased, the elk wintering on the alpine also increased. Ratcliff (1941) reported elk increasing on the alpine in 1939 to 1941 during a period when the overall elk population reached its peak prior to direct reduction. Packard (1947) believed these wintering elk on the alpine in Rocky Mountain National Park were "old non-breeding bulls." The present study, however, does not indicate this to be the case. Although adult male groups are common, the sex and the classification is similar to the low elevation winter range areas (Stevens 1974).

This study tends to indicate that elk wintering on the alpine have an influence on the vegetation cover. However, on the tundra turf sites, the five-year transect data were not substantiated by the annual observation and pellet group counts, which were low. I feel that more data are needed to document these changes. Marr and Willard (1970) did not note any lasting effects by elk.

On the willow sites, however, all of the data indicate a loss of willow cover and vigor. although the cages could form a micro-environment favoring willow growth, it is believed that the indicated impact of elk is real. If these effects persist over the long term, influence on other species that use the alpine tundra sympatrically could be expected. Reduction in the willow habitat on the alpine would affect white-tailed ptarmigan populations. Willow is the primary item in the diet of the ptarmigan (May, 1970). However, the level of change at present appears to be within tolerance and can be considered a natural ecological influence. No indication was noted of elk use of the alpine being related to human activities.

It has been hypothesized by some investigators, including Ratcliff (1941), Ratcliff and

Sumner (1945), and Contor (1958) that the decline of the bighorn population and its failure to increase is related to elk competition. This question is presently being investigated.

## LITERATURE CITED


BELL, K. 1974. Autecology of *Kobresia bellardii*. Ph.D. thesis, University of Alberta, Edmonton. 167 pp.

CAPP, J. C. 1967. Competition among Bighorn Sheep, Elk and Deer in Rocky Mountain National Park, Colorado. M.S. thesis, Colorado State University, Fort Collins. 133 pp.

CONTOR, R. J. 1958. A Survey of the Bighorn Sheep in Rocky Mountain National Park. Unpublished report, Rocky Mountain National Park, Colorado. 11 pp.

DAUBENMIRE, R. F. 1959. A Canopy Coverage Method of Vegetational Analysis. Northwest Science 33(1):43-64.

GILL, R. B. 1967. Elk Seasonal Movements, Rocky Mountain National Park. Job Completion Report W-38-R-21. pp. 191-208.

GLIDDEN, D. E. 1974. Analysis of Alpine and Subalpine Wind conditions in Winter in Rocky Mountain National Park. Unpublished report, Rocky Mountain National Park. 91 pp.

GRIGGS, R. F. 1956. Competition and Succession on a Rocky Mountain Fellfield. Ecology 37:8-20.

HOUSTON, D. B. 1976. The Northern Yellowstone Elk. Parts III and IV, Vegetation and Habitat Relations. Unpublished report, Yellowstone National Park. 444 pp.

KEINER, W. 1939. Sociological Studies of the Alpine Vegetation on Longs Peak. Ph.D. thesis, University of Nebraska, Lincoln. 68 pp.

MARR, J. W. 1961. Ecosystems of the Front Range, Colorado. University of Colorado Studies, Series in Biology No. 8. 134 pp.

MARR, J. W. 1964. Utilization of Front Range tundra. pp. 109-118 *in* Grazing in terrestrial and marine environments. D. J. Crisp (ed.). Blackwell Scientific Publications, Oxford.

MAY, T. A. 1970. Seasonal Foods of White-Tailed Ptarmigan, Colorado. M.S. thesis, Colorado State University.

PACKARD, S. M. 1947. An Ecological Study of Bighorn Sheep in Rocky Mountain National Park, Colorado. Journal of Mammalogy 27(1):3-28.

RATCLIFF, H. M. 1941. Winter Range Conditions in Rocky Mountain National Park. Transactions, North American Wildlife Conference, No. 6:132-139.

RATCLIFF, H. M. and L. SUMNER. 1945. National Park Wildlife Ranges. Transactions, North American Wildlife Conference, No. 10:246-250.

SCHWAN, H. E. and D. F. COSTELLO. 1951. The Rocky Mountain Alpine Type. U.S. Forest Service Report, U.S. Department of Agriculture. 18 pp.

STEVENS, D. R. 1974. Ungulate Ecology Studies, Rocky Mountain National Park. Annual Report, National Park Service. 2 pp.

WILLARD, B. E. 1960. Ecology and Phytosociology of the Tundra Curves Area, Trail Ridge, Colorado. M.S. thesis, University of Colorado. 144 pp.

WILLARD, B. E. 1963. Phytosociology of the Alpint Tundra of Trail Ridge, Rocky Mountain National Park, Colorado. Ph.D. thesis, University of Colorado. 245 pp.

WILLARD, B. E. and J. W. MARR. 1970. Effects of Human Activities on Alpine Tundra Ecosystems in Rocky Mountain National Park. Biological Conservation 2(4):257-265.

WILLARD, B. E. and J. W. MARR. 1971. Recovery of Alpine Tundra under Protection after Damage by Human Activities in Rocky Mountain National Park, Colorado. Biological Conservation 3(3): 181-190.

# A POPULATION MODEL OF THE NORTHERN YELLOWSTONE ELK HERD[1]

Charles W. Fowler[2] and William J. Barmore[3]

## INTRODUCTION

The elk (*Cervus canadensis*) of the northern Yellowstone herd spend their winters on about 715 $km^2$ (385 $mi^2$) in the northern part of Yellowstone National Park and southwestern Montana. This herd has been cited as an example of an ungulate population increasing beyond the carrying capacity of its winter range following near extirpation of its natural predators and man-caused changes in the herd's distribution (Allen 1954, Wagner 1969, Murie 1951, Craighead et al. 1972, and others), although recent work (Houston 1974, 1976) suggests that this may be a misinterpretation of the facts. This elk herd and its management have been of considerable scientific and administrative concern (Graves and Nelson 1919, Rush 1932, Wright and Thompson 1935, Grimm 1939, Cahalane 1941 and 1943, Kittams 1959, Leopold et al. 1963, and others) as well as public concern (Olsen 1962, and 1968, Trueblood 1963, Pengelly 1963, U.S. Senate 1967, and others) for many years.

As a result of the concern surrounding this population, numerous studies of various kinds have been conducted. These studies have produced a particularly complete collection of data concerning population size, reproductive rates, sex and age structure, especially as representative of the herd since the 1930's. These and other data have been reviewed and synthesized with results from their own research by Houston (1974, 1976) and Barmore (in prep.). However, no previous attempt has been made to better understand this herd by way of a dynamic population model. This paper reports an initial attempt to:

1) incorporate existing data into such a model, and, by using the model, to:
2) estimate the carrying capacity (population size at which the *mean* rate of change is equal to zero) for the north Yellowstone area under conditions characteristic of the last forty years, and,
3) examine the possible effects of predation on the population. Future work will concentrate on improving the model and analysis of questions concerning immigration, emigration, simulation, and management alternatives; all of which were interesting sidelights to this work but were too extensive to report here.

## THE DATA

The data used to develop the model described in this paper are from Houston (1974 and pers. comm.) and Barmore (in prep.) and in this section are described as they relate to the model.

### A. Herd size, 1935-1976

In conjunction with an intensified elk management program that began in the early 1930's, seven late winter ground censuses of the northern Yellowstone elk were made between 1935 and 1956. These were followed by fourteen aerial censuses (fixed wing and/or helicopter) through 1976. In addition, Houston (1974) estimated the size of late winter (about March) herds for all years and Barmore (in prep.) for selected years (1949-1956 and 1962-1970). The methods of estimation are described in their respective papers. Houston's estimates (1974, Figure 4 and Appendix V) are shown in Figure 1. Barmore's estimates tend to be slightly lower at high population levels and slightly higher at low population levels due to differences in estimation procedures. The population levels and trends, however, are generally the same as in Figure 1.

Through more extensive removals from both inside and outside the park between the mid 1950's and the late 1960's the population was maintained at relatively low levels when compared to previous years. Data from this reduced population, in part, provided insights into density dependent relationships between population size on the one hand, and natality and mortality on the other. Between 1968 and 1975 the herd was allowed to increase with negligible removals by man. In 1976 hunting removals characteristic of the period prior to the mid 1950's were resumed.

### B. Calf survival from birth to first winter

Calf survival (initial survival, $s_o$) was estimated by comparing pregnancy rates with calf/cow ratios obtained the following winter and by assuming pregnancy rates and birth rates are equal (see discussion of birth rates below). Figure 2 shows initial survival plotted against estimated herd size from the previous winter for ten years as estimated by Barmore (in prep.) (solid points) and mean calf survival for high (about 12,000) and low (about 5,000) population levels as estimated by Houston (1974) (open circles). Both sets of data show that initial survival increases as the population decreases, but the estimated rates of change differ. This probably reflects differences in the data used to calculate calf/cow ratios, particularly at low population levels. Barmore used only ratios calculated from field classifications as being most representative and comparable over the 1935-1969 period. Houston considered sex and age data obtained from hunter harvests outside the park and from removals (shooting and/or live trapping) inside the park in addition to data obtained by field classifications. This may have introduced an upward bias to the estimated initial survival, particularly at the low population levels during the 1960's. For example, calf/cow ratios for elk driven into live traps with helicopters would have been high because proportionately more cows than calves escaped as groups of elk were herded into the traps.

These differing interpretations were handled by separate mathematical representations of the functional relationship between initial survival and population size. These relationships were:

[1] The authors would like to express their sincere gratitude to Dr. Douglas Houston for his cooperation in reviewing an initial version of the model described here and for the unpublished data which he so kindly provided. We also wish to thank Dr. Jim Smith who also reviewed the model.

[2] Department of Wildlife Scienc, Utah State University, Logan 84322.

[3] Grand Teton National Park, Box 67, Moose, Wyoming 83012.

1) For Barmore's data: The equation for a straight line passing through the weighted means of the two clusters of points at low and high population levels (shown as the line in Figure 2) is:

$$s_o = 0.528 - 0.0144\ P$$

where:

$s_o$ = initial survival or survival from birth to first winter

P = estimated winter herd size in thousands

2) For Houston's data: The equation for a straight line between his two means is:

$$s_o = 0.915 - 0.0429\ P$$

C. Survival between first and second winters

Both Houston (1974) and Barmore (in prep.) concluded that mean survival between the first and second winters ($s_1$) was greater at low than at high population levels but varied greatly between years at both levels. Their data were used to calculate survival from the first to second winter as a function of population size and are shown in Figure 3. The two survival rates corresponding to populations of about 7,000 and 9,000 elk are notably low. They represent late winter estimates after exceptionally heavy removals of 6,535 and 3,800 elk, respectively. Calculated fall populations prior to removals for these years were 14,000 and 13,000 elk, respectively.

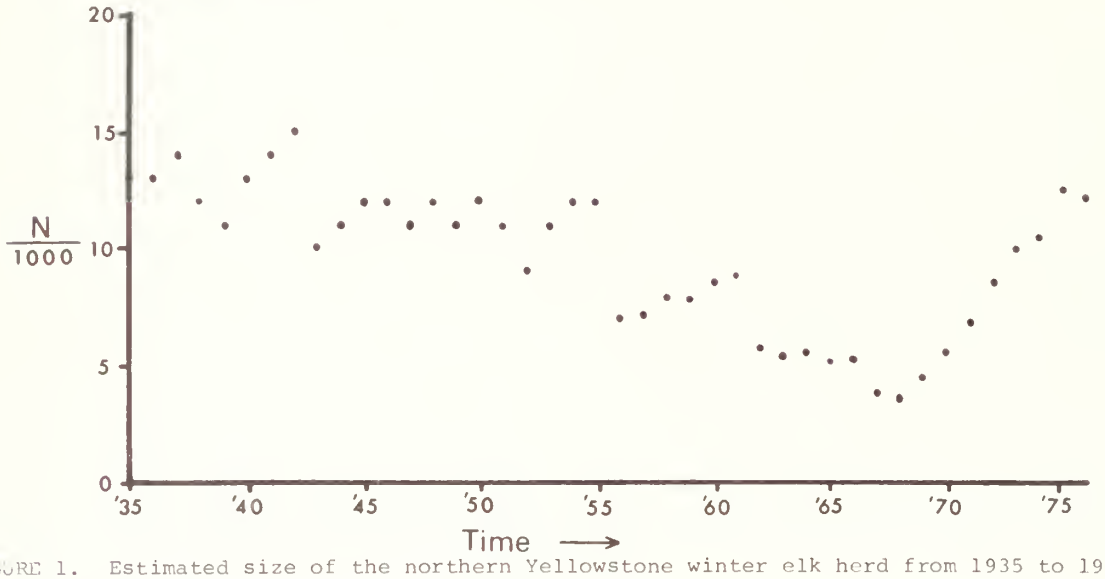



FIGURE 1. Estimated size of the northern Yellowstone winter elk herd from 1935 to 1976 (from Houston 1974 and pers. comm.).

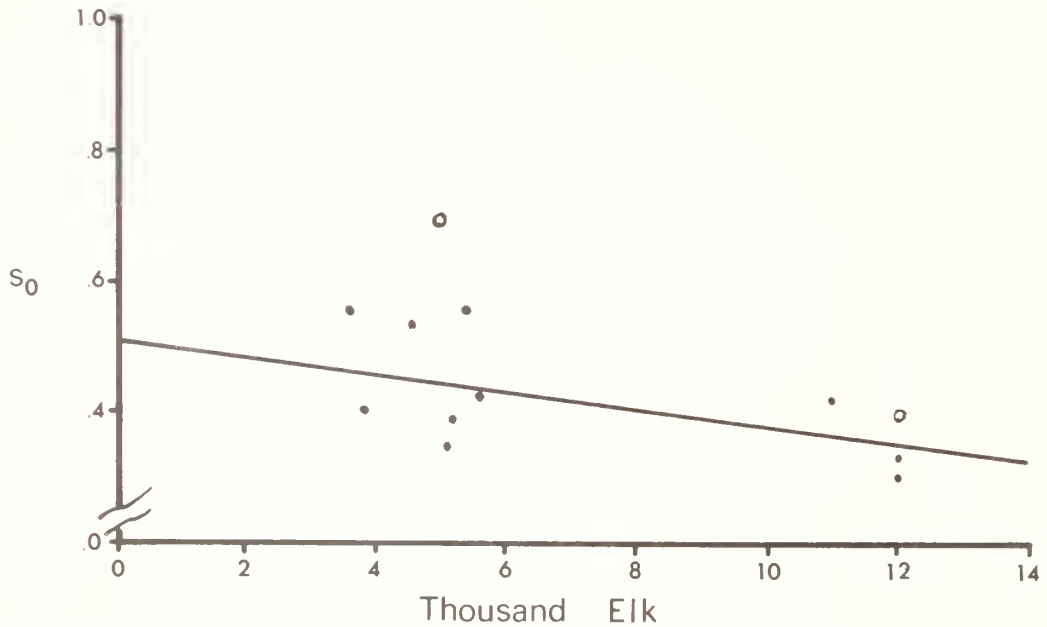



FIGURE 2. Estimated initial survival ($s_o$, from birth to the first winter) plotted against the estimated size of the herd from the corresponding previous winter for the northern Yellowstone elk. Solid points are from Barmore (in prep.) and open circles from Houston (1974). See text for explanation of line.

A linear function (shown as a line in Figure 3) was fitted to two points:

1) the midpoint between the mean of Barmore's data (solid points) and the mean (open circle) given by Houston, both for low population levels (less than 6,000 elk), and
2) Houston's estimated mean survival at high population levels (greater than 10,000 elk).

Houston's estimate for high population levels was lower than the mean of Barmore's data points by a survival value of about 0.1 and was used to give some weight to the two excluded data points for populations of 7,000 and 9,000 elk. The equation fitted to the two points described above is:

$$s_1 = 0.897 - 0.022\ P$$

where:

$s_1$ = survival between the first and second winter
P = estimated winter herd size in thousands

D. Birth rates of yearlings

Data concerning pregnancy in the northern Yellowstone elk are summarized by both Houston (1974) and Barmore (in prep.). They conclude that mean pregnancy rates for yearlings were significantly higher at low than at high population levels but varied greatly between years at both levels. Yearling pregnancy rates from Barmore (in prep.) are plotted against the corresponding population size in Figure 4. The following equation (shown as a line in Figure 4) was derived by solving for the parameters necessary to fit the weighted mean pregnancy rate for low population levels (less than 6,000 elk) and that for high population levels (greater than 10,000 elk):

$$b_1 = 0.254\ e^{-0.144\ P}$$

where:

$b_1$ = yearling pregnancy rate (portion of yearlings pregnant)
P = estimated winter herd size in thousands

A curvilinear equation was used to represent this relationship in order to avoid negative pregnancy rates at high population levels. This also provides a realistic maximum mean pregnancy rate at very low population levels since it corresponds well with values reported in the literature (see Follis 1972, for example). We assume, as did Houston (1974) and Barmore (in prep.) based on data in Greer (1966), that birth rates are equivalent to pregnancy rates. Thus, in this case, the dependent variable in the equation above ($b_1$) may also be defined as the yearling birth rate for our purposes.

E. Birth rates for two year olds

Pregnancy rates from the same sources discussed above were used to establish the relationship between pregnancy rates for two-year-olds and winter herd size shown in Figure 5. The following quadratic equation (shown as a line in Figure 5) was fitted to the weighted mean pregnancy rates at the low and high population levels (as defined in the previous section) in order to avoid a rate greater than 1.0, since few if any multiple births occur at any population level (Greer 1966):

$$b_2 = 1.0 - 0.00912\ P - 0.00019\ P^2$$

where:

$b_2$ = estimated pregnancy rate for two year olds (also birth rate)
P = winter herd size in thousands

Note that, here again, pregnancy rates and birth rates are assumed to be the same.

F. Birth rates for elk older than two years

Age specific pregnancy rates for elk more than two years old are meager for high population levels and can only be expressed for broad age classes at low population levels. Available data summarized in Barmore (in prep.) suggest mean pregnancy rates (range in parenthesis) of 97 percent (92-100) for 3-7 year olds, 85 percent (81-97) for females older than seven years, and 33 percent (0-37) for females older than fifteen

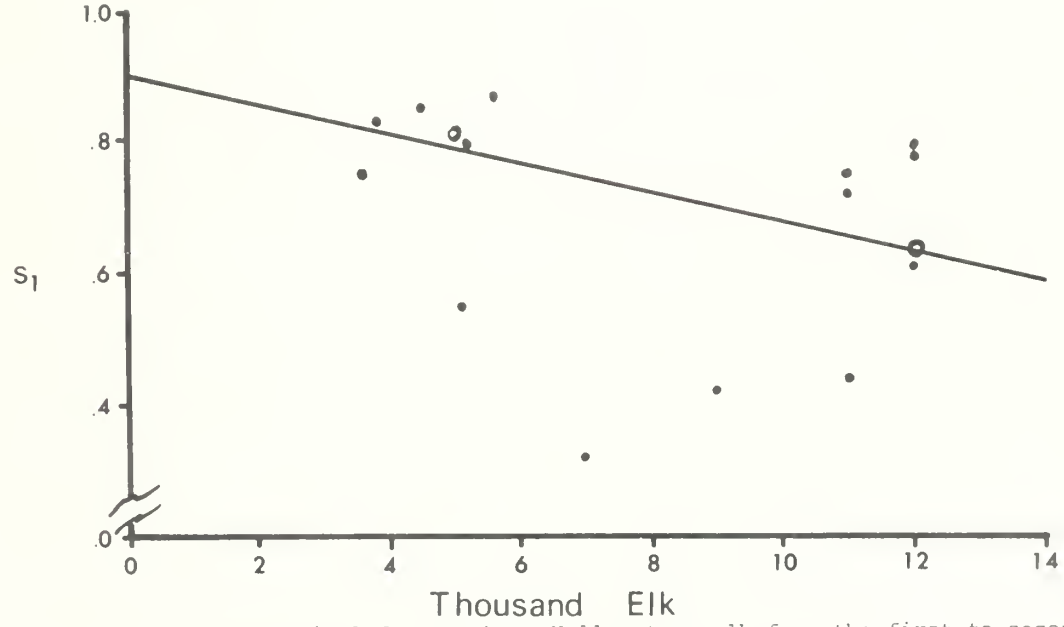



FIGURE 3. Estimated survival for northern Yellowstone elk from the first to second winter ($s_1$) plotted against population size as in Figure 2. Solid points are from Barmore (in prep.) and open circles from Houston (1974). See text for explanation of line.

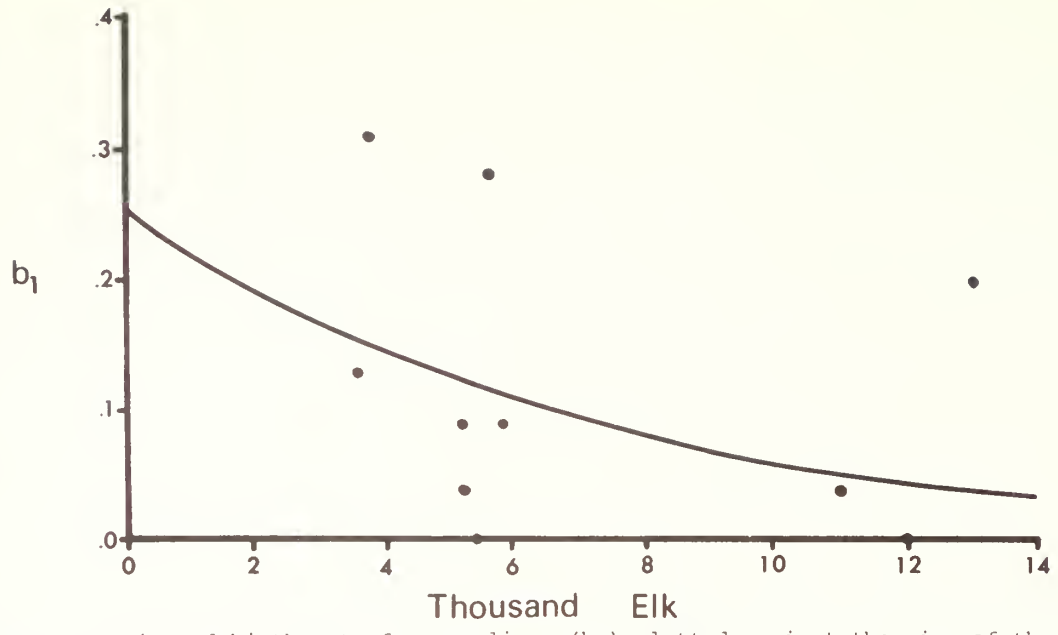



FIGURE 4. Estimated birth rate for yearlings ($b_1$) plotted against the size of the northern Yellowstone elk herd as in Figure 2. Data are from Barmore (in prep.). See text for explanation of line.

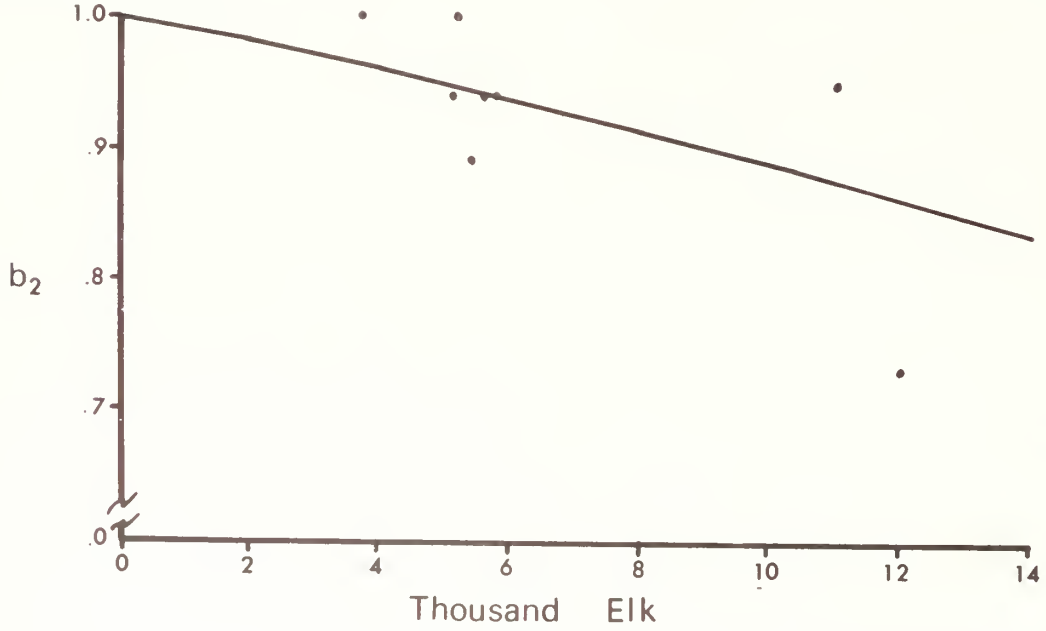



FIGURE 5. Estimated birth rate for two-year-olds ($b_2$) plotted against the size of the northern Yellowstone elk herd as in Figure 2. Data are from Barmore (in prep.). See text for explanation of line.

years. Houston (1974) found no significant differences among age classes from two to fifteen years but significantly lower rates for sixteen to twenty-one years of age at both low and moderately high population levels.

By assuming female longevity of 20 years (Murie 1951, Flook 1970) and considering the mean age structure expected from the survival data, the mean pregnancy rates of broad age classes were interpreted as the age specific birth rates ($b_i$) shown in Figure 6. Without data indicating otherwise, these were assumed to apply at all levels of the population on the basis that the older individuals may be less sensitive to environmental conditions than the younger age classes discussed above.

The general pattern of age specific birth rates, then, appeared to be one of:

1) low and highly variable birth rates for yearlings that tended to decrease with population size,
2) higher and less variable rates for two year olds that also tended to decrease with population size,
3) still higher rates for three to ten year olds that gradually decline with age, and
4) lower rates for older females that decrease more rapidly with increasing age to near zero at 20 years of age.

Rates for the oldest age classes may be unrealisti-

cally low; however the small percent of the population in these age classes both in reality and in simulations prevents any error from being a major problem.

3. Survival of females older than two years

Houston (1974) constructed several survivorship curves from data obtained in 1950-51, 1961-62, and 1962-67, but indicated the nature of the data was such that the curves were anything but a perfect representation of what was happening. Nevertheless, data for 1950-51 (Houston, pers. comm.) were used to construct a female survivorship ($s_i$) curve (Figure 7) which is considered to adequately represent the total set of conditions (including man) under which the herd existed and adequate for an intitial attempt to describe the internal dynamics of the population.

## THE MODEL

The relationships discussed above are sufficient to construct a variable projection matrix model of the northern Yellowstone elk herd. Construction, implementation, and analysis of this type of model are discussed in detail in Smith (1973), Fowler and Smith (1973), and Fowler and Smith (1972). Only details unique to the application of this type of model to the northern Yellowstone elk herd are discussed here.

The matrix representing this herd was constructed with each of the twenty elements of the top row as a product of an age specific birth rate ($b_i$) multiplied by the initial survival ($s_o$) all divided by two. Thus, the first element, corresponding to calves, contains a zero. The second element, corresponding to yearlings, contains the yearling birth rate ($b_1$, which varies with population size) multiplied by the initial survival ($s_o$) and divided by two. The third is similarly the birth rate of the two year olds ($b_2$, which varies as a function of population size) multiplied by the initial survival and divided by two. The fourth and remaining elements of the top row contain the constant and corresponding birth rates ($b_i$) as plotted in Figure 6 multiplied by the initial survival ($s_o$) and divided by two. Each element of the top row is divided by two to account for an even sex ratio at birth (Houston 1974 and Barmore in prep.). The subdiagonal was constructed with the yearling survival ($s_1$) as the first ( and variable) element. The survival values for the older females ($s_i$, Figure 7) are contained in the subsequent and corresponding subdiagonal elements.

Since initial survival ($s_o$), yearling survival ($s_1$), yearling birth rates ($b_1$), and birth rates of two year olds ($b_2$) are all functions of population size, the matrix is variable. It, as a model of the female portion of the northern Yellowstone elk herd, is a function of the estimated size of the winter herd. Application of the matrix to the females, divided into age classes of one year, projects an estimated female population for the following winter, assuming no emigration or immigration and levels of human predation (hunting and/or live trapping) typical of the time during which the data used in this study were collected.

## RESULTS

As outlined by Fowler and Smith (1973), a model such as that developed above, permits estimation of the mean carrying capacity for a species, its productivity as a function of population size, and the effects of additional mortality such as natural predation. Finally, assumptions made in constructing the model may be examined through simulation and analysis in an attempt to improve upon the model.

A. Carrying capacity

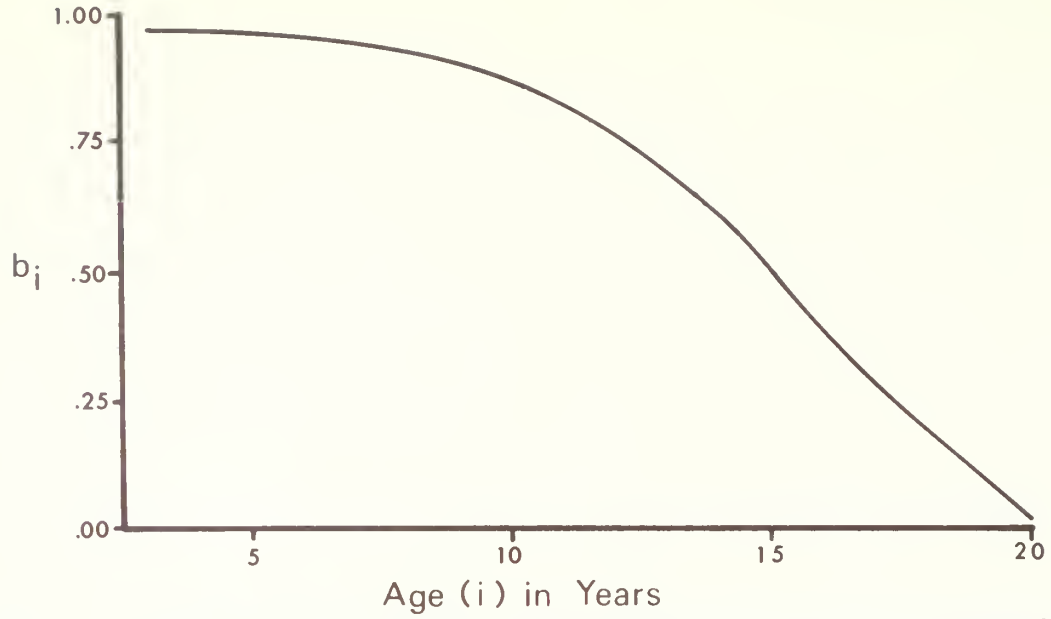
The natural log of the eigen value of a matrix such as described above is an estimate of the specific rate of growth (r) for the population represented at any particular size (Fowler and Smith 1973). Estimated rates of change observed under field conditions cannot be expected to conform exactly to those predicted by this model due to random variation in the system (weather, age structure etc.). Nevertheless, rates for the model should tend, *on the average*, to correspond with those observed in the field.

For any population with density dependent population dynamics, the population size where the average rate of increase is zero (eigen value equals one) is the estimated carrying capacity for the conditions existing when the data incorporated in the model were obtained. Figure 8 shows how the predicted rate of growth calculated from this model varies with population size. A rate of growth equivalent to zero occurs at about 11,000 elk using Barmore's estimate of initial survival ($s_o$). Using Houston's data for initial survival, the estimated carrying capacity is slightly over 12,000 elk and the maximum rate of growth is about 0.175 compared to about 0.1 for Barmore's data (see Figure 8). Considering the variability inherent in most of the data, the two estimates of carrying capacity differ relatively little. An empirical estimate of carrying capacity from examination of Figure 1 would probably fall in this range. Houston (1974) also estimated the carrying capacity at about these levels after considering the available information.

B. The possible effects of predation on calves

The role that predation may have played in the regulation of ungulate populations in North America in primeval times is unclear and controversial (Errington 1946, 1956, Cowan 1947, Hornocher 1970, Mech 1970, Murie 1944, Pimlott 1967, Pimlott et al. 1969, and others). Large predators such as wolves and mountain lions were nearly extirpated from the park by the 1920's (Murie 1940). This removal of predation is sometimes considered a primary factor allowing the northern Yellowstone elk herd to increase to (and perhaps, for a while, beyond) the carrying capacity of the winter range. However, the actual role of predation in regulating the northern Yellowstone elk herd under pristine conditions is unknown. Growing evidence suggests that predation alone was not a major factor (Barmore in prep.). An initial examination of this question in the context of the model was made by determining the magnitude of initial survival that would lead to zero population growth (eigen value of one) at various population levels using both Houston's and Barmore's data for initial survival ($s_o$). The results were transformed into numbers of calf mortalities based on the projected calf crop from the eigen vector (stable age distribution) determined for each case. The results (Figure 9) show the number of calves which, on the average, would have to be killed, in addition to other mortalities, to maintain zero growth.

Using Houston's data for initial survival, a maximum loss of about 1,200 calves per year to additional predation would strongly regulate the population. Using Barmore's data, removal of about 600 calves per year would reduce the population to about half of its estimated carrying capacity. Calves weigh about 16 kilograms (35 pounds) at birth (Murie 1951) and 113 kilograms (250 pounds) at 8-10 months (Murie 1951, Greer 1967). Assuming a mean weight of 68 kg (150 pounds),




FIFURE 6. Estimated age specific birth rates ($b_i$) plotted against the corresponding age class for the northern Yellowstone elk. (Adapted from Barmore in prep.) See text for explanation.

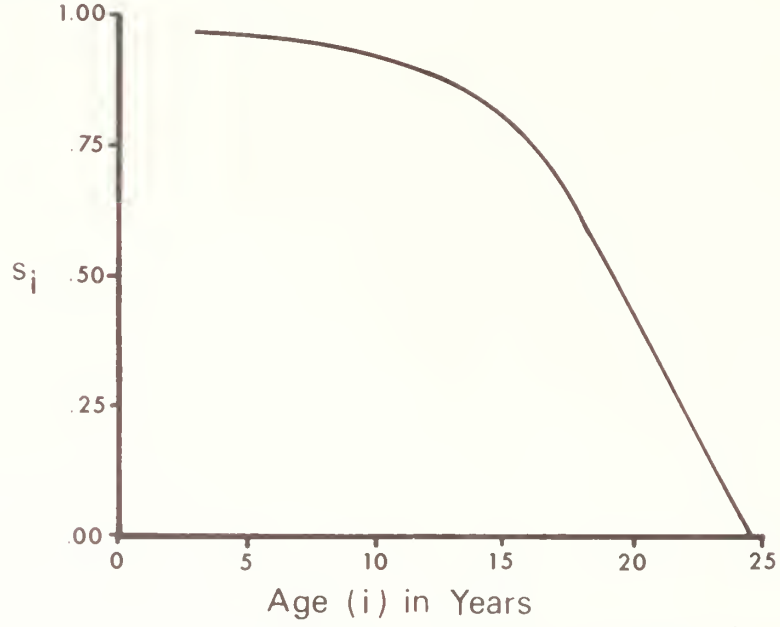



FIGURE 7. Estimated age specific survival ($s_i$) for female elk older than two years from the northern Yellowstone herd plotted against age (i). (From Houston 1974 and pers. comm.)

1,200 calves would weigh 81,600 kilograms (180,000 pounds). If seventy-five percent (61,200 kilograms or 135,000 pounds) is available for consumption by predators and if predation is spread evenly from birth to the age of 10 months, 6,120 kilograms (13,500 pounds) per month or about 200 kilograms (450 pounds) per day would have to be consumed to account for 1,200 calves. A wolf may consume about 4.5 kilograms (10 pounds) per day (Mech 1970). Assuming a consumption rate of only 2.25 kilograms (5 pounds) per day, about 90 wolves feeding only on elk would be required to remove 1,200 calves of up to 10 months of age.

Distributed over the range occupied by the elk in summer (about 4,650 $km^2$ or 1,800 $mi^2$, Houston 1974), this represents a density of about 52 $km^2$ per wolf (or 20 $mi^2$ per wolf), a density entirely within the observed ranges as reported by Mech (1970). Balancing the fact that wolves would prey on other than just calves against the low consumption purposely used above, then, it seems entirely conceivable that predation could influence the size of the northern Yellowstone elk herd. This is particularly true if only 600 calves need be removed to reduce the population to half its carrying capacity as suggested by the model using Barmore's data for initial survival. Note that both models represented by the relationships shown in Figure 9 predict a dome shaped yield curve for calves. At lower population levels fewer calves are produced while at higher levels other sources of mortality assume greater importance.

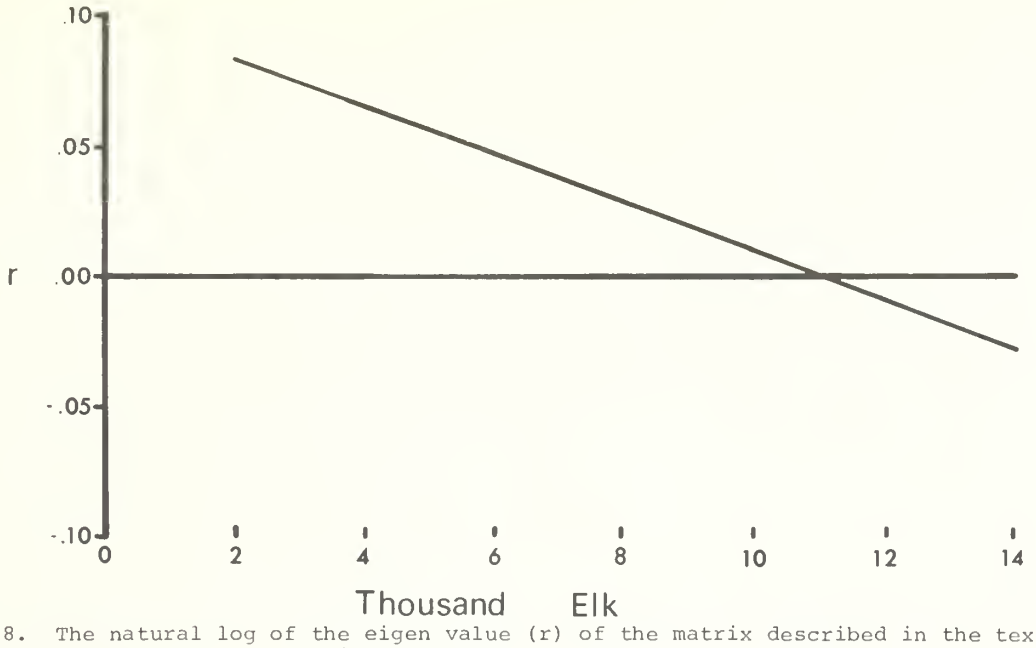



FIGURE 8. The natural log of the eigen value (r) of the matrix described in the text calculated at various levels of the population of northern Yellowstone elk using Barmore's (in prep.) data for initial survival.

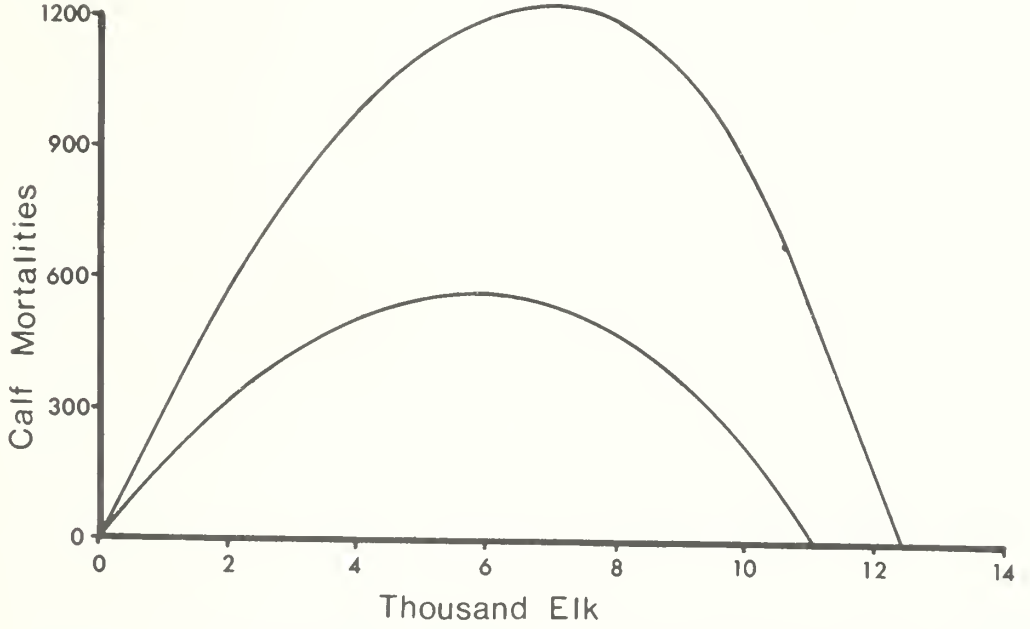



FIGURE 9. The number of calves which, on the average, would have to be removed annually from the northern Yellowstone elk herd to maintain winter herds of the size indicated on the abcissa as predicted by the model described in the text. The top line is from the model using Houston's (1974) data for initial survival and the lower is from Barmore's (in prep.) data. See text for interpretation.

## DISCUSSION

Conceptually, the most important factor to keep in mind is that the modeling efforts reported here reflect the conditions surrounding the northern Yellowstone elk herd since about 1935. Long term (longer than the period encompassed by this study) changes in the environment are not included in this model. For example, the model would not apply if a major shift occurred in the composition of the vegetation. Predators, especially wolves and cougars, are not present in numbers comparable to those in primeval times. If they were reintroduced, or their populations were to increase, the model would not apply. Conceptually, however, the model could be extended to include these and other factors.

The relationships depicted in Figures 8 and 9, then, reflect dynamic properties of the elk population characteristic of the period from 1935 to 1976. This includes hunting and the present levels of predation. Without harvest by hunters the estimated carrying capacity of the winter range (combined with weather, present natural predation, etc.) would increase. Also without harvest by man interpretations of the impact of predation change. The synergistic effect of predation and hunting may

reduce the population to levels considerably below those which would result from either factor acting in the absence of the other. We do not mean to imply, however, that other environmental factors (for example, weather and food availability) do not contribute to population regulation. In our view, regulation, by definition, reflects the interaction of most, or all, environmental factors.

Future work will concentrate on improvement of the model and examination of other questions about the dynamics of the elk population including the stochastic components of its environment. Initial work suggests that separate estimates of man induced mortality and natural mortality may provide insights into alternative management strategies. Simulation with an improved model may help evaluate the effects of immigration and emigration, which preliminary studies indicate may be important. Most importantly, the work reported here suggests that this overall approach can contribute to our understanding of this elk population.

## LITERATURE CITED


ALLEN, D. L. 1954. Our wildlife legacy. Funk and Wagnalls Co., New York. 422 pp.

BARMORE, W. J. (In Prep.). Population characteristics, distribution, and habitat relationships of six ungulate species in northern Yellowstone National Park. Ph.D. Dissertation, Utah State University.

CAHALANE, V. H. 1941. Wildlife surpluses in the national parks. Trans. North American Wildl. Conf. 6:355-361.

CAHALANE, V. H. 1943. Elk management and herd regulation - Yellowstone National Park. Trans. North American Wildl. Conf. 8:95-101.

COWAN, J. MCT. 1947. The timber wolf in the Rocky Mountain national parks of Canada. Canadian J. Res. 25 (section D):139-174.

CRAIGHEAD, J. J., G. ATWELL, and B. W. O'GARA. 1972. Elk migrations in and near Yellowstone National Park. Wildl. Mono. No. 29. 48 p.

ERRINGTON, P. L. 1946. Predation and vertebrate populations. Quart. Rev. Biol. 21:147-177, 221-245.

ERRINGTON, P. L. 1956. Factors limiting higher vertebrate populations. Science 124:304-307.

FLOOK, D. R. 1970. A study of sex differential in the survival of wapiti. Canadian Wildl. Service Rept. Series No. 11. 71 pp.

FOLLIS, T. B. 1972. Reproduction and hematology of the Cache elk herd. Utah State Div. of Wildl. Res. Publication No. 72-8. 133 p.

FOWLER, C. W. and T. SMITH. 1972. A matrix method for determining stable densities and age distributions and its application to African elephant populations. Quantitative Science Paper No. 31. Center for Quantitative Science in Forestry Fisheries and Wildlife, Univ. of Wash., Seattle.

FOWLER, C. W. and T. SMITH. 1973. Characterizing stable populations: An application to the African elephant. J. Wildl. Manage. 37:513-523.

GRAVES, H. S. and E. W. NELSON. 1919. Our national elk herds: A program for conserving the elk on national forests about the Yellowstone National Park. U.S. Dept. Agric. Circ. 51. 34 pp.

GREER, K. R. 1967. Special collections - Yellowstone elk study. Montana Fish and Game Dept. Job Compl. Rept. W-83-R-10, Job B-1. 15 pp.

GREER, K. L. 1966. Fertility rates of the northern Yellowstone elk populations. Ann. Conf. W. Assoc. State Fish and Game Comm., No. 46. 10 pp.

GRIMM, R. L. 1939. Northern Yellowstone winter range studies. J. Wildl. Manage. 3:295-306.

HORNOCKER, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive area. Wildl. Mon. No. 21. 31 pp.

HOUSTON, D. B. 1974. The northern Yellowstone elk: Parts I and II, History and demography. Report, U.S. Nat. Park Serv., Yellowstone National Park, Wyoming. 185 pp.

HOUSTON, D. B. 1976. The northern Yellowstone elk: Parts III and IV. Vegetation and habitat relations. U. S. Nat'l. Park Serv., Yellowstone National Park, Wyoming. 444 pp.

HOUSTON, D. B. Pers. Comm. Memo to the senior author dated 5/18/76.

KITTAMS, W. H. 1959. Future of the Yellowstone wapiti. Naturalist 10:30-39.

LEOPOLD, A. S., S. A. CAINE, C. M. COTTAM, I. N. GRABRIELSON, and T. L. KIMBALL. 1963. Wildlife management in the national parks. North Amer. Wildl. Conf. 24:28-45.

MECH, L. D. 1970. The Wolf: The ecology and behavior of an endangered species. The Natural History Press, New York. 385 pp.

MURIE, A. 1940 Ecology of the coyote in the Yellowstone. U. S. Nat'l. Park Serv. Fauna Series No. 4. 206 pp.

MURIE, A. 1944. The wolves of Mount McKinley. U.S. Nat'l. Park Serv., Fauna Series No. 5. 238 pp.

MURIE, O. J. 1951. The elk of North America. Stakpole Co., Harrisburg, Pa. 376 pp.

OLSEN, ARNOLD. 1962. Yellowstone's great elk slaughter. Sports Afield 148:40-41, 87-88.

OLSEN, ARNOLD. 1968. The elk slaughter, a sensible sequel. Sports Afield, July, 160:33.

PENGELLY, W. L. 1963. Thunder on the Yellowstone. Naturalist 14:18-25.

PIMLOTT, D. H. 1967. Wolf predation and ungulate populations. Am. Zool. 7:267-278.

PIMLOTT, D. H., J. A. SHANNON, and G. B. KOLENSKY. 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ontario Dept. of Lands and Forests. 92 pp.

RUSH, W. M. 1932. Northern Yellowstone elk study. Montana Fish and Game Comm. 131 pp.

SMITH, T. D. 1973. Variable population projection matrix models: Theory and application to harvesting strategy. Ph.D. Dissertation, U. of Wash. 120 pp.

TRUEBLOOD, T. 1963. Too many elk. Field and Stream, July:36-39, 72-74.

U. S. SENATE. 1967. Hearings before a subcommittee of the committee on appropriations, United States Senate, Ninetieth Congress, First Session, on control of elk population, Yellowstone National Park. U.S. Government Printing Office, Washington, D. C. 142 pp.

WAGNER, F. H. 1969. Ecosystem concepts in fish and game management. pages 259-307. *In:* G. M. Van Dyne (ed.), The ecosystem concept in natural resource management. Academic Press, New York and London.

WRIGHT, G. M. and B. H. THOMPSON. 1935. Wildlife management in the national parks. U.S. National Park Service, Fauna Series No. 2. 142 pp.

# DESERT BIGHORN SHEEP, LIVESTOCK, AND LANDFORMS IN CANYONLANDS NATIONAL PARK

Clay Dean[1]

During the last 100 years, bighorn sheep (*Ovis canadensis*) have undergone a great decline throughout North America. The desert bighorn (*O.c. nelsoni*) has been particularly susceptible to the western movement of white man and his domestic livestock (Beuchner 1960). Canyonlands National Park, located in southeastern Utah, harbors one of the few remaining native desert bighorn populations. The National Park Service, and the Utah Cooperative Wildlife Research Unit funded this study to examine the distribution, abundance, movements, and human encroachment of the bighorn sheep in Canyonlands. The bighorn sheep-livestock interaction was examined closely.

Canyonlands National Park contains 1300 km$^2$ of rugged isolated canyon and mesas. The Park is divided into three districts by the Colorado and Green rivers. Rainfall averages 18-23 cm coming primarily in the forms of winter snows and late summer cloudbursts. The vegetation is typical of the lower and upper Sonoran Zones described by Merriam (1898).

## METHODS

During the first field session a general survey of the Park was conducted to determine vegetative communities, water sources, landforms, livestock use, mule deer distribution, and bighorn sheep distribution. A hypothesis was formulated depicting the role of landforms in the restriction of livestock grazing and the consequent preservation of bighorn sheep. To test this, canyons in the Island in the Sky District which harbors the majority of the bighorn in the Park, were classified into four types on the basis of their landforms. With the assistance of Walter Loope of Utah State University, vegetation and landform were mapped to determine the percent composition of at least two canyons for each type. These canyons were surveyed regularly to determine current bighorn sheep and mule deer distributions. Cattlemen were interviewed to determine the historical bighorn sheep range and extent of domestic livestock use.

## RESULTS

Canyon type I was characterized by vertical cliffs, steep slopes, and a broad level floor at the same level as the river providing unrestricted access (Figure 1). Although cattlemen reported seeing bighorn in these canyons frequently prior to the introduction of cattle and domestic sheep, no bighorn were observed in type I canyons during the study. However, deer were observed commonly in the canyons and on the adjacent river bottoms. Livestock and deer were able to utilize most of the available forage due to the absence of physical barriers.

Canyon type II was characterized by vertical cliffs, steep slopes, a single broad level area, and a vertical jump in the wash resticting access to the river (Figure 2). Livestock have never grazed in type II canyons. Nineteen bighorn sheep sightings totaling 40 rams, 20 ewes, and 1 lamb were recorded in type II canyons. Deer were never observed in these canyons.

Canyon type III was characterized by vertical cliffs, benches, and a vertical jump in the wash restricting access to the river (Figure 3). Livestock have entered only one type III canyon, remaining for one season. They were restricted to the wash by cliffs and steep slopes. In type III canyons, 31 bighorn sightings totaling 37 rams, 37 ewes, and 13 lambs were recorded. Deer were observed only on the rims above type III canyons.

Canyon type IV was characterized by vertical cliffs, benches, and an unrestricted access to the river (Figure 4). There has been a limited but continued use of these canyons by cattle and domestic sheep. However, cliffs and steep slopes restricted livestock to the washes and to a limited portion of the adjacent slopes, leaving 80 percent of the canyon untouched by livestock. Seventeen bighorn sheep sightings totaling 10 rams. 25 ewes and 12 lambs were recorded in type IV canyons. Although deer were observed frequently in the washes or on the rims, only once were deer sighted on the benches where the majority of the bighorn sightings were recorded.

## DISCUSSION

Although the percent composition and cover of plant communities varied there were no discernible trends relating vegetation to bighorn sheep distribution. Rather it appears that the bighorn sheep distribution is dependent upon whether physical barriers prevented livestock and deer from using either the entire canyon or the majority of the canyon. This relationship can be effectively described by examining the bighorn sheep decline in the Park.

Prior to the 1930's bighorn sheep ranged throughout the Island in the Sky District. Cattlemen reported a decline in bighorn sightings in number and distribution after the introduction of cattle and domestic sheep and greatly reduced bighorn sheep distribution was very much in evidence during this study. The role of diseases introduced by livestock in reducing the bighorn sheep populations has been discussed by Smith (1954), Beuchner (1960), and Post (1962). The first two authors believed the scabies mite (*Psoroptes ovis*) to be the culprit. Post (1962) suggested that *Pateurellosis* precipitated by stress was the decimating factor.

However, there is a predisposing condition for either disease theory. This is a shifting energy regime for bighorn sheep in the face of introduced competitors. Desert ruminants are under severe energy limitations as they must consume large quantities of forage to meet their metabolic requirements. This must be balanced with the increased energetic costs of procuring energy in the sparsely vegetated desert. The introduction of more than 2000 ruminants definitely would result in increased competition for the limited supply of energy. Additionally, when disturbed by man and other animals, bighorn sheep ceased grazing, assumed an alarm posture and retreated to escape terrain. This reaction would serve to create an energy deficit if re-

[1]Route 1, Box 41B, Navasota, Texas 77868.

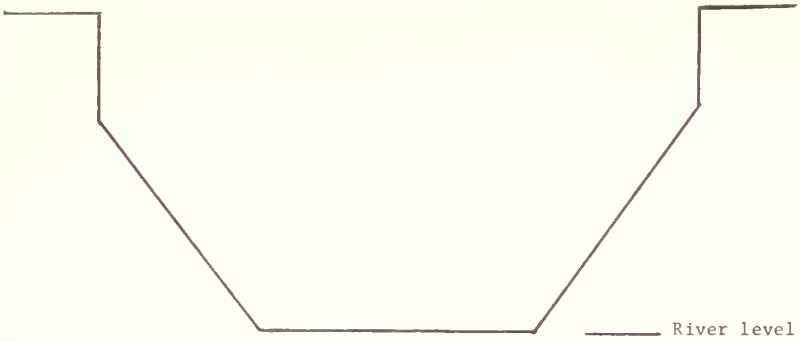



FIGURE 1. Canyon type I is characterized by vertical cliffs, steep slopes, and a braod floor at the same elevation as the river.

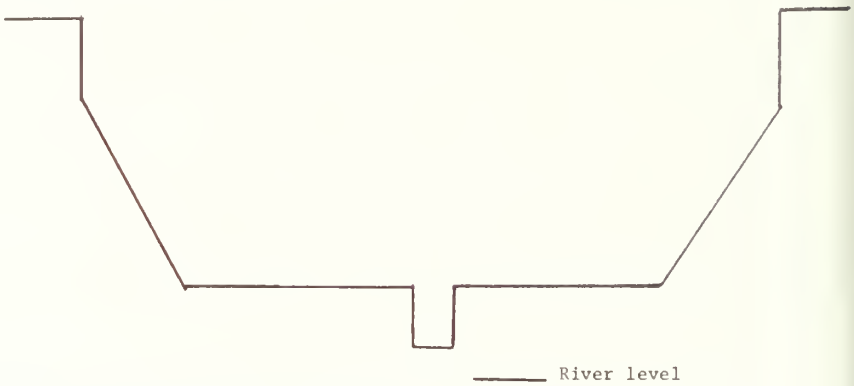



FIGURE 2. Canyon type II is characterized by vertical cliffs, steep slopes, a broad level area, and restricted access to the river.

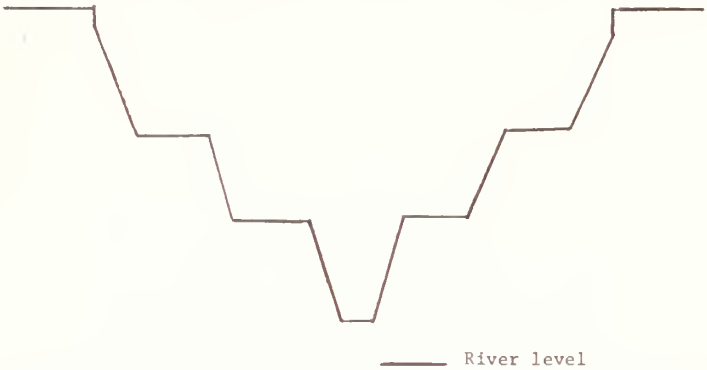



FIGURE 3. Canyon type III is characterized by vertical cliffs, benches, and restricted access to the river.

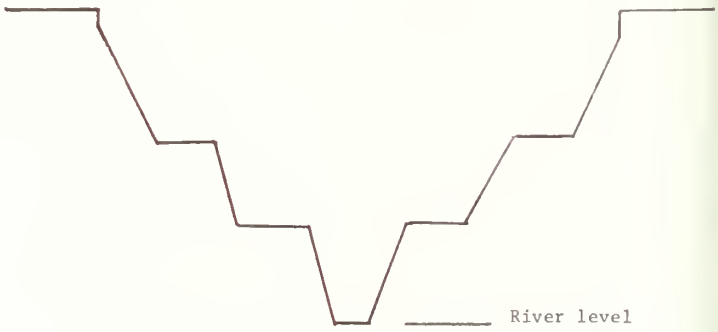



FIGURE 4. Canyon type IV is characterized by vertical cliffs, benches, and an unrestricted access to the river.

eated too many times during the foraging period. onsequently, bighorn were forced to choose between ompeting directly with livestock where energy out- ut would be increased or to retreat permanently o escape terrain where there is less available nergy, but fewer disturbances by man, livestock, nd deer. This was accomplished by utilizing type I or type III canyons where total isolation was btained or type IV canyons where physical barriers nabled bighorn sheep to isolate themselves and till utilize over 80 percent of the canyon. What ffect does this spacial separation within a canyon ave on bighorn numbers? In type III canyons with otal isolation, there were 4.6 bighorn sheep ighted per $km^2$. In type IV canyons which are dentical to type III canyons except for the unre- tricted access, there were 1.9 bighorn sheep ighted per $km^2$.

Do bighorn sheep prefer rocky areas which are ore energetically costly to inhabit? In isolated anyons, bighorn were most frequently seen on evel areas and in the washes.

One final piece of evidence for the bighorn heep energy crisis concerns the differences in ighorn ram and ewe distributions. Whereas big- orn rams ranged throughout the entire elevation f the Park, ewes remained in the isolated lower anyons. This could be explained by the gravid or lactating ewe having its highest energy requirements during the late spring when livestock use and human use were heaviest.

Finally, how appropriate is this paper since livestock grazing has been terminated in much of Canyonlands National Park? Bighorn sheep declined as a result of the introduction of livestock. The presence of physical barriers such as cliffs and steep slopes have isolated only enough terrain to support a reduced number of bighorn sheep. This study indicated there were tentative similarities in the bighorn sheep-livestock interaction and the bighorn sheep-tourist interaction. With the tourist's ability to penetrate physical barriers which were prohibitive to livestock, how much isolation will bighorn sheep be able to maintain?

LITERATURE CITED

BUECHNER, H. K. 1960. The bighorn sheep in the United States, its past present, and future. Wildl. Mono. No. 4:174.

MERRIAM, C. H. 1898. Life zones and crop zones of the United States. Div. of Biol. Survey, USDA BULL. 10:79.

POST, G. 1962. Pasteurellosis of Rocky Mountain bighorn sheep *(Ovis canadensis canadensis)*. Wildl. Diseases. 23:1-14.

SMITH, D. R. 1954. The bighorn sheep in Idaho, its status, life history, and management. Idaho Fish and Game. 154.

# MOVEMENTS OF DESERT BIGHORN SHEEP IN THE RIVER MOUNTAINS OF LAKE MEAD NATIONAL RECREATION AREA

David M. Leslie, Jr.[1] and Charles L. Douglas[2]

## INTRODUCTION

The desert bighorn (*Ovis canadensis nelsoni*) has received considerable attention in the past with specific reference to management plans reflecting the species' needs. A great deal of data exist for various populations based to a large extent on 1) waterhole counts, conducted during the hot summer months when bighorn are forced to congregate around permanent water, and 2) random observations, the majority of which are from summer months when bighorn are more confined in their movements and more readily observed. Numerous publications exist on the species, but very little specific information on their movements has been documented.

The present study is jointly funded by the National Park Service and the Nevada Department of Fish and Game, and coordinated by Dr. Charles Douglas, leader of the Cooperative National Park Resource Studies Unit at the University of Nevada, Las Vegas. The study was initiated with a trapping and marking project in the River Mountains during the summer of 1973. The overall objectives were to gain insight into the life history of the herd, examining such parameters as population densities, sex ratios, range utilization, and movement patterns.

## DESCRIPTION OF THE STUDY AREA

The River Mountains are a relatively small range located in Clark County, Nevada, roughly 15 miles southeast of Las Vegas (Figure 1). Of the total land mass of approximately 39 square miles, half of the range lies within the Lake Mead National Recreation Area; the remainder is under the jurisdiction of the Las Vegas District of the Bureau of Land Management.

The topography is diverse, ranging from low, rolling hills to extremely rugged terrain, which is comprised mainly of steep slopes and sheer canyons, covered with weathered and eroded talus. Such topography provides excellent escape cover for bighorn (Figure 2). Shallow caves and shaded overhangs are found throughout the River Mountains and are heavily used by bighorn, particularly during the hot summer months.

Certain areas of the range could better be described as low, rolling country, and although it may be rough in isolated areas, is mainly comprised of alluvial fans and washes, within and surrounding the range.

Elevation varies from 1260 feet at Boulder Beach on the eastern side to 3789 feet. The entire range lies within the creosote bush community defined by Bradley and Deacon (1965). Although such communities most often occur along the valley floor and on gentle slopes, the terrain near the Colorado River is notably rougher (Bradley and Deacon, 1965). This would include the River Mountains. No elevational change in floral communities is evident; however, several species of plants occurring in the washes are largely absent on the surrounding ridges (Bradley and Deacon, 1965).

Currently there are two permanent water sources, one at the Park Service horse corral and the other at the Southern Nevada Water Project, Pump #2. Both are located on the eastern periphery of the range, roughly 1.75 miles apart. Numerous rock encatchments or natural tanks are found throughout the River Mountains which provide temporary water sources after rainfall. A seasonal artificial water source is available to bighorn during the summer, located 1.25 miles south of the horse corral. However, it is very rarely used for it is located several hundred yards from escape cover and is obstructed by powerlines. Only a single set of tracks was noted at this site during the last year.

The River Mountains have received considerable impact since the construction of Hoover Dam. Powerlines from the dam cross the range at a number of points, mostly in the south, and adjacent roads afford accessibility into the area. The range is completely surrounded by roads, heavily used by park visitors. However, human use is primarily concentrated around the Visitor Center, and the Boulder Beach and Las Vegas Wash areas.

## BACKGROUND

Water has long been noted as a key limiting factor in most desert environs. Prior to the construction of Hoover Dam in the early 1930's, desert bighorn probably frequented the River Mountains only after rainfall and when forage conditions were optimal, for no permanent water sources were present. They no doubt remained at lower elevations along the Colorado River, where there was no problem of water. After the dam was completed and waters of the river began filling the Boulder Basin between 1935-1938, bighorn were forced to move west into the River Mountains, or south along the Eldorado Mountains. Early sightings from the late 1930's and 1940's indicate that bighorn from the Rivers watered in Lake Mead at Hemenway Wash, moving across low, flat country of distances up to 1.5 miles. At this point, interchange between adjacent populations on the north end of the Eldorados was undoubtedly common.

In 1935, the National Park Service and Bureau of Reclamation formed the Boulder Dam Recreation Area. The name was officially changed to Lake Mead National Recreation Area in 1964. The recreation area is one of the largest in the National Park Service system.

The construction of sewage lagoons or leach fields in the early 1940's to accomodate Park Service housing provided the first permanent watering site other than the lake for bighorn of the River Mountains. It consisted of a single settling pond; a second pond was dug in 1973. As visitor use in the park increased and more powerlines from the dam crossed the south end of the range, sightings of bighorn moving across Hemenway Wash to the lake decreased. Random observations indicated an increased dependence by the sheep on the leach fields in the 1950's and 1960's. Observations at the lake and on the highways did

[1]University of Nevada, Las Vegas 89121.

[2]NPS/University of Nevada Las Vegas Cooperative Resources Studies Unit, Las Vegas 90121.

continue; however, the trend has steadily decreased. Over the last few years, not a single observation of sheep moving from the Rivers has been documented.

The location of the leach fields provided a far more suitable setting at which to water. It is located immediately adjacent to the most rugged expanse of the range and affords ample escape cover in the form of steep, talus covered slopes, a number of means of approach, and an unobstructed view of the surrounding area. All of these points must be of major consideration in spring and guzzler development for desert bighorn. The sheep, by nature, will often stand motionless for considerable amounts of time, surveying the area before approaching the water.

In the early 1960's, Alan Denniston, under the auspices of the Park Service, conducted research on the herd. His results were based primarily on waterhole counts conducted at the leach fields during the summer months and included a basic inventory of sheep habitat within the River Mountains. Population estimations were calculated from these counts (assuming that a given percentage of the population watered in a given number of days), and were based to a great degree on recognition of individual bighorn by predominant physical characteristics. It was concluded that 37 bighorn inhabited the River Mountains with the possibility that as many as 60 animals frequented the range (Denniston, 1965).

In 1969, the Nevada Department of Fish and Game, under cooperative agreement with the National Park Service, trapped and removed ten bighorn from the herd at the leach fields. These animals were transported to the 600 acre Dutch Creek enclosure at Hawthorne, Nevada and were to serve as a breeding population for future transplants throughout the state (McQuivey, 1975). At this point, the Nevada Department of Fish and Game estimated a population of 80 bighorn in the River Mountains. Trapping at this location warranted the fencing of the settling pond to force bighorn to approach the water through a six drop-panel gate trap. In 1971, a trough was provided near the fenced pond, filled by pumping runoff from the Park Service housing. The second settling pond was built in 1973 and fenced immediately.

Trapping again resumed during the summer of 1973 at the leach fields. Trap structure was modified to enclose the water trough. Twenty-two individual animals were handled. Ten of these were sent to Zion National Park to serve as a breeding population for re-introduction on historical ranges in southern Utah. The remaining 12 animals were marked and released back into the River Mountain herd.

In 1971, the construction of a multi-phased pumping facility, referred to as the Southern Nevada Water Project, Purp #2(SNWP), located 1.5 miles northwest of the leach fields, provided bighorn with another permanent watering site. It was finished by 1973 and a good percent of the population began watering at it. Blow-off from the main pumps was channeled to a wash a couple of hundred yards from the station. Although extremely close to the pumps themselves, this site provided the three elements described above: escape cover, multiple approach, and an unobstructed view of the watering area.

Trapping continued at SNWP during the summer of 1974 and 1975, during which time 23 and 61 bighorn, respectively, were handled. Eight of the animals trapped in 1975 were transplanted to Stonewall Mountain in Nye County, Nevada by the Department of Fish and Game. The remainder were marked and released.

During the summer of 1975, a third water source was provided at the National Park Service horse corral, located just south of the leach fields. This consists of run-off from a swamp cooler and is available year round. Sheep began to use this source within a week, and water to the trough at the leach fields was left off.

Thus, since 1973, eighty-two bighorn were marked and released, with an overall composition of 27 ewes, 15 lambs (10 males and 5 females), and 40 rams. The rams included the following age breakdown in 1975: 14 yearlings, 14 two year olds, 5 three year olds, and 1 seven year old.

## MATERIALS AND METHODS

My field work began July 1, 1975. The primary objectives were to determine home range and movement patterns of the desert bighorn of the River Mountains.

Trapping operations were conducted on the herd during the summers of 1969, 1973, 1974 and 1975. Throughout this time, with several modifications on the trap structure, the waterhole method for trapping desert bighorn was greatly perfected. A detailed description of trap structure is given by Cooper and McLean (1974). Basically, the trap was a netted structure supported by piping and stakes from the outside. Drop-gate panels were triggered electrically and simultaneously. A trap of this nature could be easily modified to suit a given location. The flexible netting insured maximum safety against injury. Only two mortalities have occurred with over 130 animals handled in Nevada, and these were not the result of trap structure. Trapping on the Rivers was never conducted for more than two consecutive days.

Techniques for marking desert bighorn also developed throughout the project. The most successful method for marking adult bighorn was color-coded 3 1/2" x 3 1/2" metal discs attached to leather collars (Figure 3). The disc hangs parallel to the animal's body. Scotch Lite tape has had the greatest longevity of any coloring method. It is felt that the natural oils from the bighorn's pelage prevents the leather from drying and cracking in the arid desert conditions. Of the four animals marked in this fashion in 1973, two have retained their collars. The others could represent natural mortalities, although this has not been documented.

Color-coded T-lock ear tags were used in 1975 to mark lambs. Although they cannot be seen from as great a distance, their longevity appears to be comparable to that of the collars. Silver ear tags, bearing an identification number, also were used on all the animals.

In 1973, five bighorn (2 ewes/3 rams, aged 1-4-5) were collared with solar cell transmitters, supplied by Electronics Unlimited, Sacramento, California. A twelve channel receiver was supplied by A.R. Johnson Electronics, Moscow, Idaho. Unfortunately, follw-up was extremely limited by technical difficulties (Cooper and McLean, 1974).



FIGURE 1. Aerial view of the northern part of the River Mountains toward Las Vegas Valley.



FIGURE 2. Typical habitat of the River Mountains, which provide excellent escape cover for bighorn. Note radio collar on 4-year-old ram to the right.



FIGURE 3. Color-coded 3½ X 3½ metal discs attached to leather collars have provided the best marking technique of desert bighorn.

In 1975, ten bighorn (5 ewes/5 rams, aged 1-2-3-5-6) were equipped with radio telemetry collars supplied by Telonics, Inc., Tempe, Arizona. The transmitter, lithium battery pack, and antenna were molded into a collar of urelane. The transmitters operate on 159.360 MHz, and the battery has life expectancy of 18-24 months. A ten-channel receiver and two types of antenna have been used for follow-up. The equipment was designed to have a range of 10-15 miles; however, the topography, for the most part, determined the range.

In documenting bighorn movements, primary attention has been directed toward these ten radioed animals. A great deal of supplemental information has been derived from the other marked individuals. Three techniques have been used for locating the radioed bighorn throughout the course of this study.

The first and most obvious method has been direct observation by means of radio tracking. It has been most desirable to observe the animals to accurately record the location and classify the group, noting any other marked bighorn. Most observations have been made using 7 x 35 binoculars and on occasion, a Bausch and Lomb 15 x 60 variable power spotting scope. The desert bighorn of the River Mountains are habituated to man's presence, and in many cases, they can be approached well within the range of 7 x 35 binoculars for observation without affecting their normal behavior.

The second method has been radio triangulation. Directional fixes have been taken on radioed bighorn from two to three different locations, usually not less than half of a mile apart. The intersect of these lines, plotted on a topographical map using a compass, gave the location of the animal. This technique was tested by tracking the animal and was shown to be accurate to an eighth of a mile.

The final method has been aerial location using either the Park Service's Cessna 206 or the Nevada Fish and Game's Super Bell helicopter. Fixed-wing flights have been conducted on a bi-monthly basis between August 26, 1975 and June 8, 1976, and at irregular intervals thereafter. The sole purpose of these flights has been to record radio locations on the telemetried bighorn, and no attempt was made to directly observe the animals. Previous work from the Cessna 206 had shown that location and classification of bighorn groups were extremely difficult due to air speed. Each flight has lasted approximately 45 minutes, and on the average, 90% of the signals have been received. Initially, ground follow-up ensued immediately after the flights. It was documented that such a technique was accurate to the quarter-mile section.

A total of nine helicopter surveys has been conducted in the River Mountains by the Nevada Fish and Game between 1969 and 1976, in addition to a number of others using an EPA helicopter. The use of the helicopter in censusing desert bighorn populations has been reviewed by Jett (1969), Tsukamato 1971), Copper (1972 and 1974), and McQuivey (1975). At present, the River Mountain herd serves as an index to evaluate population estimations throughout the state, based on the percentage of marked animals observed during the surveys (Cooper and McLean, 1974; McQuivey, 1975). The surveys also have given excellent distributional information and observations of radioed and marked individuals.

## PRELIMINARY RESULTS AND DISCUSSION

The findings below are of a preliminary nature; final analysis of data collected to date has just begun.

Since 1973, a total of 1550 observations of individually marked bighorn has been collected, by means of fixed-wing aerial locations, helicopter surveys, waterhole counts, and random observations. Based on 82 marked bighorn, this would indicate an average of 19 sightings per animal; however, 11 animals were only observed several times shortly after being marked and never again. Seventy-three percent of these were lambs, which could represent mortalities.

Between July 1975 and October 1, 1976 a total of 458 observations has been collected for the ten radioed bighorn, or an average of 45.8 sightings per animal. A minimum of 16 sightings has been recorded for the 6-year-old ram, with a maximum of 78 for a radioed ewe. At least 2000 observations of marked and unmarked bighorn were collected between July 1, 1975 and June 30, 1976 in the River Mountains.

The Lincoln Index is being used to estimate population levels from data collected by means of 1) individual helicopter surveys, 2) waterhole counts, and 3) random observations. Naturally, the number of marked animals within the range is not constant, due to mortality, loss of tags (at least four bighorn have silver ear tags and no other markings), or migration out of the River Mountains (although not documented). Thus, careful attention has been directed toward documenting the number of marked animals within the range during a given survey or period of time. At present, at least 51 bighorn are marked within the range. Critical analysis of this information is currently being prepared. It is estimated, however, that approximately 200 bighorn inhabit the River Mountains, with a herd composition of about 90 rams per 100 ewes.

Movement of desert bighorn can be directly related to permanent water sources, rainfall, vegetation, and time of year. During the hot summer months, bighorn movements are confined to areas near permanent water sources. Thunder showers, which temporarily fill natural tanks, disperse the animals throughout the range.

Cooling temperatures in the fall are not the only prerequisite necessary to decrease water dependence. Wilson (1971) noted the importance of vegetation, particularly succulent species, and its influence on bighorn movements. Movement patterns of the River Mountain herd change in relation to temporary water sources and also to plant phenology.

Spring showers and subsequent plant growth provide a source of temporary and "free water", and movements become less erratic and more confined. Under these conditions, sheep utilize ridges and more remote areas for foraging. Washes and lower country are extremely important to bighorn, particularly when summer heat and/or lack of rainfall have dried the less resilient plant species found among the ridges, Under such circumstances, bighorn are largely observed foraging in washes. It is important to note, however, that such locations are never far from adequate escape cover.

The River Mountains received little rainfall throughout the fall and early winter, 1975-1976. Dry conditions persisted until February 5. Numerous bighorn were observed at permanent water sources, despite cooler temperatures. In most cases, movements of ewes, lambs, and young rams were limited to these areas. Thus it appears that if rainfall and subsequent plant growth is marginal, bighorn remain dependent on permanent water sources; cooler temperatures allow frequency of visits to decrease somewhat, for less body water is lost to the environment.

During the breeding season, profound changes in the movements of rams have been noted. Prior to the rut in 1976, rams in excess of three years remained almost exclusively on the western part of the range in bachelor ram groups. Individual movement throughout the winter, spring, and early summer was very limited, and no doubt related to water conservation. Ewes and lambs remained on the eastern part of the range, while one- and two-year-old rams frequented both areas. As the breeding season approached in mid-summer, prime rams were observed more often among ewe groups. Information from telemetered and marked rams indicated extremely erratic movements during this period.

Ewes have moved freely within a defined home range, displaying no apparent seasonal preference to one area, except during the summer months, when movements are confined to areas around permanent water, and during lambing, which limits movement only temporarily. Lambs aged two to three weeks have been observed at permanent water sources and moving with groups of sheep. Newborn lambs have been observed throughout the River Mountains. No one particular area of "lambing ground" is evident. Fidelity of a given ewe to lamb in one particular area year after year has not been documented.

Home ranges of individual animals overlap greatly and include one or both of the permanent water sources. Total home range for rams is considerably larger than ewes. However, as mentioned above, during a good part of the year, rams remain sedentary, occupying only a small portion of their total range. From information generated thus far, it is evident that offspring adopt portions of their mother's home range, which is similar to Geist's (1971) observations on mountain sheep. Knowledge of such behavioral patterns is fundamental to proper management and future transplants.

## LITERATURE CITED


BRADLEY, W. GLEN, JAMES E. DEACON. 1965. The biotic communities of southern Nevada. Desert Research Institute, Univ. of Nevada, Preprint No. 9. 86 pp.

COOPER, J. R. 1972. Nevada's desert bighorn sheep status report 1971. Desert Bighorn Council Trans. 1972:66-78.

_____. 1974. Nevada's desert bighorn sheep - 1973 status report. Desert Bighorn Council Trans. 1974:31-37.

COOPER, J. R., D. J. MCLEAN. 1974. Cooperative management and research of the River Mountain herd, Nevada. Desert Bighorn Council Trans. 1974:53-60.

DENNISTON, ALAN. 1965. Status of Bighorn in the River Mountains of Lake Mead National Recreation Area. Desert Bighorn Council Trans. 1965:27-34.

GEIST, VALERIUS. 1971. Mountain sheep: A study in behavior and evolution. Univ. Chicago Press, Chicago. 383 pp.

JETT, JAMES E. 1969. Helicopter surveys of the desert bighorn in northwestern Arizona. Desert Bighorn Council Trans. 1969:48-54.

MCQUIVEY, ROBERT P. 1975. Bighorn research in Nevada. Desert Bighorn Council Trans. 1975: 15-18.

_____. 1975. Bighorn reintroduction efforts in Nevada. Desert Bighorn Council Trans. 1975:39-40.

TSUKAMATO, G. K. 1971. Nevada's desert bighorn sheep activities. Desert Bighorn Council Trans. 1971:12-17.

WILSON, LANNY O. 1971. The effect of free water on desert bighorn home range. Desert Bighorn Council Trans. 1971:82-89.

# EWE-LAMB VOCALIZATION AND RECOGNITION IN CAPTIVE DESERT BIGHORNS AT ZION NATIONAL PARK, UTAH

Henry E. McCutchen[1]

## INTRODUCTION

In 1973 the National Park Service, in coopera-
on with the Utah State Division of Wildlife Re-
urces and the Nevada Department of Fish and Game,
leased 12 desert bighorn sheep (*Ovis canadensis
lsoni)* from Nevada into an enclosure in Zion
tional Park, Utah. The purpose of the project
to propagate the bighorns until the population
large enough to release into the wild. The
story of the project has been discussed in further
tail by McCutchen (1975). Support of the project
Park Superintendent Robert C. Heyder and the
on Natural History Association is acknowledged.

In August 1974, a limited behavioral study
s initiated on the bighorns to obtain information
at could be applied to the management of the sub-
ecies. One interesting component of behavior
at was noted was the loud seasonal vocalizations
the ewes and lambs. An analysis of these vocali-
tions, their association with other behavioral
tterns and habitat use and observations related
recognition between the ewes and their neonates
e the subject of this paper.

### *Description of the Area*

The bighorn enclosure in Zion National Park
nsists of a 32 hectare fenced area about 900
ters long and 300 meters wide. The north, west
d south sides are fenced. The fence connects to
sheer sandstone cliff about 30 meters in height
ich forms the east side of the enclosure.

The eastern one-third of the enclosure below
e cliff consists of a rugged talus slope contain-
g a plant association of pinyon-juniper (*Pinus
nophyla* and *Juniperus utahensis)* with a sparse
derstory of shrubs and grasses. The remaining
o-thirds of the enclosure is a fairly level flood
ain containing cheatgrass (*Bromus tectorum)* and
few other herbaceous species.

Following the lambing season of 1975, there
re 19 bighorns within the enclosure. These
nsisted of 4 rams, 8 ewes and 7 lambs.

## MATERIALS AND METHODS

The period of observation selected for this
udy was from August 1974 to September 1975.
wn to dusk observation periods were conducted
ch month on an irregular basis. Additional
servations were made whenever time permitted.
casional short periods of nocturnal observations
re made. Observations were made from a parked
hicle on a service road on the west side of the
closure. The vehicle made an excellent blind and
id not disturb the bighorns because they had be-
me conditioned to it. The distance between the
ighorns and the observer was generally within the
nge of 100 to 500 meters. A pair of 7 X 50
inoculars and a 15-60x spotting scope were used
make the observations. All of the bighorns
cept the lambs were individually identifiable
d the birth dates of the lambs were known.

[1]National Park Service, Zion National Park,
ringdale, Utah 84767.

## RESULTS AND DISCUSSION

### *Seasonal and Diurnal Activity*

Even though their movements were restricted, the bighorns in the Zion enclosure had established diurnal and seasonal activity patterns.

From the initiation of the rut in late summer until lambing in early spring the bighorns formed a loosely knit band consisting of rams, ewes and lambs. The band would bed overnight in the crevasses of the lower cliff and in the rocks of the upper talus slope. After daylight they would leave their beds and feed downward across the talus slope and onto the flood plain. On the plain they divided their activities into two or three feeding and resting periods during the day. As twilight approached they left the plain, traveled up the talus slope and by dark would be resting in their night beds.

About a week before lambing, which began in mid-March in 1975, the ewe behavior markedly changed. The pregnant ewes left the band individually and sought the seclusion of the talus slope. Each ewe avoided the others until she had lambed. After lambing, the ewes began to be seen in company of the other ewes with lambs and eventually they formed a small nursery band of 7 ewes and 7 lambs. The nursery band remained separate from the rams and from the ewe which had no lamb.

For several months the ewes, and particularly the lambs, spent most of the time on the talus slope. The ewes would leave their lambs in the nursery band on the slope for short periods of time and graze out onto the flood plain. By the end of July, the nursery band was being used less frequently and the lambs had matured to the point where most of the day they were observed on the flood plain grazing with their dams. They would even leave their dams to feed and then return to them to nurse. At this time the rut began, the rams joined the ewes and lambs and the annual activity cycle was repeated.

### *A Review of Ewe-Lamb Vocalization*

Vocalization of bighorn sheep has been reported in literature. Seton (1929) indicated that while he had heard bighorn lambs bleat, he had never heard mature bighorns make any sound except a loud snort.

On the other hand, Welles and Welles (1961) reported hearing both sexes and all age classes of bighorn vocalize. They noted ewes and lambs calling and approaching humans, apparently mistaking them for bighorns. They observed frightened lambs running to their mothers and bleating until they were in sight of them and ewes calling their lambs to them. They also noted that the lambs voiced their demands for food and protection and observed large bands of 15 to 20 animals vocalizing frequently and loudly for recognition and identification. Hansen and Deming (1971) reported a large band of 69 ewes and lambs and yearlings calling in a mild form of bedlam to

keep in contact. They also stated that ewes called their lambs to them for security. Wilson (1968) observed ewes to return from feeding and watering periods and call their lambs to them from their hiding places. He also heard a lamb return a call from its dam. Geist (1971) observed ewes and lambs calling and searching for each other. He also heard ewes bleat as they returned to their lambs from an extended absence.

*Ewe-Lamb Vocalization at Zion National Park*

At the enclosure at Zion National Park, the vocalization of the ewes and lambs was not heard from the initiation of the behavioral study in August 1974 until eight months later in April 1975. Lambing began on 18 March 1975 and on 18 April 1975, several ewes were heard to make loud diurnal vocalizations. Additional ewe and lamb vocalizations were noted after that time.

The ewe vocalizations heard in the enclosure were much lower in pitch than those of domestic ewes. Wilson (1969) best described the desert bighorn ewe call as a "coarse, burping, frog-like sound." the lamb vocalizations at Zion were very similar to domestic lambs; Seton (1929) and Hanson and Deming (1971) also indicated that the lamb calls were similar between the two.

Generally when the ewes and lambs were heard to vocalize, they showed some visual indication that they were doing so such as assuming a posture, opening their mouths or flexing their bodies to call. The vocalizations at Zion were very loud and clear, often being heard from a distance of over 500 meters.

*Ewe Vocalization in Relation to Month*

The ewe vocalizations noted in the enclosure were seasonal and were found to be uncommon. Throughout the year of observation, the vocalizations occurred only during the months of April, May and June. For example, between March and July of 1975 only 19 vocalization bouts (situations where the ewe called her lamb) were noted in 179 hours of observation (Table 1).

Most of the vocalizations occurred in April (Figure 1) and the frequency of vocalization bouts decreased form .27 bouts per observation hour in this month to .08 and .09 respectively in May and June. A temporal decrease in frequency of vocalization was noted for lambs on the Desert Game Range in Nevada by Hanson and Deming (1971).

*Ewe volcalization in Relation to Nursing*

The ewe vocalizations at Zion were associated with the need for them to locate and nurse their lambs. Of the 19 ewe vocalization bouts recorded, 14 of these were terminated when the ewe located and nursed her lamb. In two other instances, the ewes joined their lambs and moved out of sight. In two additional observations, the ewes were calling as they moved out of sight. In the remaining instance, a ewe vocalized immediately after she had nursed her lamb. The ewe vocalizations were not common in relation to the nursing activities.

The ewes displayed three general behavioral sequences that preceded nursing during the nursery band period. The first and most common of these sequences occurred when the ewe completed a resting period on the talus slope with the nursery band and arose. After she was up, her lamb would run to her from several meters away and begin to nurse. The second sequence occurred when the ewe would begin a feeding period and would leave the lamb with the nursery band or in a juvenile band for several hours. When the ewe returned and approached to within a few meters of the band, the lamb would leave it and run to her to nurse. The third sequence was a modification of the second. In this situation, the ewe would return from a feeding bout and approach the area where she had left the lamb. If the nursery band had moved out of sight and she could not find it or if her lamb had mingled with the other lambs and did not respond to her return, she would begin to vocalize.

These behavioral sequences are shown in Table 2. During 1975, 161 individual nursing bouts were noted which were related to the sequences. Among these 109, or 64 percent, occurred when the ewe arose and nursed the lamb in the nursery band. In 38 instances, or 24 percent of the observations, the ewe left the nursery band for a short time then returned to it and was not observed to vocalize. In 14 instances, or 9 percent of the sequences, the ewe left the band, returned and found it necessary to vocalize to locate her lamb for nursing. These observations suggest that during this period, the ewes generally 1) maintain a close proximity to their lambs 2) are fairly successful in keeping the lambs located in small nursery band situations by means other than vocalization, and 3) would vocalize and search only rarely to locate their lambs.

Of the 14 instances of vocalization noted above, six instances occurred when the ewe returned to the area where she had last left her neonate and it had moved out of sight with the nursery band. In seven instances, ewes were observed to return to the area and call their lambs to them from the nursery band and in the remaining instance a ewe was observed to call after nursing her lamb.

*Ewe Vocalization in Relation to Habit Use*

The ages of the lambs were known. Ewe vocalization was not heard for any individual lamb earlier than two weeks or later than 14 weeks or 3 and 1/2 months postpartum. At the earlier time, the ewes and lambs were in seclusion from other bighorns, however, the sampling periods may also have missed vocalizations during this time. At the later time, the lambs appeared to have reached a stage of maturity where they were less reluctant to leave the security of the slope and were more frequently following their dams onto the flood plain to feed.

*Ewe Vocalization in Relation to the Age of the Lamb*

Ewe vocalization was related to the habitat the ewes and lambs were located upon. All of the 19 ewe vocalizations were observed to occur on the talus slope and none were observed to occur on the flood plain. This is depicted in Figure 2. Observations of the habitat the lambs nursed on were quantified to provide an index of the amount of diurnal time each habitat was used. From April to September 1975, 185 nursing bouts were observed which were related to habitat. In April, 100 percent of the nursings observed durin that month occurred on the talus slope. This decreased to 90 percent in May, 35 percent in June, 40 percent in July and 0 percent in August. A reciprocal increase in the use of the flood plain was noted from 0 percent in April to 100 percent in August and September. The most significant observations relating to habitat use and vocalizations were made in June. During this month, all

of the vocalizations were observed to occur on the talus slope even though 65 percent of the nursings were made on the flood plain. This would tend to support a strong correlation between ewe vocalizations and the talus slope.

It is difficult to explain the reason for this phenomenon, partly because the sample size is small. It may simply be that in the enclosure on the rugged talus slope and in the small nursery band situation, the ewes occasionally lose sight of their lambs and must resort to vocalization to locate or identify it. However, the act of calling would appear to have the potential to attract predators, which could home in on the call and prey on the ewe and lamb. It would appear that there is the possibility that natural selection has affected this behavior. Perhaps ewe vocalization on steep, rugged terrain such as the talus slope has not been selected against by predation because it is escape terrain in which the bighorn can easily detect and evade predators. On the other hand, the trait of ewe vocalization on habitat such as the flood plain may have been selected against because it is terrain in which they would be less likely to detect and evade predation.

During the later part of the nursery band period on the talus slope, ewe vocalization ceases and becomes unnecessary apparently because the lamb has reached a stage of maturation where it is following the ewe most of the time, is not using the nursery band as frequently and the ewe and lamb are more able to identify and locate each other by visual or other means.

*Lamb Vocalizations*

Lamb vocalizations were very rare at Zion. Only three were noted. These occurred on 7 and 6 May and 19 July 1975. In two instances the lambs were observed on the talus slope alone calling loudly. In the other instance, a lamb was heard to call after dark. Apparently a lamb would call when it found itself alone and separated from its dam or from the nursery band. Perhaps hunger also prompted the call. It would appear that a calling lamb would be vulnerable to predation.

*Other Vocalizations of Ewes and Lambs*

It was suspected that a call, which could be heard only within a few meters, was also given by the ewes and lambs. This was looked for and listened for, and although occasionally the action of recognition between the ewes and lambs suggested it, it could not be heard nor could it be detected in the posture of the animals. Ewe-lamb vocalizations may have also occurred at night but continual nocturnal observations were not made.

Other ewe-lamb vocalization situations such as those recorded by Welles and Welles (1961), Hansen and Deming (1971), Geist (1971) and Wilson (1969) in wild populations were not noted in the Zion herd.

*Ewe and Lamb Recognition*

Ewe vocalization at the Zion enclosure was only one of several means of recognition used by the ewes and their neonates. Geist (1971) reviewed recognition phenomena between the ewe and lamb bighorns. He indicated that the ewes recognized the lambs by olfaction and perhaps by vocalization. Lambs, he believed, recognized their dams primarily by sight and there was evidence that they also recognized their dams by their vocalization. Welles and Welles (1961), Wilson (1968) and Hansen and Deming (1971) also presented observations that the lambs recognized their dams by voice.

At the Zion enclosure, the bighorn ewes appeared to recognize their lambs by visual and olfactory means. No response was observed from the ewes when a lamb vocalized. The lambs appeared to recognize their dams by visual and auditory means. There was no observation to indicate that they recognized their dams by olfaction although this possibility should not be ruled out.

Usually it appeared to require a combination of recognition cues to reunite the ewe and lamb. In addition to vocalization, the ewes exhibited at least two maternal behavioral patterns which appeared to elicit an approach response from the lambs. One of these patterns was when a ewe would rise after a resting period. The other was when a ewe approached to within a few meters of her lamb in the nursery band. A ewe's direct gaze was also suspected of eliciting these responses from the lambs, however, this could not be confirmed.

The ewes apparently used olfaction as the most positive test to recognize their lambs. Although quantitative data were not obtained on most nursing bouts, the ewe would sniff the anal region of the lamb as it nursed as if to confirm its identity. A ewe was only observed once to use olfaction to locate her lamb among a group of lambs.

Ewes recognized their lambs secondarily by vision. One observation indicating that a ewe identified her lamb by visual means was made on 22 April 1975, when a ewe which had been resting with the nursery band arose from her bed, walked a few meters to her lamb which was resting near another ewe and nudged it to its feet for nursing.

Generally, however, the ewes appeared to have difficulty in identifying their lambs by vision. On 22 April 1975, a ewe was observed to return to the nursery band from a feeding period and run from lamb to lamb sniffing each until she located her lamb and nursed it. On 16 May, a ewe who had been on a feeding period joined the nursery band as it was traveling away from its resting place on the talus slope. After traveling with the group for a few minutes, the ewe suddenly reversed her direction and ran over 100 meters on the contour toward the previous resting place, then she again reversed her direction and returned to the nursery band calling. She ran into the band, located her lamb and nursed it. Apparently, the ewe did not recognize her lamb by sight among the others in the nursery group when she initially joined it and it did not observe her. Because of her need to nurse, it is believed that she ran back to where she had remembered last leaving her lamb. It is remotely possible that she followed the lamb's scent trail in her attempt to locate it. In any event, when she did not locate it at the resting site, it was interesting to note that she appeared to know then that the lamb was in the nursery band.

The ewes were not observed to respond to the call of a lamb. On 16 May a lamb was observed by itself on the upper talus slope. The lamb called loudly and made several 400 meter treks back and forth along the contour of the slope. It called toward several ewes who were feeding on the talus slope 80 meters below. It also called toward the other ewes which were feeding on the flood plain. Even though all of the

TABLE 1. Ewe vocalization bouts and hours of observation for slected months. Zion National Park, 1975.

| Month | Number of Vocalization Bouts | Hours of Observation |
|---|---|---|
| March | 0 | 14 |
| April | 11 | 41 |
| May | 5 | 66 |
| June | 3 | 32 |
| July | 0 | 26 |
| Total | 19 | 179 |

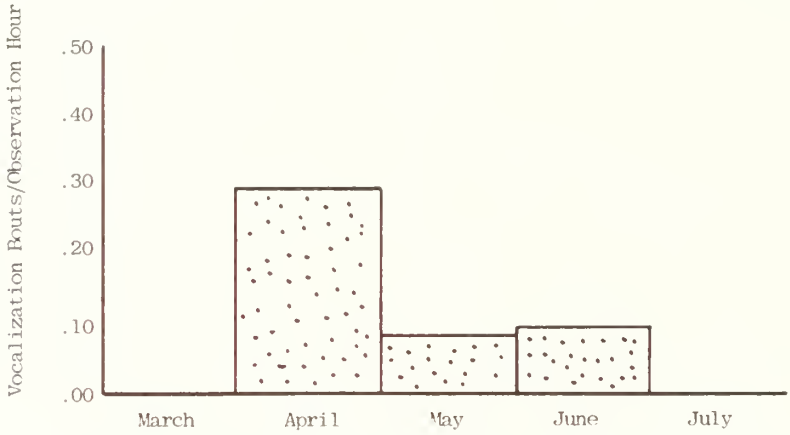



FIGURE 1. Bighorn ewe vocalization per observation hour in relation to month.

TABLE 2. Bighorn ewe behavior prior to nursing lamb.

| Behavior Sequence | Number of Times Observed | Percent of Observations |
|---|---|---|
| Ewe with or near lamb prior to nursing | 109 | 67 |
| Ewe leaves lamb to feed, returns to nurse, does not vocalize to find lamb | 38 | 24 |
| Ewe leaves lamb to feed, returns to nurse, vocalizes to find lamb | 14 | 9 |
| TOTAL | 161 | 100 |

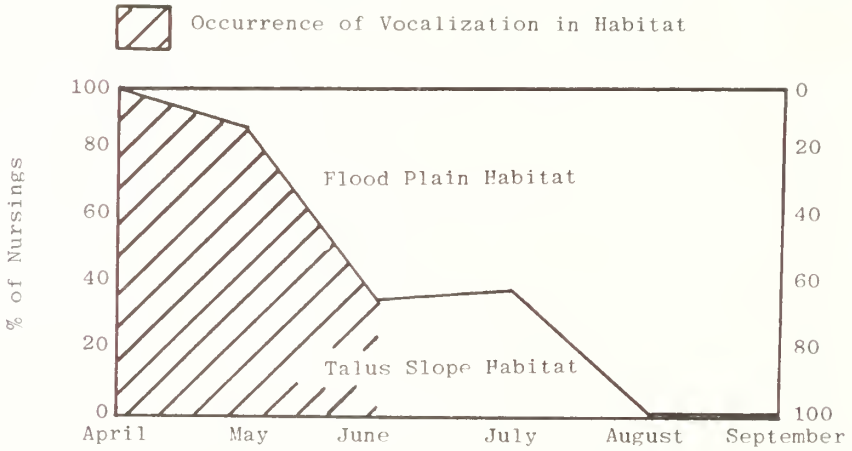



FIGURE 2. Ewe vocalization in relation to nursing habitat and month.

lactating ewes were present, they paid no attention to the lamb's call. After an hour and a half of intermittent calling, the lamb was heard to vocalize simultaneously with a ewe vocalization. The ewe was out of sight in a canyon, the lamb traveled 300 meters up into the canyon and the vocalizations stopped. It appears likely that the lamb responded to the ewe's call by going to it rather than vice versa but this could not be confirmed.

Early in the nursery band period, the lambs appeared to recognize their dams primarily by sight but only from a few meters away. On many occasions a lamb was observed to leave the band and run to join its dam, which appeared to be not vocalizing, as it approached. A typical recognition distance was observed on 16 May when a ewe was observed to walk to within 20 meters of a juvenile band, stand and look at it. Her lamb responded by leaving the group and running to her to nurse. Later in the nursery band period, when the lambs were spending more time on the flood plain, it is believed that this distance greatly increased. Also at this time, lambs would feed away from their dams then return to them to nurse.

The lambs also recognized their dams by call even though ewe vocalization was not common. On 16 May, a ewe was noticed on the upper talus slope to stop feeding and begin to vocalize. Her six-week-old lamb, which was located out of her sight behind several large boulders 40 meters below her, immediately stopped feeding and ran to her to nurse. This was the greatest distance over which a response to a call was confirmed.

When a ewe vocalized usually only her lamb was observed to respond to the call. Apparently, it is a fairly specific recognition signal for the lamb. A possible exception to this was observed on 30 April when a ewe, vocalizing for her lamb, approached a juvenile band of 4 lambs. As she approached all of the lambs ran to her and one nursed form her while the others frolicked nearby. In this case, it was suspected that only her lamb responded to her call and the others either followed her lamb or responded to her approach rather than to her vocalization.

There was no observation to indicate that a lamb identified its dam by olfaction although this possibility needs to be investigated further.

Usually it appeared to require a combination of visual, olfactory and/or auditory recognition cues to reunite a ewe and lamb during the nursery band period. There also appeared to be a reciprocal exchange of various cues between the lamb and its dam as they reunited. One of the most common interactions involving recognition occurred when a ewe, which had been resting for a period of time with the nursery band, would stand. This activity seemed to be the stimulus for her lamb, which was usually resting a few meters away with other lambs, to run to her and nurse, then as it nursed the ewe would sniff the lamb's anal area as if to confirm its identity. On rare occasions, an unrelated lamb would see the ewe rise and it would run to her and attempt to nurse. The ewe would respond by butting at the lamb or would step over its neck to prevent nursing. In these cases, the ewes apparently recognized their lambs by vision and olfaction and the lambs would recognize their dams by visual means. The act of rising also appeared to be a general signal of readiness to nurse that would elicit a response from non-related lambs.

The next most common situation observed was when a ewe would leave her lamb in the nursery band so that she could feed. As the ewe fed, she would frequently raise her head and look back toward the nursery band area where her lamb was located. The peak frequency of these looks were timed at one per minute on several occasions, usually they were less frequent than this. After several hours, the ewe would terminate the feeding and return to the area where she had left the lamb or she would go to the nursery band if it had moved but was still within sight. When she approached to within a few meters of the band, her lamb would leave the group and run to her to nurse, then while it nursed she would sniff the lamb's anal area. Again a combination of visual, olfactory and other behavioral recognition cues appeared used by the ewe and lamb.

Occasionally, the ewe could not find her lamb by other means and would begin to vocalize in search for it. As she approached her lamb, it would respond by running to her. In several instances, the lambs appeared to respond to their dam's call blindly. On 18 April, a calling ewe was observed to approach a nursery band. When she was about 15 meters away, a lamb left the group and ran toward her. Another ewe was feeding halfway between the ewe and lamb, the lamb ran directly to this feeding ewe and began to nurse. The startled ewe kicked the lamb away and it immediately left her and ran on to its dam to nurse.

From the above observations, it appears that the ewes used at least five general strategies to help relocate their lambs after they had left them for feeding periods. The first was to apparently maintain a watch of the area the lamb had been left in. The second was to return to the area where the lamb had been left. The third was to seek out the nursery or juvenile band. The fourth was to call and search for the lamb and the fifth was to smell each lamb until the neonate was found.

In the second, third and fourth strategies, it appeared that the ewe made an effort to place herself in the vicinity of the lamb and when this occurred the burden of identification was shifted to the lamb. If these efforts failed, the ewe most likely would resort to calling and searching or sniffing each individual lamb. These observations would tend to indicate that the ewe appears to favor lamb locating strategies that result in less energy expenditure and/or risk of predation.

### *Some Additional Considerations*

There appear to be different patterns of ewe-lamb vocalization which are related to the size of the social groups. These patterns may vary in increasing complexity from the single ewe with lamb to an intermediate situation such as the small nursery band situation at Zion National Park to the large ewe-lamb bands observed by Hanson and Deming (1971).

Wilson (1968) described the single ewe-lamb situation in detail. The ewe let the lamb select a hiding place and then watched until it was settled. She then left the lamb for several hours and upon her return, as she neared the vicinity of the hiding place, she vocalized. The lamb then left its hiding spot and ran to her to nurse. Wilson (1968) believed that this hiding procedure favored lamb survival because the lamb would be at its mother's side before a predator would be able to notice it. It would appear from Wilson's (1969) description that the ewe-calling-lamb response distance was short so that even though the

call might serve as a lure to a predator, the lamb would be with its dam for maternal protection by the time the predator had also responded to the call.

In the Zion enclosure, the ewes and lambs formed a small nursery band. The nursery band probably favors lamb survival but it also presents problems to the ewe in locating and recognizing her neonate. One problem is that the nursery band is mobile. The lambs stay together and tend to follow any ewe so that if they move the other ewes must resort to various strategies to find their neonates. Another problem is that in a group, the individual lambs appeared to be difficult for the ewes to identify so that the ewes occasionally had to vocalize in order for their lambs to identify them. Rarely the ewes must also hunt for and sniff each lamb to locate their offspring from among a group. This appears to be an energy and time consuming activity. The problems of identification were mitigated in most cases by the lambs, who most likely conditioned by hunger would recognize their dams from a distance, would leave the group and join their dams as they approached.

In the larger ewe-lamb groups, the problems of ewe-lamb location and recognition would almost appear to present a threat to lamb survival in that it could be left behind and not found. It would appear that loud vocalizations by both the ewe and lamb would be necessary to provide a reunion. Perhaps in this situation the ewes might even learn to recognize and respond to their lamb's calls.

The ewe-lamb vocalizations appeared to have several functions in the Zion enclosure in the small nursery band situation. First, vocalization enabled the ewes to locate the lambs from a distance, out of sight and in rugged terrain, for nursing. Second, it stimulated the lamb to respond by leaving the nursery band and running to her. This saved energy that would otherwise have been wasted hunting for the lamb among the group. Thirdly, it served as a specific recognition cue which apparently reinforced the mother-infant social bond and facilitated later recognition by sight. Nocturnal ewe-lamb vocalization data were not obtained at Zion, however, another possible function, and perhaps the most important of all, would be that vocalization might enable the ewe and lamb to reunite in the dark. This was suggested by Bromley (1967) for pronghorn antelope (*Antelocapra americana*) and it may also be the case for desert bighorns.

There are management implications associated with the observations of the bighorn ewe-lamb vocalizations. A portion of the herd at Zion National Park will soon be released into the wild. It appears that the ewe vocalizations are of survi value to the lamb because they enable the lamb to be located, identified and nursed by its dam. The vocalizations also appear to be a potential beacon to predators. When the bighorns are released, it will be interesting to determine if their survival is affected or if their vocalization or other behavior is modified by the presence of predation.

A major problem of the observations of ewe-la vocalization in the Zion enclosure was that the bighorns were in a captive situation which may have modified their behavior in comparison to that of a wild situation. Also, nocturnal observations were not made, the observation distances were so great that vocalizations low in volume may have be missed and the vocalizations that were recorded were so few in number that they made a small sampl size. It is hoped, however, that the observations and analysis presented here will contribute to an understanding of this interesting aspect of bighorn behavior.

## REFERENCES CITED


BROMLEY, P. T. 1967. Pregnancy, birth, behavioral development of the fawn, and territoriality in the pronghorn *(Antilocapra americana Ord)* on the National Bison Range, Moiese, Montana. Master's thesis, University of Montana.

GEIST, V. 1971. Mountain sheep: A study in behavior and evolution. 413 pp. Chicago: University of Chicago Press.

HANSEN, C. G. and D. V. DEMING. 1971. Lambs *in* Sumner and Monson (eds.). The Desert Bighorn, Its Life History, Ecology and Management. (In Press)

MCCUTCHEN, H. E. 1975. Desert bighorn restoration at Zion National Park, Utah. Trans. Desert Bighorn Council. 19:19-27.

SETON, E. T. 1929. Lives of game animals. Vol. 3. Doubleday, Doran and Co. New York. 780 pp.

WILSON, L. O. 1968. Distribution and ecology of the desert bighorn sheep in southeast Utah. Utah Div. of Fish and Game 68(S):220 pp.

WELLES, R. F. and F. B. WELLES. 1961. The bighorn of Death Valley. Fauna of the National Parks of the U.S. Fauna Series, No. 6. 242 pp.

# DALL SHEEP IN MOUNT MCKINLEY NATIONAL PARK: IMPLICATIONS FOR CONSERVATION[1]

Edward C. Murphy[2]

I have previously discussed changes in Dall sheep population numbers in McKinley Park from the mid-1920's through 1972 and year-to-year (temporal) variation in natality and survivorship of cohorts (Murphy and Whitten 1976). Figure 1 depicts variation both in initial size and in age-specific survivorship of six of the cohorts comprising the 1972 population. This variation occurred during a period, 1966 to 1972 when there was no substantial change in population numbers.

Lamb:ewe ratios in early summer are strongly and inversely related to snowfall the previous winter ($r = -0.81$) and to sheep density on the summer range (see Murphy and Whitten 1976 for details). In McKinley Park, unlike other *Ovis* habitats (Geist 1971), there is no relationship between the lamb:ewe ratio and subsequent survivorship of those lambs. This suggests that the factors (e.g. snowfall and density) affecting natality and survivorship vary temporally and show low autocorrelation.

Earlier in this conference G. Petrides demonstrated that large mammalian herbivores often have long-term adverse effects on their range and food supply when at high densities. Because Dall sheep birth and death rates are so responsive to immediate conditions, long term effects must be minimal. Moreover, if McKinley Park sheep were to affect adversely their range, the impact would be greatest on winter range. Due to heavy snow cover in winter on most of the range, winter range is quite small compared to summer range (Murie 1944). During winter Dall sheep feed on dead above-ground portions of graminoids, and their winter foraging activities have but minor effects on the survivability of plants they crop. Therefore, although Dall sheep may experience food shortages during heavy winters and/or when at high densities, heavily cropped areas will recover the following spring. Although mortality factors vary greatly, they do so independently of past events.

A common scientific justification for preservation of wilderness areas in the National Park System is that such areas function as baselines in the study of effects of human activities in unprotected areas. However geographic (spatial) as well as temporal variation in a species' biology may be considerable. Our understanding of the effect of human activities may be confused with such variation unless spatial variation is quantified by collecting data in more than one protected locality in the species' range. Only then can an adequate baseline be defined.

Geographic variation in Dall Sheep individual and population attributes is considerable, and geographic trends among populations are evident. For example five years of Alaska Dept. Fish and Game unpublished data show that the average age of rams killed in the Wrangell Mountains is 6.9 years, while it is 7.4 years and 8.7 years in the Brooks Range. These differences do not reflect simply different hunting pressures but real differences in horn growth rates and longevity. Twelve-year and older rams are commonly harvested throughout the Brooks Range and only rarely in the Wrangells, even in areas of minimal hunting pressure. Horn growth rates are rapid and life expectancies low in the Wrangells, both are intermediate in the Alaska Range, and horn growth rates are slow and life expectancies high in the Brooks Range.

Inclusion of the proposed Wrangell-St. Elias and Gates of the Arctic National Parks in the National Park System would preserve, with careful management, a wide spectrum of Dall sheep habitats. Populations of Dall sheep and a wide variety of other tundra and boreal species would then be adequately protected in a range of habitats. The effects of human activities on unprotected populations of such species could be assessed once spatial variation in protected populations has been quantified. Adequate baseline data on geographically variable species cannot be gathered if only one popua ation is fully protected. For such species, e.g. caribou, the contention that National Parks might function as baselines is unjustified. Additional protection of such species should be a high-priority goal when considering future additions to the National Park System.

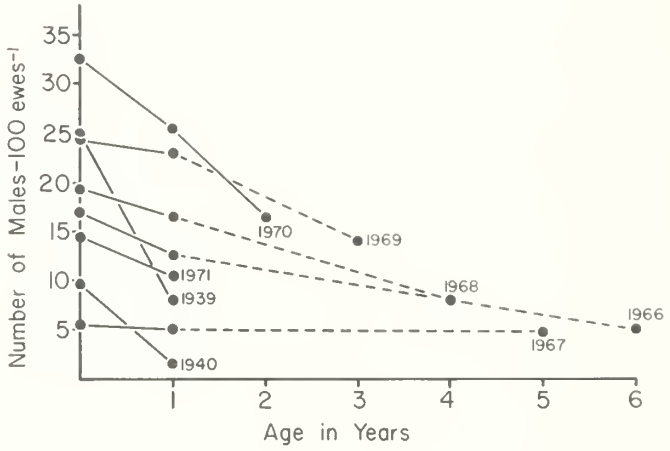



FIGURE 1. Partial male survivorship curves of six cohorts in McKinley Park, 1972. Age 0 and 1 values determined by halving the lamb:ewe ratio in year n and the yearling:ewe ratio in year n+1, respectively. Determination of values for older ages is discussed in Murphy and Whitten (1976).

[1]I wish to thank K. Whitten who assisted in the field work. W. Heimer and A. Smith who provided unpublished Alaska Department of Fish and Game data on other Dall sheep populations, and the National Park Service for its cooperation in this project.

[2]Department of Biological Sciences, University of Alaska, Fairbanks 99701. Present address: Museum of Natural History and Department of Ecology and Systematics, The University of Kansas, Lawrence 66045.

## LITERATURE CITED

GEIST, V. 1971. Mountain sheep, a study in behavior and evolution. Univ. Chicago Press, Chicago. 383 pp.

MURIE, A. 1944. The wolves of Mount McKinley. Fauna of the Natl. Parks of the U.S., Fauna Ser. No. 5, U.S. Gov. Printing Office, Washington, D.C. 238 pp.

MURPHY E. and K. WHITTEN. 1976. Dall sheep demography in McKinley Park and a reevaluation of Murie's data. J. Wildl. Manage. 40(4): 597-609.

# ECOLOGICAL RELATIONSHIPS OF MOUNTAIN GOATS *(OREAMNOS AMERICANUS)* IN GLACIER NATIONAL PARK, MONTANA[1]

Douglas H. Chadwick[2]

## STUDY AREA

Glacier Park incorporates 4,100 km$^2$ of mountainous terrain in northwestern Montana. Precambrian Belt Series argillites and limestones (Ross 1959) uplifted and sculpted by Pleistocene and Recent glaciers dominate the core of the park and form the Continental Divide. Park elevations range from 945 m to 3200 m. Just over one third of total park acreage lies within the alpine zone. Snows typically cover this zone from October through June, reaching depths of 15 m in places. Alpine vegetation which includes ledge, talus, meadow, and krummholz communities (Habeck 1970) is strongly influenced by the persistent snowpack, high wind velocities, low temperature extremes and the continual downward movement of snow, ice, water, and rock on precipitous slopes. Alpine communities grade into a mosaic of subalpine coniferous forest types in which fire plays a significant role (Kessell 1976). Ledge and talus communities are also found within the forest zone where rock outcroppings occur.

Research efforts focused on a 310 km$^2$ central portion of the park representative of mountain goat range on both sides of the Divide (Fig. 1). Mountain goats in the park are part of a large and diverse native fauna. Present in relatively undisturbed populations are potential competitors such as mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), bighorn sheep (*Ovis canadensis*) and predators including eagles (*Aquila chrysaetos, Haliaeetus leucocephalus*), wolverine (*Gulo gulo*), cougar (*Felis concolor*), lynx (*Lynx canadensis*), coyotes (*Canis latrans*), and bear (*Ursus arctos, U. americanus*).

## METHODS

Complete surveys of goat populations were conducted monthly in each of the ten major valleys comprising the study area from May through September during 1974 and 1975. The study area was comprehensively surveyed once during the 1976 May-October period. Range and habitat use during May was considered representative of the winter period. Observations were also made during fall and winter months each year. Surveys were made on foot using 7X binoculars and a 15-45X spotting telescope. Several investigators (Saunders 1955, Peck 1972, Chadwick 1974) have determined goats to be most active during early morning and late afternoon hours. Efforts were therefore directed toward obtaining prime vantage points at such times, though surveys were continuous throughout the day. Closely aligned drainages were covered on successive days to minimize possible duplication in counts resulting from movement of goats.

Each observed goat was placed in one of the following categories: kid (K), yearling (Y), two-year-old male (2M), two-year-old female (2F), adult male (AM), and adult female (AF). Sightings were located on contour field maps and then described to the nearest 100 m using Universal Transverse Mercator (UTM) coordinates. Pertinent habitat data recorded include temperature, wind velocity, snow depth, slope, exposure, elevation, vegetation zone, habitat type, ledge development (a measure of available footing for goats on a given substrate), presence or absence of shade, and location along environmental gradients of topographic moisture and primary (soil) succession (after Kessell 1976). Other parameters described for each goat sighting include type of activity, distance to nearest individual or group (groups being considered separate if further than 50 m and engaged in unrelated activities), and distance to nearest predator or competitor if simultaneously visible within 1 km. A total of 1,519 observations of 4,831 goats was made during the Glacier Park study. Various aspects of social behavior were investigated through intensive observations of selected herd units which included some naturally and artificially marked animals. A total of 4,126 social interactions was analyzed. Occasional surveys were conducted in other parts of Glacier Park for comparative purposes. Additional comparative data were drawn from a previous three-year investigation of native mountain goats in the Swan Mountains some 80 km south of Glacier National Park in the Flathead National Forest.

## RESULTS

### *Population Characteristics*

Survey results from 1974 through 1976 are presented in Table 1. High counts for each age and sex group were selected from monthly surveys in 1974 and 1975 to obtain total counts of 314 and 300, respectively. Repeated surveys were assumed capable of locating about 80% of the existing population so actual number of goats in the study area was probably close to 360. This establishes a density of 1.2 goats/km$^2$ throughout the 310 km$^2$ study area. Elsewhere in the park, goats were found to be abundantly distributed within suitable terrain wherever I was able to conduct sample surveys. Reports by other biologists, rangers, and naturalists confirm these impressions. Singer (1975) estimated 405 goats to be in the 883 km$^2$ portion of his study area situated within park boundaries, yielding a density of .46 goats/km$^2$. His study area (Fig.1) includes a large percentage of subalpine landforms which I judged to be marginal by comparison with my study area. Extrapolation of densities of from a lower limit of .5 goats/km$^2$ to 1.2 goats/km$^2$ to similar habitats in the park therefore seems to be justified. The result is a minimum parkwide population of 1,500 , nearly double traditional estimates exemplified by Cahalane's (1948) figure of 870. Mountain goats then assume the status of a major species, abundantly distributed within the park. Table 1 shows a fairly constant productivity of 50-60 young:100 adult females. This is consistent with population data from elsewhere in the park (Petrides 1948, Bansner 1974, Singer 1975). Mortality was heaviest in juvenile classes and appeared to vary with duration and severity of winter conditions. Bansner's

[1]Thanks are due to Clifford J. Martinka, Research Biologist, Glacier National Park, for advice and helpful criticism; Karen B. Reeves for assistance with data compilation and art work; and Sandra S. Knott for excellent secretarial work. The Glacier Park study was supported by the National Park Service, financiallt and through provision of valuable logistical support.

[2]Box 175, Polebridge, Montana 55928.

data from 1974 show an unusually high proportion of two-year-olds in the population as does data from my study area for that year. This may be attributed to the light winter conditions of 1972-73 which enhanced survival of the kid class as was found to be the case in the Swan Mountains. The high proportion of yearlings evident in the 1976 population followed the light winter of 1975-76. Juveniles were found to be subordinate to other classes and suffered socially intensified resource shortages under conditions of scarcity. Two-year-olds, yearlings and kids, in that order, were progressively less efficient at thermal conservation due to higher surface to volume ratios, lower fat reserves, higher metabolic requirements, and increased physical difficulties negotiating deep and crusted snows. Mortality to all age and sex classes resulted from avalanches, climbing accidents, and occasional predation. Avalanches accounted for 60% and climbing accidents for 15% of those 20 deaths which could definitely be attributed to specific causes. Climbing accidents were also implicated by leg injuries and broken and twisted horns in 64% of 53 observed physical abnormalities. Observations of marked animals in the Swan Mountains revealed that both sexes first participate in the rut at two and one-half years of age (Chadwick 1974). There is no evidence that females breed as yearlings, even in expanding populations with optimum range conditions (Lentfer 1955). Populations give every indication of being stable over the long term in Glacier Park. No historical records exist of notable fluctuations, nor has any evidence of range deterioration or epizootic conditions been discovered.

*Habitat Considerations*

The native distribution of the mountain goat along the northern Rocky Mountains and their coastal extensions is one of the most restricted o any North American artiodactyl. The species is typically associated with mountaintops; and in Glacier Park, goats exhibited narrow preferences for steep slopes at high elevations throughout the year (Tables 2 and 3). Rock outcroppings provided most of the precipitous habitat utilized by mountain goats in the park (Table 4) and the Swan Mountains (Chadwick 1974). Analysis of habitat use along environmental gradients (Tables 5 and 6) als located goats in the newest, uppermost stages of geological succession. An important but unquantified component of such habitats is the catastrophi downslope movement of rocks, ice, and snow which accelerate erosion, create topographic climaxes (Daubenmire 1968:232) in recognizable slide areas, and pose a constant hazard to animal inhabitants. Snowslides occurred over virtually every meter of certain winter-spring ranges and rockfalls were a constant phenomenon of the high country. Though subject to the continuous action of erosive forces plant communities on ledge and fellfield substrate tend to be stable over time and self-perpetuating by comparison with seral forest types. As Habeck (1970) notes, changes in alpine community composition occur on a geological time scale.

Occupation of a topographically defined, narr niche effectively separated goats from other speci During winter, when confining snows generally inte sify competition and predation among large mammals

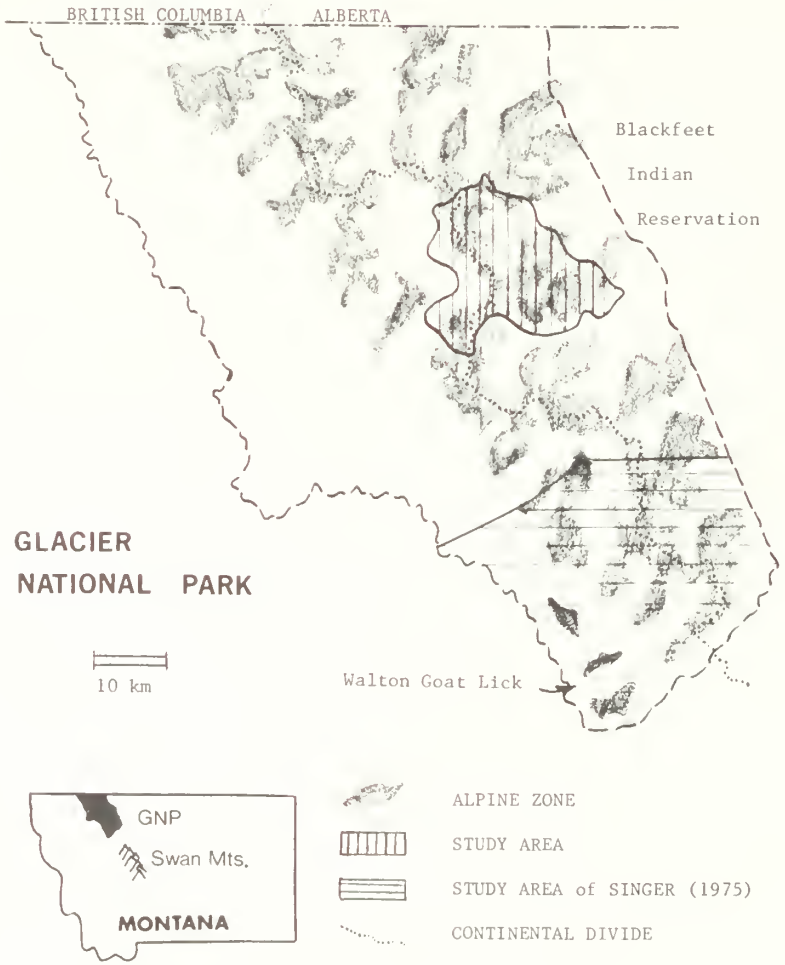



FIGURE 1. Map of study area.

TABLE 1. Mountain goat population structure in Glacier National Park.

No:100 AF/Percent of Total Population

| Class | Study Area 1974 | 1975 | 1976 | Bansner 1974 | Singer 1975 | Petrides 1948 |
|---|---|---|---|---|---|---|
| K | 56/18 | 55/19 | 57/20 | 39/ | 75/ | /42 |
| Y | 36/12 | 33/12 | 40/14 | 6/ | 33/ | |
| 2 | 36/12 | 20/7 | 28/10 | 41/ | 21/ | |
| AM[1] | 86/27 | 75/26 | 57/20 | 47/ | 52/ | |
| AF | 100/32 | 100/35 | 100/35 | 100/ | 100/ | |
| Unclassified Juvenile | | | | 12/ | 5/ | |
| Unclassified Adult | | | | 14/ | 26/ | |
| Unclassified Older than K | | | | | | /100 |
| Number Classified[2] | 314 | 300 | 232 | 171 | 745 | 132 |

[1]Proportion of males observed in surveys is variable as the largely solitary males disperse early from winter ranges and become difficult to locate during summer.

[2]Study area figures are based upon complete, unduplicated counts while those of Bansner and Singer, taken at the Walton Goat Lick, and Petrides lump all goat observations, including resightings.

in northern biomes, mountain goat niche isolation increased. Nearly two-thirds of the population wintered completely above timber line. Use of cliff exposures and steep slopes increased during winter months. As late as May when snow depths were diminishing, 88% of all foraging and 97% of all bedding sites were on rock ledges. Singer (1975) used Namen monograms to illustrate niche separation between mountain goats and sympatric cervids in southern Glacier Park. Similar patterns were evident in my study area where goats were clearly isolated from cervid populations and less than 10% of the total goat population shared winter ranges with bighorn sheep to any extent. A full complement of predators was present in the study area and attempted predatory actions by several species in relation to goats were observed. The overall impact of predation on mountain goats, however, appeared to be quite small. Adult goats, which possess sharp dagger-like horns, drove away medium-sized predators such as lynx, wolverine, and coyotes, succumbing only to cougars and grizzly bears. Predators presence on winter ranges was negligible.

As noted by Geist (1962), narrow habitat preferences by goats have led to compensatory plasticity of food habits within those habitats. Studies show goats capable of exploiting a wide variety of staple food items including lichen (Hanson 1950, Brandborg, 1955), ferns (Hjeljord 1973), grasses and sedges (Brandborg 1955, Saunders 1955, Hibbs 1967, Smith 1976), shrubs (Anderson 1940, Casebeer 1948, Holyrod 1967, Kuck 1970, Peck 1972) and conifers (Geist 1962). Goats in the Swan Range have been recorded utilizing over 180 plant species to date, including significant amounts of non-vascular plants (Chadwick 1974). Grasses and sedges comprised the bulk of the diet of certain herds in the Swan Range while other herds on ranges less than 10 miles distant favored shrubs.

*Distribution Within Habitats*

Close to 75% of all sightings were of solitary animals or pairs. Expressed as percent of all animals sighted, 36% of the population occurred alone or in pairs. Mean group size was small, varying between 1.9 and 3.3 in Glacier Park and 2.1 and 4.6 in the Swan Range (Table 7). Similar results have been obtained by Brandborg (1955), Lentfer (1955), Kuck (1970), and Smith (1976) and seem characteristic of the species. Large groups experienced some physical difficulties maintaining contact and maneuvering efficiently on steep cliffs. Table 2 showed that small groups were more common in precipitous terrain than larger groups. Snowslides may also have selected against occurrence of herds in large groups. Table 8 indicates higher aggressive rates in groups of increasing size. Analysis of behavioral interactions (Chadwick in prep.) revealed that group size, structure, and ultimately distribution reflect agonistic relationships within a social hierarchy. The most stable groupings were small, with clearly defined rank orders. Males, inhibited from behaving agonistically toward other classes outside the rut, tended to be more solitary than other classes and occupied areas peripheral to or separate from female-subadult herd components. All groups were generally well spaced within ranges rather than aggregated, with monthly average intergroup distances varying between 221 m and 577 m (Table 9). A picture therefore emerges of a semi-gregarious rather than a true herd species; one which is characterized by small herd subunits well dispersed throughout steeply rugged terrain.

## DISCUSSION

Mountain goat populations in Glacier Park appear to be influenced primarily by the extrinsic abiotic factors of alpine climate and the demands

TABLE 2. Percent slope utilization by mountain goats in the Glacier National Park study area.

| | Slope (Degrees from horizontal) | | | | | |
|---|---|---|---|---|---|---|
| | Feeding | | | Bedding | | |
| Month | ≤40 | 41 - 60 | >60 | ≤40 | 41 - 60 | >60 |
| May | 31 | 53 | 16 | 30 | 50 | 20 |
| June | 13 | 71 | 16 | 19 | 77 | 4 |
| July | 33 | 59 | 8 | 40 | 57 | 3 |
| August | 41 | 53 | 6 | 24 | 62 | 14 |
| September | 51 | 46 | 3 | 40 | 57 | 3 |
| Average, All Groups | 34 | 56 | 10 | 30 | 61 | 9 |
| Average, Groups Larger than 5 (N=135) | 66 | 31 | 3 | 45 | 42 | 13 |

TABLE 3. Percent elevation utilization by mountain goats in the Glacier National Park study area.

| | Month | | | | |
|---|---|---|---|---|---|
| Elevation (ft.) | May | June | July | August | September |
| 3100-4000 | 2 | - | - | - | - |
| 4100-5000 | 22 | 2 | 1 | - | 1 |
| 5100-6000 | 43 | 17 | 3 | 4 | 16 |
| 6100-7000 | 31 | 54 | 30 | 38 | 38 |
| 7100-8000 | 2 | 25 | 52 | 50 | 42 |
| 8100-9000 | - | 2 | 14 | 8 | 3 |

TABLE 4. Percent habitat type utilization by mountain goats in Glacier National Park study area.

| | Percent of Utilization | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | May | | June | | July | | Aug. | | Sept. | |
| Habitat Type | F* | B** | F | B | F | B | F | B | F | B |
| Permanent Snow/ Icefield | 1 | - | - | - | 1 | 4 | 1 | 2 | - | - |
| Dry Ledge | 68 | 74 | 61 | 58 | 50 | 51 | 29 | 52 | 24 | 48 |
| Wet Ledge | 20 | 23 | 16 | 15 | 14 | 16 | 12 | 16 | 17 | 28 |
| Talus/Scree/Moraine | 4 | 1 | 6 | 3 | 18 | 13 | 13 | 10 | 12 | 8 |
| Dry Meadow | 4 | 2 | 10 | 14 | 10 | 13 | 28 | 14 | 18 | 8 |
| Wet Meadow | 1 | - | - | - | 2 | 3 | 8 | 2 | 3 | - |
| Shrub/Krummholz | 2 | - | 6 | 10 | 5 | - | 9 | 4 | 26 | 8 |
| Forest | - | - | 1 | - | - | - | - | - | - | - |

* F=Feeding
** B=Bedding

TABLE 5. Percent habitat utilization along a soil seccession gradient by mountain goats in the Glacier National Park study area.

| | Month | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | May | | June | | July | | Aug. | | Sept. | |
| Habitat Type | F* | B** | F | B | F | B | F | B | F | B |
| Glacier/Icefield | - | - | - | - | 1 | 4 | 2 | 2 | - | - |
| Solid Outcrop | 62 | 67 | 47 | 48 | 35 | 31 | 24 | 44 | 26 | 48 |
| Broken Outcrop | 33 | 32 | 14 | 21 | 23 | 27 | 15 | 19 | 14 | 28 |
| Boulders and Talus | 1 | 1 | 3 | - | 9 | 12 | 4 | 9 | 8 | 5 |
| Talus | 1 | - | 7 | - | 3 | 7 | 6 | 1 | 3 | 3 |
| Talus and Meadow | 1 | - | 9 | 10 | 17 | 7 | 21 | 12 | 15 | 6 |
| Meadow | 1 | - | 1 | 4 | 8 | 12 | 8 | 2 | 9 | 8 |
| Meadow and Shrub Krummholz | 1 | - | 1 | 17 | 3 | - | 18 | 11 | 18 | 2 |
| Shrub/Krummholz | - | - | 6 | - | 1 | - | 1 | - | 5 | - |
| Shrub/Krummholz and Forest | - | - | 1 | - | 1 | - | 1 | - | 2 | - |
| Typical Forest | - | - | 1 | - | - | - | - | - | - | - |

* F=Feeding
** B=Bedding

TABLE 6. Percent habitat utilization along a topographic moisture gradient by mountain goats in the Glacier National Park study area.

| | | Month | | | | |
|---|---|---|---|---|---|---|
| | | May | June | July | August | September |
| Wet | Hydric Basin | - | - | - | 2 | - |
| ↓ | Ravine | 2 | 1 | - | 3 | 1 |
| | Draw | - | 1 | 1 | 4 | 6 |
| | Sheltered Slope | 19 | 18 | 17 | 20 | 34 |
| | Open Slope | 76 | 74 | 30 | 58 | 54 |
| | Peaks and Ridges | 3 | 6 | 50 | 11 | 5 |
| Dry | Xeric Flats | - | - | 2 | 2 | - |

TABLE 7. Monthly mean group size in the Glacier National Park and Swan Mountains study area.

| | Month | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Area | J | F | M | A | M | J | J | A | S | O | N | D |
| Glacier Park | | | | | 1.9 | 2.1 | 2.4 | 2.9 | 3.3 | | | |
| Swan Range | 3.1 | 3.3 | 3.6 | 2.8 | 2.1 | 4.5 | 4.6 | 2.9 | 2.6 | 3.6 | 2.4 | 2.6 |

TABLE 8. Relationship of mountain goat group size to frequency of agonistic behavior.[1]

| | Number of Agonistic Encounters/Goat/Hour | | | |
|---|---|---|---|---|
| | Swan Mountains | | | GNP |
| Group size | Bedded (N=549) | Foraging (N=1055) | Licking Salt (N=43) | Foraging (N=95) |
| 2 | .06 | .26 | 1.47 | 1.08 |
| 3 | .06 | .63 | 3.04 | .94 |
| 4 | .39 | .83 | 4.17 | 2.75 |
| 5 | .22 | .82 | 3.69 | 1.83 |
| 6 | .52 | .89 | | 2.47 |
| 7 | .47 | .65 | | 4.64 |
| 8 | .80 | 1.30 | 6.06 | 5.20 |
| 9 | 1.25 | 1.50 | | 3.01 |
| 10 | .44 | 1.82 | | 1.12 |
| > 10 | .54 | 1.87 | | 4.24 |

[1]Data from Swan Range and Glacier Park are not quantitatively comparable due to different sampling techniques.

TABLE 9. Degree of dispersion of mountain goat groups in the Glacier National Park study area as estimated from monthly records of intergroup distances.

| | Average Intergroup Distance (m)* | | | | |
|---|---|---|---|---|---|
| Year | May | June | July | August | September |
| 1974 | 221 | 421 | 577 | 425 | 470 |
| 1975 | 288 | 462 | 484 | 571 | 405 |

*Based on measurements of distance to nearest individual or group for each sighting. Since ridgelines and rugged topography prevented simultaneous observation of many isolated goats, a maximum intergroup distance of 1 km was assigned to goats which may have been separated by greater distance. All intergroup distance averages are likely underestimates and are therefore useful primarily in describing relative changes.

of precipitous mountain topography. Numbers were regulated principally by variable juvenile mortality in response to winter stress and by hazards such as snowslides and climbing mishaps incurred while negotiating cliffy terrain. Living higher, steeper, and more snowbound than any other large mammal in the park, goats were less subject to biotic influences such as predation, competition, and plant succession.

Exploitation of available foods was facilitated by physical specializations, such as pelage and climbing abilities, and flexible food habits. Niche efficiency was further enhanced by a complex social system with learned home range traditions. Social forces led to occurrence of the population in small groups, including a large percentage of solitary individuals. Small average group size distributed zootic impacts in fragile alpine habitats, created stable social situations with regulation of intraspecific competition, and permitted reliance upon limited and extremely localized food resources under severe winter conditions.

These characteristics enabled mountain goats to maintain unexpectedly high densities within their narrow and relatively uncontested niche without adversly affecting native ranges. Such ecological relationships are far more difficult to interpret outside park ecosystems, in areas such as the Swan Mountains, for example, where human disturbances have altered goat populations along with predator and competitor species. Within Glacier Park, which is managed as a natural area, this study suggests that native mountain goat populations are abundant, naturally regulated, and stable over time. This substantiates, at least for this species, the hypothesis of Cole (1971:420) that "...populations of native ungulates cannot, without overriding successional influences or habitat limitations imposed by man, progressively reduce food resources that limit their own density."

## LITERATURE CITED


ANDERSON, N. A. 1940. Mountain goat study. Washington Department of Game, Biol. Bull. 2. 21 pp.

BANSNER, U. 1974. Mountain goat-human interactions in the Sperry-Gunsight area of Glacier National Park. U. of Montana, Progress Report. 38 pp.

BRANDBORG, S. M. 1955. Life history and ecology of the mountain goat in Idaho. Idaho Dept. Fish Game Wildl. Bull. 2. 142 pp.

CAHALANE, V. J. 1948. The status of mammals in the U.S. National Park system. J. Mammal. 29:247-259.

CASEBEER, R. L. 1948. A study of the food habits of the mountain goat *(Oreamnos americanus missoula)* in western Montana. Unpubl. M.S. thesis, Montana State U., Bozeman. 4 pp.

CHADWICK, D. H. 1974. Mountain goat ecology-logging relationships in the Bunker Creek Drainage of western Montana. Unpubl. M.S. thesis, U. of Montana, Missoula. 262 pp.

COLE, G. F. 1971. An ecological rationale for the natural or artificial regulation of native ungulates in parks. Trans. 36th N. Am. Wildl. Conf.:417-425.

DAUBENMIRE, R. 1968. Plant communities. Harper and Row, N.Y. 300 pp.

GEIST, V. 1962. Observations on the habitat-directed behavior of Stone's sheep *(Ovis dalli stonei)* and the mountain goat *(Oreamnos americanus)*. Proc. 13th Alaskan Sci. Conf. 29-30.

HABECK, J. R. 1970. The vegetation of Glacier National Park, Montana. Special Report, U. of Montana, Missoula. 132 pp.

HANSON, W. O. 1950. The mountain goat in South Dakota. Unpubl. Ph.D. thesis, U. of Michigan 92 pp.

HIBBS, L. D. 1967. Food habits of the mountain goat in Colorado. J. Mammal. 48(2):242-248.

HJELJORD, O. 1973. Mountain goat forage and habitat preference in Alaska. J. Wildl. Manage. 37(3):353-362.

HOLYROD, J. C. 1967. Observations of Rocky Mountain goats on Mount Wardle, Kootenay National Park, British Columbia. Can. Field Nat. 81(1):1-22.

KESSELL, S. R. 1976. A gradient vegetation, resource, and fire management model for Glacier National Park, Montana. Unpubl. Ph.D. thesis, Cornell University, Ithaca, N.Y. 578 pp.

KUCK, L. 1970. Rocky Mountain goat ecology. Project Completion Report, P-R Project W.144-R-1, Idaho Fish and Game Dept., Boise. 37 pp

LENTFER, J. W. 1955. A two-year study of the Rocky Mountain goat in the Crazy Mountains, Montana. J. Wildl. Manage. 19(4):417-429.

PECK, S. V. 1972. The ecology of the Rocky Mountain goat in the Spanish Peaks area of southwestern Montana. Unpubl. M.S. thesis, Montana State U., Bozeman. 54 pp.

PETRIDES, G. A. 1948. Mountain goat age ratios in Montana. J. Mammal. 29:158.

ROSS, C. B. 1959. Geology of Glacier National Park and the Flathead Region of Northwestern Montana. Geological Survey Paper #296.

SAUNDERS, J. K., JR. 1955. Food habits and range use of the Rocky Mountain goat in the Crazy Mountains, Montana. J. Wildl. Manage. 19(4):429-437.

SINGER, F. J. 1975. Behavior of mountain goats, elk, and other wildlife in relation to U.S. Highway 2, Glacier National Park. Federal Highway Administration, Denver. 96 pp.

SMITH, B. L. 1976. Ecology of Rocky Mountain goats in the Bitterroot Mountains, Montana. Unpubl. M.S. Thesis, U. of Montana, Missoula. 203 pp.

# APPLICATION OF A RUMINANT ENERGETICS MODEL TO A STUDY OF ELK WINTER RANGE CARRYING CAPACITY

D. M. Swift, J. E. Ellis and N. T. Hobbs[1]

## INTRODUCTION

The elk (*Cervus elaphus*) winter range on the lower east side of Rocky Mountain National Park is about 5000 ha in size, ranges in elevation from 2300 to 2700 m and supports some 400 elk. The foraging activities of this herd are beginning to have an adverse effect on its food resource. Direct evidence of this is found in very heavy elk use of aspen (*Populus tremuloides*). Aspen suckers are browsed heavily and mature trees are severely barked. The result is very poor aspen reproduction and an apparent loss of vigor in mature stands. For more information on the extent of this problem see the paper by C.F. Olmstead in this volume.

A number of recent observations of young elk dying in the early spring (D.R. Stevens, pers. comm.) is indirect evidence of a deteriorating range condition. This may indicate that the herd is reaching a state of poor nutrition on the winter range and these infrequent deaths may portend more serious problems for the future.

Both the direct and indirect evidence are cause for concern and led us and the personnel of Rocky Mountain National Park to the question, "What is the carrying capacity of this winter range?"

## PRELIMINARY STUDIES

Although the eventual determination of carrying capacity must be a management decision, we felt that we could shed some light on the nutritional status of the elk herd through simulation modeling. We had available to us a generalized mammalian energetics model developed by J. C. Anway (1) as part of the Grassland Biome study of the US/IBP. Using this model in conjunction with data on herd size and forage resources in the winter range, we simulated a typical winter situation.

The results of this exercise were interesting in two respects. First, the model estimated that no more than 1/3 of the available forage would be consumed by the resident elk herd, indicating that the animals are not energy limited per se on this range. Second, we observed that the weight changes in the simulated elk were very sensitive to an empirical relationship in the model between forage digestibility and forage intake. The model first estimates an animal's forage intake from its calculated maintenance energy requirement but then permits the actual forage intake to vary slightly with forage digestibility. On highly digestible diets, an animal consumes forage in excess of its maintenance requirement, while on poorly digestible diets it consumes less than that requirement. By modifying our estimates of forage digestibility and of the effect of digestibility on forage intake, we were able to produce simulations in which animals gained weight all winter and others in which weight loss was so severe that death by starvation was indicated. On this winter range, the actual situation normally falls between these two extremes.

The Anway model had shown us that changes in weight or animal condition were not being controlled by absolute forage availability but rather by the rate at which that energy could be ingested. Unfortunately, the model gave us no insight into the mechanisms controlling forage intake nor into the basic characteristics of winter forages which are responsible for making them more or less readily ingestible. Control of voluntary intake was essentially an empirical black box controlling animal condition. If we wished to understand how the resources of this range were controlling animal condition, we needed to understand the mechanisms represented by that black box.

It should be noted that the inability of this model to address the question at hand should not be considered a shortcoming of the model. It was developed for purposes of a much more general nature and has served well when applied to appropriate problems. We were simply stressing the model beyond its original objectives. In a larger sense, the model worked very well for us. Because it is a cohesive set of explicitly stated hypotheses, it led us very quickly to the central problem--the control of voluntary intake.

A literature search was conducted to determine the mechanisms controlling voluntary food intake. On high roughage diets voluntary food intake in ruminants is controlled by the rate of passage of digesta from the reticulorumen (2, 3) and not by energy requirements (4). This rate of passage is controlled by the rate of physical and microbial breakdown of the ingesta (5) which is in turn controlled by two factors: *(i)* the innate digestibility of the forage, and *(ii)* the rumen environment. Forage digestibility is a function of the content of protein, cellulose, lignin, and other similar components. The rumen environment is strongly influenced by the amount of nitrogen in the rumen which controls the rate of microbial protein synthesis (6). The level of nitrogen in the rumen depends largely upon the protein content of ingested foods as does forage digestibility.

Food intake rate is thus highly dependent upon the level of dietary protein. That is, low protein diets usually have low total digestibility and support low microbial populations so that the rate of digestion is reduced. Thus, on low protein diets less energy is released to the ruminant, more undigested material remains in the rumen and the rate of energy intake is reduced. The result of this is that low protein forage may not satisfy a ruminant's energy requirement. An adequate supply of energy may be present in the forage, but the animal is simply not able to process it fast enough to maintain positive energy balance.

In addition to this relationship between protein content of the forage and ruminant energy balance, the animal has direct requirements for food protein to replace nitrogen being lost from the body in urine and feces. If these losses cannot be made up from dietary sources, the animal will enter negative nitrogen balance. Nitrogenous body tissues will continue to be lost physically from abrasion of the gut, and through tissue catabolism, but the losses will not be completely compensated for by the production of new tissue. Maintenance of a positive nitrogen balance is thus as important to animal condition as is maintenance of a positive energy balance.

Given the relationship between forage protein and voluntary intake, it is probable that while energy availability is not controlling animal con-

[1]Natural Resources Ecology Laboratory, Colorado State University, Fort Collins 80523.

dition on this range, the ability of the animals to process that energy is. If this is true, it explains the heavy aspen use, as our literature search suggests aspen to be higher in protein than any other forage on the winter range (7-10).

## CURRENT RESEARCH

Our present research, directed toward determining the carrying capacity of the RMNP winter range, is funded by the National Park Service, the U.S. Forest Service, and the Colorado Division of Wildlife. Elk calves have been provided by the Wyoming Game and Fish Department and the Denver Zoological Gardens. We are studying elk/range relationships on the Rocky Mountain National Park winter range and assessing the quantity and quality of forage there. Our objectives are to estimate forage use under varying elk densities and estimate animal condition under various range conditions so that the park management can make an informed decision on carrying capacity of the winter range.

To achieve these objectives we have designed a research program which combines field and laboratory studies with simulation modeling. A new simulation model, more appropriate to the needs of this study, is being used. It was developed by the senior author under the US/IBP Grassland Biome Study.

Table 1 shows the information necessary to me our objectives and shows which of the information items will be measured and which will be estimate via simulation.

TABLE 1. Information required.

| To measure | To simulate |
|---|---|
| Dietary mix | Energy requirements |
| Forage quality | Protein requirements |
| Forage quantity | Voluntary intake |
| Elk numbers | Energy partitioning |
| | Changes in lean body and fat |

The decision to measure or to simulate was based on technical feasibility and cost effectiveness. For instance, diet selection is not being simulate because the mechanisms controlling diet selection are not well understood and thus cannot be stated as a model with a high level of confidence. Instead, we are measuring diet selection by observin the feeding habits of tame elk. Total forage inta

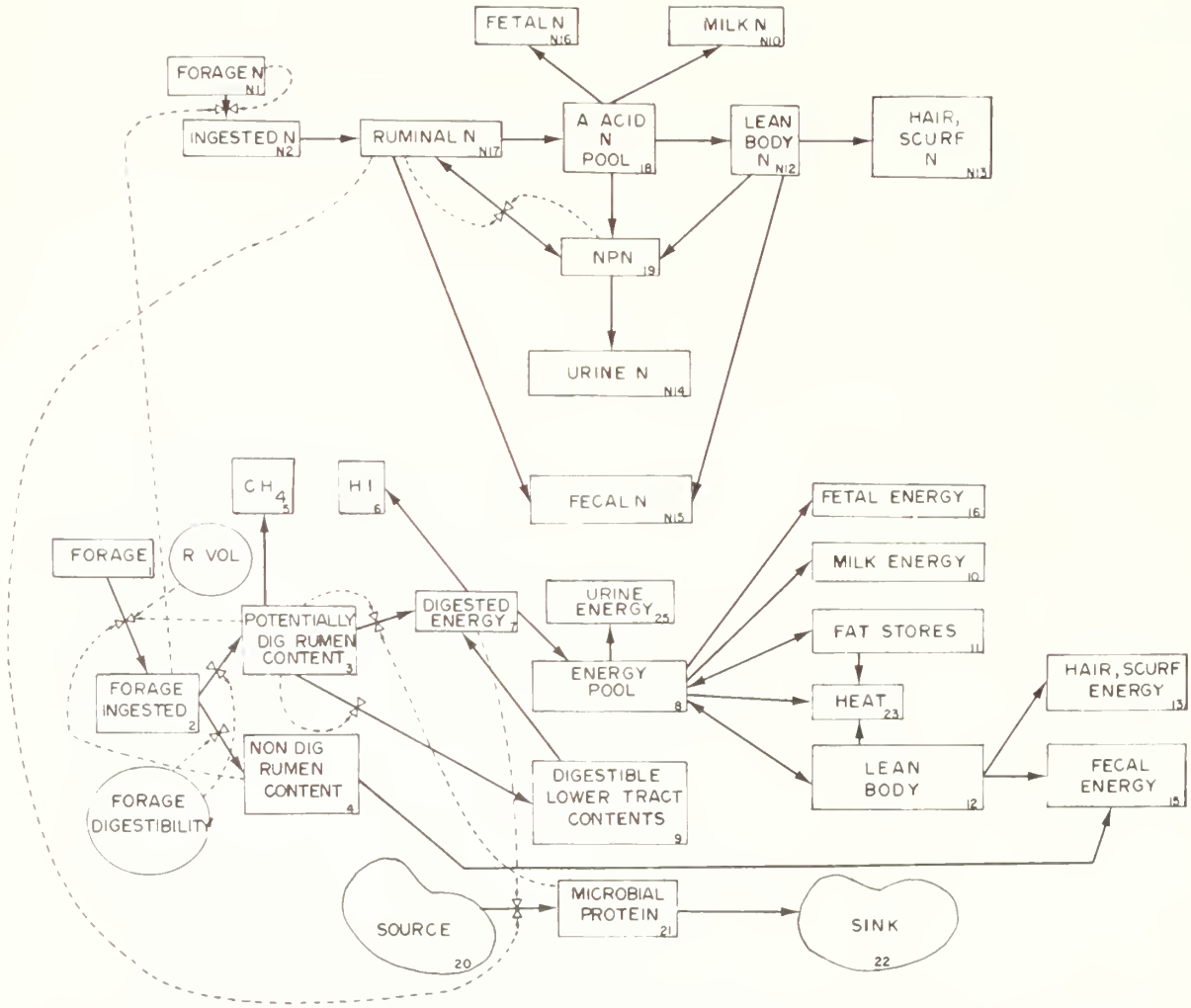



FIGURE 1. A generalized model of ruminant energy and nitrogen balance. Solid lines represent material flows, dashed lines represent information flows--not all information considered in the model are shown.

is much more difficult to determine in the field but we feel we can simulate it accurately based on a knowledge of rumen function and forage quality.

Our model serves a wide range of purposes other than estimating parameters which we cannot measure.

(i) The model acts as an integrator of information from field, laboratory, and literature; it provides us with a clear conceptual framework within which to work.

(ii) The model provides us with a gaming capability. For instance, we would like to investigate the question, "How will elk condition change if aspen were to disappear from the winter range?" We cannot readily study this in the field but can address this question with the model.

(iii) The model can provide a dynamic solution to questions that are usually posed and answered in a static context. As an example, we feel it is unsatisfactory to cite a single figure as representing forage protein requirements for wintering elk. Any such figure will surely be different for different sex and age classes and, for any one class, will vary within and between winters as a function of weather. It will also change as a function of the level of protein deprivation deemed acceptable by the herd manager. The model will demonstrate the effects of varying levels of dietary protein and varying degrees of protein deprivation, so that managers can gain a better understanding of protein requirements.

(iv) The model can guide further research. The construction and exercise of the model pinpoints processes that are either poorly represented or poorly understood and thus require further study.

The model currently being used in this study is a generalized model of ruminant energy and nitrogen balance. The structure of the model is shown as Fig. 1. Not all information flows are indicated. The model simulates energy and nitrogen requirements, voluntary intake of forage, the release of nitrogenous and non-nitrogenous compounds via digestion, and the joint metabolism of the energy and nitrogen thus released. The result is a dynamic determination of energy and nitrogen balance and concomitant changes in the mass of lean body tissue and depot fat reserves; indices of animal condition and possible future performance.

Energy and nitrogen metabolism are simulated jointly because of the intimate relationship between the two. For example, urinary energy loss depends primarily upon the nitrogenous compounds excreted and can be predicted from total urinary nitrogen production (11). The amount of urinary nitrogen excreted depends in part upon the extent to which amino acids are deaminated to provide energy for maintenance and upon the ability of the animal to recycle nonprotein nitrogen internally. Thus this important component of energy balance is a function of both energy and nitrogen metabolism in the animal.

This model has been implemented as a difference equation model of pronghorn (*Antilocapra americana*) energy and nitrogen dynamics. It is currently undergoing refinement and adaptations necessary to represent elk of various age and sex classes.


## SUMMARY

The foraging activity of elk on the primary winter range in Rocky Mountain National Park is beginning to have a detrimental effect upon the range resource. In order to insure a balance between the wintering elk and their forage resource, we must determine:

(i) The effect of different densities of elk upon the range resource through removal of forage.

(ii) The effect of different quantities and qualities of forage upon the elk, as represented by changes in animal condition.

With this information available, management decisions concerning the carrying capacity of the winter range can be made. Our approach is to gather this information in an efficient way by combining field and simulation techniques to provide a more complete picture of elk/range relationships than could be provided by either technique alone.


## LITERATURE CITED


1. ANWAY, J. C. 1977. A canonical mammalian model *in* Ecological Study Series, G. S. Innis (ed.), Springer-Verlag, Inc., New York. (In press).
2. CAMPLING, R. C., FREER, M. & BALCH, C.C. 1961. Factors affecting the voluntary intake of food by cows. 2. The relationships between the voluntary intake of roughages, the amount of digesta in the reticulorumen and the rate of disappearance of digesta from the alimentary tract. Br. J. Nutr. 15, 531.
3. JONES, G. M. 1972. Chemical factors and their relation to feed intake regulation in ruminants: A review, Can. J. Anim. Sci. 52, 207.
4. CRABTREE, J. R. & WILLIAMS, G. L. 1971. The voluntary intake and utilization of rough-age-concentrate diets by sheep. 2. Barley and soya bean meal supplementation of hay diets, Anim. Prod. 13, 83.
5. CAMPLING, R. C. 1970. Physical regulation of voluntary intake, *in* Physiology of Digestion and Metabolism in the Ruminant, A. T. Phillipson (ed.), Oriel Press, Newcastle upon Tyne, England. pp. 226-234.
6. HUME, I. D., MOIR, R. J. & SOMERS, M. 1970. Synthesis of microbial protein in the rumen. I. The level of nitrogen intake, Aust. J. Acric. Res. 21, 283.
7. MCCULLOUGH, D. R. 1969. The Tule Elks, its History, Behavior and Ecology, University of California Press, Berkeley and Los Angeles, Univ. Calif. Publ. Zool., Vol. 88, pp. 209.
8. PERRY, L. L., JR. & MOSER, L. E. 1974. Carbohydrate and organic nitrogen concentrations within range grass parts at maturity, J. Range Manage. 26(1), 37.
9. WILLARD, E. E. & SHUSTER, J. L. 1973. Chemical composition of six southern Great Plains grasses as related to season and precipitation, J. Range Manage. 26(1), 37.
10. OLDEMEYER, J. L. 1974. Nutritive value of moose forage, Nat. Can. (Que.) 101, 217.
11. STREET, J. C., BUTCHER, J. E. & HARRS, L. E. 1963. Estimating urine energy (cattle, sheep) from urine nitrogen, J. Anim. Sci. (Agstr.) 22, 847.

# JUNCO HABITATS IN THE WESTERN UNITED STATES[1]

John R. Haldeman[2]

## INTRODUCTION

There are several taxa of western juncos which may or may not be true species. The status of the populations of the junco complex has been debated, recently the former Oregon Junco (*Junco oreganus*) was considered a subspecies of the Dark-eyed Junco (*Junco hyemalis*) while the Gray-headed Junco (*Junco caniceps*) still under study was retained as a separate species (the American Ornithologist's Union 1973). The purpose of this study is to compare habitats of several junco populations from two species to determine if there are greater differences within populations of a species or between population of two species. The techniques used to make this determination can also be applied to species management through identification of pertinent habitat variables. The application of this method shall be described.

It has been demonstrated that a multivariate numerical classification based entirely on ecological characteristics can yield meaningful classifications similar to those based on morphological characteristics. Since habitats involve aspects or variables, my study was confined to numerous vegetational aspects of the habitat but nevertheless treated the habitat configuration as a multidimensional space and thus employed the techniques of multivariate analysis.

## JUNCO STUDY AREAS

There were five areas and fifty junco territories analyzed in each area (Figure 1). Areas administered by the National Park Service were selected whenever feasible with hopes that the best guarantee of continually undisturbed habitat would be found within. Two populations of Dark-eyed Juncos were investigated, one in Crater Lake National Park and the other near Lake Tahoe, California, and there were three populations of Gray-headed Juncos, one in the Paniment and Grapevine Mountains of Death Valley National Monument north to the Charleston Range, and the others from the south rim of the Grand Canyon to Flagstaff, Arizona, and near Luna, New Mexico. Each population was designated by the name of the state in which it was located.

## METHOD AND MATERIALS

Junco breeding territories were determined by a modified spot-map method (Kendeigh 1944). The geometrical center of the territory was designated the center of a 0.016 hectare transect which was oriented toward the nearest edge.

The transect was divided into four equal segments (quarters), each 0/01 acre in size, and was traversed to measure vegetational characteristics. These were either direct measurements of heights, numerical counts, percent of cover or distribution and visibility measurements.

The percent of ground cover, shrubs, and canopy cover was determined by using a crosshair sighting tube (Winksworth and Goodall 1962). Dispersion of understory and ground cover was determined with an umbrella frame (Breckenridge 1956), while visibility was measured with a density board (Wight 1938). Tree size was measured using a "Biltmore reach stick" (James and Shugart 1970). Trees were divided into five classes depending on their DBH in inches; 3.1 to 6.0, 6.1 to 9.0, 9.1 to 12.0, 12.1 to 15.0 and greater than 15.0 DBH. From this the total basal area could be calculated for each territory. Maximum, minimum, and average were determined for canopy cover, ground cover and tree density data. Each of the four quarter transect values in a territory was used to calculate the vegetational diversity within the transect (Pielou 1966).

Other vegetational and topographic characteristics measured within the transect were greatest tree height, average height of upper and lower canopy and average shrub height. Some measurements were taken within the territory limits rather than being confined to the transect boundaries. These were song tree height and height above ground of the singing male bird.

## DATA ANALYSIS

An IBM Model 50 digital computer and a Calcomp Plotter were used to analyze the field data. Statistical programs were modified from these in the computer library at the University of Arkansas computing center.

When biological data involve several variables the total variance can be partitioned into principal components (PC) (Cooley and Lohnes 1971; Morrison 1967). Each fraction of the total variance is dominated by a group of variables that are correlated. Each corresponding PC is a new variable derived from the original variables and represents a variance axis that is based on a linear combination of the original variables. Since the PC's are multivariate they are thus multidimensional and in environmental studies can be used to describe a multidimensional hyperspace, which corresponds to the ecological niche of a species (Hutchinson 1957).

Separation of several groups by their measured multiple differences has recently been applied to avian studies (Cody 1968; James 1971). Canonical variable analysis maximizes the differences between the multiple factors of habitats in a way that determines whether the habitats are significantly different or not. The multiple factors are reduced to a linear axis, the canonical variable, for a better separation when all measurements are accounted for simultaneously (Anderson 1958).

## RESULTS

### *Habitat Comparisons*

A comparison of the habitat parameters are given

[1]Sincere gratitude is expressed to Dr. Douglas A. James whose ideas on experimental design and statistical analysis were most useful. Statistical guidance and computer programs were provided by Dr. James E. Dunn. I am particularly grateful to Drs. Frances C. James and Alan F. Posey for stimulating discussions on ordination and for helpful suggestions throughout. Financial support was provided by the University of Arkansas, Museum of Northern Arizona and the Society of Sigma Xi.

[2]Museum of Northern Arizona, Flagstaff 86001; and Florida Southern College, Lakeland, Fla. 33802.

for each of the species (Table 1). When comparing the parameters of the study area, each area had the highest value for some parameters, and the lowest value for others, thus no discernible trends were observed.

TABLE 1. Average values of habitat characteristics for each species.

| Habitat characteristics | Gray-headed Junco | Dark-eyed Junco |
|---|---|---|
| Maximum per cent ground cover (PC) | 53.9 | 62.2 |
| Minimum per cent ground cover (PC) | 12.8 | 14.4 |
| Average per cent ground cover (PC, CV) | 32.7 | 36.8 |
| Diversity of ground cover (PC) | 1.6 | 1.4 |
| Ground cover sum times ground cover diversity (PC) | 55.4 | 48.5 |
| Maximum per cent ground cover dispersion (PC) | 77.2 | 68.7 |
| Minimum per cent ground cover dispersion (PC) | 34.7 | 39.8 |
| Average per cent ground cover dispersion (PC) | 49.8 | 48.8 |
| Diversity of ground cover dispersion (PC) | 1.8 | 1.4 |
| Ground cover dispersion sum times ground cover dispersion diversity (PC) | 91.6 | 67.7 |
| Diversity of shrubby ground cover (PC) | 0.6 | 0.9 |
| Shrubby ground cover sum times its diversity (PC) | 31.6 | 45.7 |
| Shrub height in centimeters (PC) | 45.6 | 77.9 |
| Maximum per cent understory dispersion (PC) | 49.7 | 40.2 |
| Minimum per cent understory dispersion (PC) | 7.7 | 7.0 |
| Average per cent understory dispersion (PC) | 30.9 | 28.4 |
| Diversity of understory dispersion (PC, CV) | 1.5 | 1.2 |
| Understory dispersion sum times understory dispersion diversity (PC) | 46.1 | 37.4 |
| Maximum number of saplings per acre (PC) | 167.2 | 230.0 |
| Average number of saplings per acre (PC) | 93.2 | 117.8 |
| Diversity of saplings (PC,CV) | 1.0 | 1.0 |
| Sapling number sum times sapling number diversity | 95.2 | 122.7 |
| Maximum per cent canopy cover (PC) | 63.6 | 64.8 |

| Habitat characteristic | Gray-headed Junco | Dark-eyed Junco |
|---|---|---|
| Minimum per cent canopy cover (PC) | 17.8 | 14.4 |
| Average per cent canopy cover (PC, CV) | 42.5 | 41.6 |
| Diversity of canopy cover (PC,CV) | 1.7 | 1.4 |
| Canopy cover sum time canopy cover diversity (PC) | 72.3 | 57.1 |
| Minimum number of trees 3.1-6.0 in. DBH per acre (PC, CV) | 1.9 | 2.5 |
| Average number of trees 3.1-6.0 in. DBH per acre (PC) | 20.8 | 28.7 |
| Diversity of trees 3.1-6.0 in. DBH (PC, CV) | 0.8 | 0.7 |
| Maximum number of trees 6.1-9.0 in. DBH per acre (PC) | 35.0 | 41.0 |
| Minimum number of trees 6.1-9.0 in. DBH per acre (PC) | 0.3 | 0.7 |
| Average number of trees 6.1-9.0 in. DBH per acre (PC, CV) | 13.0 | 15.5 |
| Diversity of trees 6.1-9.0 in. DBH per acre (PC, CV) | 0.5 | 0.6 |
| Trees 6.1-9.0 in. DBH sum times diversity of trees 6.1-9.0 in. DBH (PC) | 6.5 | 8.7 |
| Maximum number of trees 9.1-12.0 in. DBH per acre (PC) | 23.3 | 30.0 |
| Average number of trees 9.1-12.0 in. DBH per acre (PC, CV) | 8.6 | 10.3 |
| Diversity of trees 9.1-12.0 in. DBH per acre (PC, CV) | 0.3 | 0.3 |
| Trees 9.1-12.0 in. DBH sum times diversity of trees 9.1-12.0 in. DBH per acre (PC) | 2.7 | 3.4 |
| Maximum number of trees 12.1-15.0 in. DBH per acre (PC) | 20.3 | 23.3 |
| Average number of trees 12.1-15.0 in. DBH per acre (PC, CV) | 7.5 | 8.7 |
| Diversity of trees 12.1-15.0 in. DBH (PC, CV) | 0.3 | 0.4 |
| Trees 12.1-15.0 in. DBH sum times diversity of trees 12.1-15.0 in. DBH (PC) | 2.3 | 3.4 |
| Maximum number of trees greater than 15.0 in. DBH per acre (PC) | 0.1 | 0.1 |
| Minimum number of trees greater than 15.0 in. DBH per acre (PC) | 2.3 | 0.8 |
| Average number of trees greater than 15.0 in. DBH per acre (PC, CV) | 44.0 | 42.9 |
| Diversity of trees greater than 15.0 in. DBH (PC) | 0.4 | 0.5 |
| Trees greater than 15.0 in. DBH sum times diversity of trees greater than 15.0 in. DBH (PC) | 18.6 | 21.8 |
| Basal area in board feet (PC) | 220.2 | 250.1 |

| Habitat characteristics | Gray-headed Junco | Dark-eyed Junco |
|---|---|---|
| Visibility at 0 to 2 feet | 81.7 | 79.5 |
| Height of singing bird in meters | 10.3 | 10.0 |
| Song tree height in meters | 14.4 | 13.0 |
| Lower canopy height in meters (CV) | 5.2 | 3.4 |
| Upper canopy height in meters | 14.7 | 15.5 |
| Greatest tree height in meters | 18.3 | 18.0 |

PC = characteristics considered for principal component analysis

CV = characteristics considered for canonical variable analysis

*Habitat Separation*

Only seventeen of the habitat characteristics could be transformed to a state that gave a homogenous variance (Table 1). Thus the other variables were eliminated in doing canonical variable analysis. Using this analysis, the territories for the five junco populations were ordered in a linear fashion arranged to maximize the differences in habitat relationships. Therefore, the mean canonical variable for each population is a measure of the maximum habitat differences between populations. These mean values for each study area were: New Mexico, 30.91; California 24.48; Oregon 19.42; Arizona, 18.40; and Nevada 4.05 (Table 2). There was a significant difference among the means for at least two or more states at the $\alpha = 0.05$ level of significance ($P \approx 0$).

The difference in the means between the Dark-eyed Junco population was small (5.06) whereas the difference between parapatric populations of the Dark-eyed and Gray-headed Junco was large (20.43) (see Table 2 and Figure 1). Between adjacent populations of the Gray-headed Junco, there were moderate differences (14.35 and 12.51), but the overall difference between extreme Gray-headed Junco populations was greater (26.86) than the difference between adjacent poulations of the Gray-headed and Dark-eyed Junco (20.43).

Canonical variables wer obtained from paired comparisons between each of the study areas to determine which of the areas were significantly different from each other in habitat characteristics. At the $\alpha = 0.05$ level of significance all areas were significantly different from each other with the exception of New Mexico and Oregon ($p = 0.09$) the extreme areas in the study, although these two areas were not adjacent along the canonical axis derived from all areas combined (Table 2). Different factors affected the separation when all areas were considered together than when paired comparisons were made.

When all areas were combined, average ground cover was the only significant factor separating populations. It also was the only significant factor separating territory habitats in New Mexi and Arizona, New Mexico and Nevada, and Californ and Nevada populations. The other significant vegetational feature that separated populations lower canopy height, which separated Oregon and Nevada populations. The other areas that were significantly different were not separable by an single factor but instead by a combination of factors.

## DISCUSSION

The ecological similarities within the junco complex have been well recognized (Amadon 1950; Peterson 1948; Mayr 1942; Miller 1941). Thatche (in Bent 1968) states that "presumably all junco are ecological equivalents and occupy the same niche in essentially similar habitats." Althoug Miller (1941) noted differences in the habitats different juncos with respect to moisture, studi of junco habitats have not stressed vegetational composition of individual junco territories. It has been shown that ecological and morphological studies may yield similar taxonomic results (Fujii 1969), thus a habitat study may aid in re olution of taxonomic problems.

Any study on habitat selection imposes limitations by its sampling method but the method used seemed to be adequate for studying an edge specie Another self-imposed limitation is set by the selection of characteristics which usually are visual and assumed to include the stimuli necessa for habitat selection.

This study did deal with habitats and general it showed that despite significant differences f population to population, based primarily on differences in amount of ground cover, these differences were not concordant with supposed junco ta nomic differences (American Ornithologist's Unior 1973). In fact there were greater differences within supposed species than between species, and

the ends of the cline were the least different of all when all populations were compared.

TABLE 2. Mean canonical variable scores in parenthesis for the territory habitats in each study area, and the canonical variable distance separating populations. The largest value is in the upper right with variables decreasing to the left and downward.

| Study area | California | Oregon | Arizona | Nevada |
|---|---|---|---|---|
| New Mexico (30.91) | 6.43 | 11.49 | 12.51 | 26.86 |
| California (24.48) | | 5.06 | 6.08 | 20.43 |
| Oregon (19.42) | | | 1.02 | 15.37 |
| Arizona (18.40) | | | | 14.35 |
| Nevada (4.05) | | | | |

These relationships were based on the maximal differences emphasized by canonical variable analysis. But the straightforward approach, using principal components analysis, showed the same general trends (Figure 2 and 3) but with less obvious habitat differences than with canonical variable analysis. Principal component analysis, with respect to naturally occurring vegetational properties, produce a representation of realized habitat niches. Again similarity was observed between populations of the Dark-eyed Junco (California and Oregon, Figure 2); while little similarity with respect to habitat niches was observed between Nevada and New Mexico populations of the Gray-headed Junco (Figure 3). In keeping with the concept that principal components are representative of realized habitat niches, many more habitat variables were used in principal components analysis than in canonical variable analysis (Table 1).

From the various types of analyses, it becomes apparent that habitat differences are rarely attributable to single factors but are associated

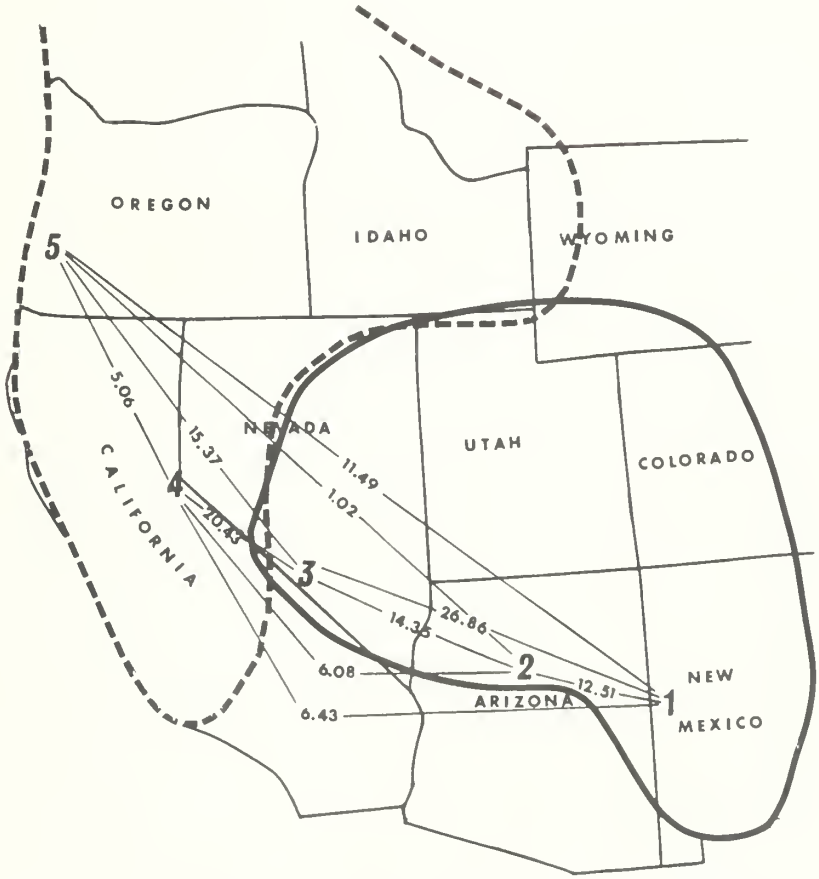



FIGURE 1. General ranges of the Gray-headed Junco (solid line) and Dark-eyed Junco (broken line) in western United States. Numbered areas represent study sites designated by state name. The values on the lines connecting the study areas are the differences between the mean canonical variable values for the respective areas.

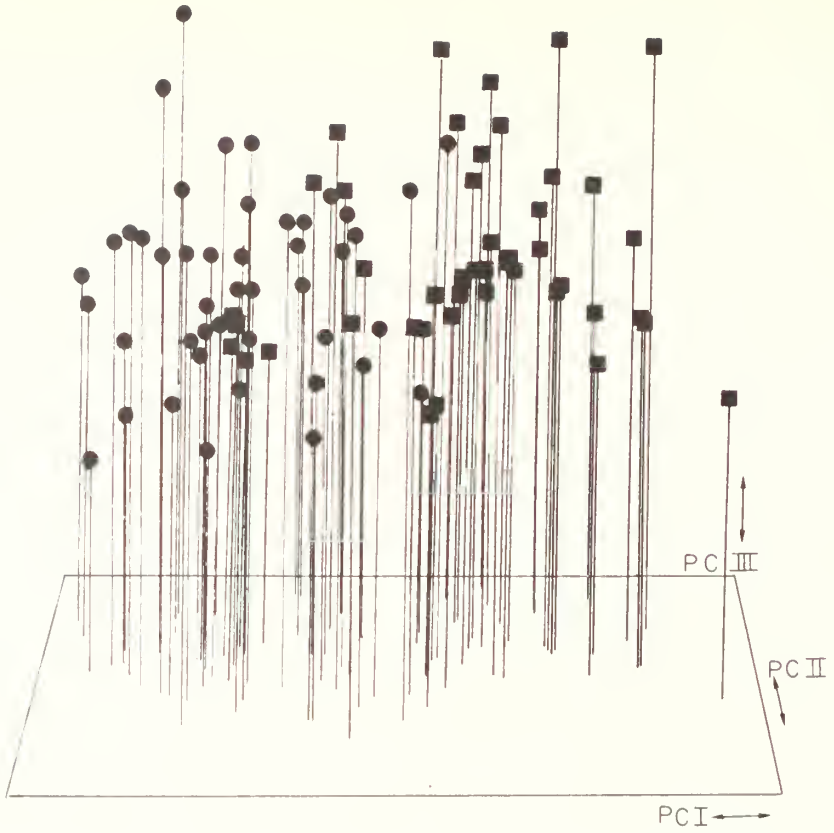



FIGURE 2. Three-dimensional habitat ordination of two Dark-eyed Junco populations according to the first three principal components. The first component, extending from right to left, is highly correlated with all the ground cover variables. The second principal component, extending from front to back, represents increasing canopy cover, while the third principal component, extending from low to high, represents the presence of middle sized trees. The 50 squares represent California territories and the 50 circles represent Oregon territories.

with several interacting factors. The habitat evidence does not support taxonomic separation in the juncos studied, because despite some significant differences, probably due to physiognomic differences, there is no consistent separation of taxa. In fact, more habitat differences occur within species than between species and the ends of the generic cline are the most alike in habitat.

*Multivariate Techniques and Management Problems*

In the management of biological species, plants and animals, the limiting factors and niche parameters must be identified prior to attempts at increasing desirable species while decreasing undesirable competitors. If a niche hyperspace can be constructed for the several species within a given community and paired comparisons made to determine which species differ significantly, a community ordination can be constructed (Figure 4).

From this community structure, it is readily apparent that management for one species dictates management for several species having similar requirements. Thus, desirable and undesirable species may have similar niche configurations and management to increase one desirable species may also increase an undesirable species. If species B (Figure 4) was considered undesirable and species C desirable, it would be necessary to manage for species D (hence C) rather than for C directly which would imply simultaneous management for both C and undesirable B. Note (Figure 4) that B and C are underscored (not significantly different) while B and D are not underscored (significantly different); thus some factor separates B from D but not C from D.

If the species are significantly different, the difference may be attributed to major differences in a single factor or subtle differences in multiple interrelated factors. A step-down procedure, sub-

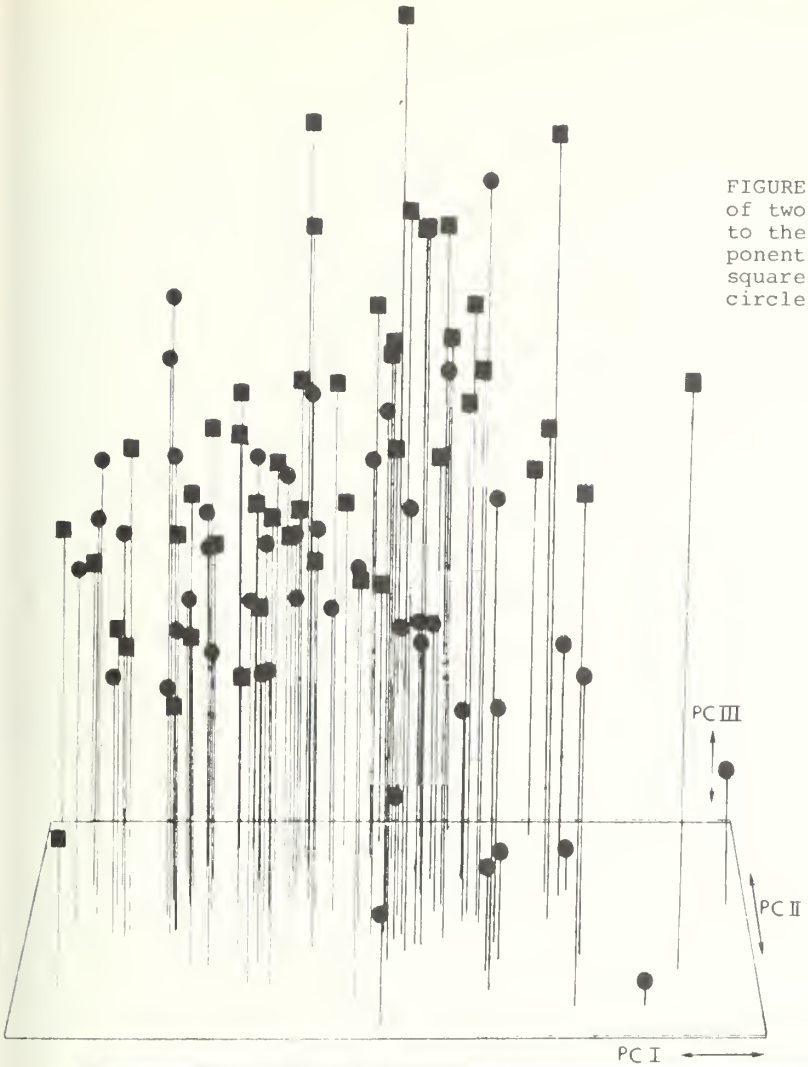



FIGURE 3. Three-dimentional habitat ordination of two Gray-headed Junco populations according to the first three principal components. The components correspond to those in Figure 2. The 50 squares represent Nevada territories and the 50 circles represent New Mexico.

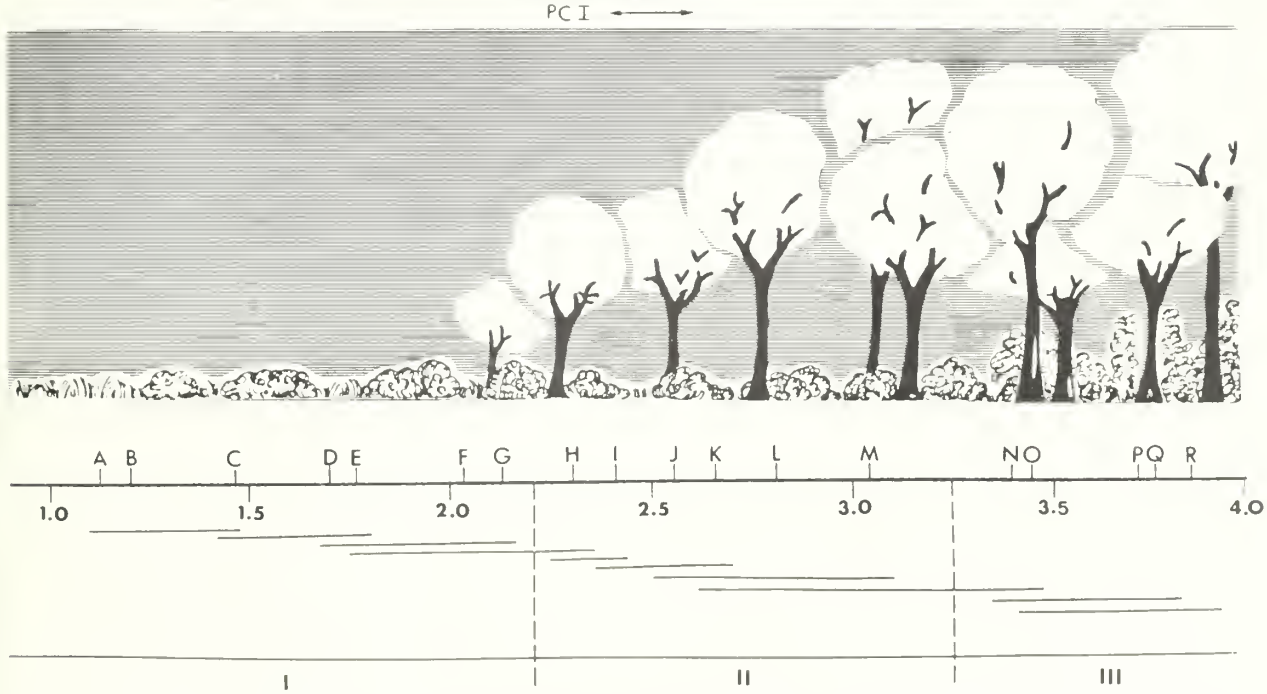



FIGURE 4. A habitat continuum with species ordination along a canonical variable axis. Each hypothetical species is designated by a letter and is placed along the axis relative to its canonical variable score. Overlapping horizontal lines underscore species groups lacking statistical significance in their habitat differences. The Roman numerals represent discernable avian communities within the habitat gradient.

routine to canonical variable analysis, would identify any single or multiple factors, if any exist, and separate the niche configurations of the two species.

Community management, in lieu of species management, presents a more feasible approach since desirable management is possible without the need to identify critical limiting factors for each species. Thus, a determination could be made concerning desirable communities rather than desirable species, and management could be for the broader aspects of the community, i.e., biomass of the trophic levels, species diversity, age and size structure, etc. Even when a continuum exists, distinct communities may still be recognizable, i.e., field, edge and forest (Roman numerals I, II, and III, respectively on Figure 4).

In situations where a single undesirable species becomes dominant, specific requirements for control need to be identified, however community management would in most cases be the feasible alternative for management programs. Both approaches require a knowledge of the limiting factors operant under local conditions.

LITERATURE CITED


AMADON, D. 1950. The species ---- then and now. Auk 67:492-498.

AMERICAN ORNITHOLOGISTS' UNION. 1973. Thirty-second supplement to the American Ornithologists' Union Check-list of North American Birds. Auk 90:411-419.

ANDERSON, T. W. 1958. An introduction to multivariate statistical analysis. John Wiley, N.Y.

BENT, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and allies. (part 2) U.S. Nat'l. Mus. Bull. no. 237.

BRECKENRIDGE, W. J. 1956. Measurements of the h[illegible]itat niches of the Least Flycatcher. Wilson Bull. 68:47-51.

CODY, M. L. 1968. On the methods of resources d[illegible]ision in grassland bird communities. Amer. Natur. 102:107-147.

COOLEY, W. W., and P. R. LOHNES. 1971. Multivari[illegible]e data analysis. John Wiley, N.Y.

FUJII, K. 1969. Numerical taxonomy of ecological characteristics and the niche concept. Syst. Zool. 18:151-153.

HUTCHINSON, G. E.1957. Concluding remarks. Cold Spri. Harb. Symp. Quant. Biol. 22:415-427.

JAMES, F. C. 1971. Ordination of habitat relatic[illegible]ships among breeding birds. Wilson Bull. 83: 215-236.

JAMES, F. C., and H. H. SHUGART. 1970. A Quantit[illegible]tive Method of Habitat Description. Aud. Fiel[illegible] Notes 6: 727-736.

KENDEIGH, S. C. 1944. Measurement of bird popula[illegible]tion. Ecol. Monogr. 14:67-106.

MAYR, E. 1942. Speciation in the junco. Ecology 23:378-379.

MILLER, A. H. 1941. Speciation in the avian genus *Junco*. Univ. Calif. Publ. Zool. 44:173-434.

MORRISON, D. F. 1967. Multivariate statistical m[illegible]ods. McGraw-Hill, N.Y.

PETERSON, R. T. 1948. Arizona Junco. Wilson Bull 60:5.

PIELOU, E. C. 1966. Species-diversity and patter[illegible] diversity in the study of ecological successi[illegible]. J. Theoret. Biol. 10:370-383.

WINKWORTH, R. E., and D. W. GOODALL. 1962. A cro[illegible]wire sighting tube for point quadrat analysis Ecology 43:342-343.

WIGHT, H. M. 1938. Field and laboratory technic wildlife management. Univ. Mich. Press, Ann Arbor.

# COLIMA WARBLER STATUS AT BIG BEND NATIONAL PARK, TEXAS

Roland H. Wauer[1]

The Colima Warbler (*Vermivora crissalis*) is a peripheral avian species in the United States, known only from the Chisos Mountains in Big Bend National Park, Brewster County, Texas (Figure 1). Its breeding range extends from the Chisos Mountains south for about 350 miles in disjunct mountains in the Mexican states of Coahuila, Nuevo Leon, and southwestern Tamaulipas. Its wintering grounds are on the Pacific slope of southern Sinaloa south to western Guerrero (Friedmann, et al., 1957).

The Colima Warbler is a little studied species, primarily because of the relative inaccessibility of its breeding habitats. Although its entire range within Big Bend National Park is protected from cultural impacts such as habitat removal, its status there must be assured. It is one of the Park's most significant resources, and the species' condition is useful as a remarkably fine indicator of the health of the natural ecosystem within the Big Bend National Park wilderness.

Baseline data were therefore obtained, and a long-term monitoring program was established. This paper serves as the initial report on the Colima Warbler's status within the Chisos Mountains ecosyste

## BACKGROUND

Until 1928 the Colima Warbler was considered to be a Mexican species only. Then on July 20 of that year, Frederick M. Gaige secured a specimen from near Boot Springs in the Chisos Mountains (Van Tyne, 1929). It represented only the 13th known species and the first from north of the border. Earlier specimens had been taken in the mountainous parts of southwestern Mexico, including the state of Colima in 1889, which resulted in the first description and naming of the bird (Salvin and Goodman, 1889).

An expedition to the Chisos Mountains for the purpose of finding a nest of the warbler was organized by Jossely Van Tyne of the University of Michigan in May 1932. On May 7, he succeeded in finding a Colima Warbler nest near Boot Spring where he reported the bird to be "quite common" (Van Tyne, 1936). Since the 1932 discovery many more nests have been found in the Chisos Mountains and south throughout its breeding range (Blake, 1949; Wauer, 1973; Wauer and Ligon (in press); Friedman et al., 1957; Sutton, 1935).

## METHODS OF STUDY

In order to learn more about the status of the Colima Warbler in the United States, I initiated a census in the Chisos Mountains during a four-day period of May 12 to 15, 1967. All locations where Colimas previously had been reported were searched by ten counters. Eight areas were selected for censusing, and the largest count areas were later divided into smaller, more practical units. All are situated between 5,600 feet (1707 meters) elevation on the eastern slope of Pulliam Ridge to the upper ridge of Emory Peak, the high point in the Chisos Mountains, 7,835 feet (2,388 meters) elevation (Figure 2). A total of 11 count units were utilized. Those units include:

1. Laguna Meadow Canyons include the drainages along the western side of Emery Peak and north and west of Laguna Meadow. This unit includes the area along the Chisos Basin trail to about 5,800 feet (1,903 meters) elevation.

2. Toll Mountain unit includes the upper slopes of the southeastern corner of the Chisos Basin, or the northwest side of the Toll Mountain, between approximately 6,000 to 6,800 feet (1,968 to 2,231 meters) elevation.

3. North Boot Canyon unit begins along the summit of Toll Mountain and follows the drainage to the Boot which lies at the lower edge of main Boot Canyon. This unit ranges in elevation from approximately 5,800 to 6,300 feet (1,903 to 2,067 meters).

4. Lower Boot Canyon unit runs from the Boot up Boot Canyon to Boot Spring and the Boot Spring cabin, and varies in elevation from 5,800 to 6,300 feet (1,903 to 2,067 meters).

5. Middle Boot Canyon is the heart of the Chisos Mountains. This unit includes Boot Canyon up canyon from the spring to the East Rim Trail fork, as well as the side canyon that runs northwest from the spring area to the pass between Boot Canyon and Blue Creek Canyon. Elevations range from 6,300 to 6,700 feet (2,067 to 2,198 meters).

6. Upper Boot Canyon unit extends above the East Rim Trail fork to the South Rim, and varies from 6,500 to 7,100 feet (2,133 to 2,319 meters) in elevation.

7. The East Rim Canyon unit includes several short canyons east of Boot Canyon between Juniper Canyon and the East Rim. Elevations vary from 6,400 to 7,100 feet (2,100 to 2,329 meters).

8. The South Rim Trail unit extends from near Laguna Meadow to the South Rim, an area along the western edge of the Chisos Mountains highlands. Elevation varies from 5,900 feet (1,936 meters) just above Laguna Meadow to 7,200 feet (2,362 meters) elevation near the South Rim.

9. Emory Peak Ridge unit runs along the upper ridge of Emory Peak from the trail in North Boot Canyon to the summit of the peak. This is the highest of the units and varying in elevation between 6,800 and 7,800 feet (2,231 to 2,559 meters).

10. Pine Canyon unit extends along the eastern edge of Lost Mine Trail and runs south and turning southeast between 6,500 and 5,600 feet (2,133 to 1,837 meters) in elevation.

11. Maple Canyon unit is a small isolated canyon along the eastern edge of Pulliam Peak on the western side of Green Gulch. Elevation there varies from 5,800 to 6,000 feet (1,903 to 1,969 meters).

Counters were asked to record information about the localities where birds were found, including dominant vegetation and degree of cover and slope, distance from the nearest singing or non-singing bird, and general behavior, including singing, courting, nest-building and aggressiveness.

[1]National Park Service, Southwest Regoional Office, Santa Fe, New Mexico 87501.



FIGURE 1.

The census total was derived from counts of singing birds as well as sightings. A singing bird was considered to be paired only when it was found singing 500 feet (164 meters) or more from another singing Colima. Sightings were treated in the same manner, while many sighted birds were considered to be a female of a pair if they were seen within a distance of 500 feet of a singing male. There is, of course, no way of knowing how many individuals were missed by the counters, although I am reasonably sure that no birds were counted twice.

As a follow-up to the 1967 census, additional counts were made on the second weekends of May in 1968, 1969, 1970, 1974, and 1976. All of the areas included in the 1967 census, plus one additional area that was added in 1968, were searched.

Also, in 1976, John Egbert assisted me by quantifying some of the data gathered by counters. He lived at Boot Spring from May 7 through June 20, and studied, among other things, Colima Warbler distribution, density and habitat preference within Boot Canyon and its immediate tributaries. Territory sizes and shapes were determined by observation of territorial birds, plotting their movements upon a topographic map (enlarged to 5 in. = 1 mile) and measuring the plots. Habitat preference was derived from circular plots located at five active nests and five nest sites found on previous years. The Colima Warbler is a ground-nester. The ten nests served as centers of the plots, and all vegetation within a 16 meter circumference was plotted and analyzed for abundance and significance to nest proximity.

## DISCUSSION

The Colima Warbler arrives at the Chisos Mountains as early as April 10 and may remain as late as September 19 (Wauer, 1973). In all instances counters found it in pinyon-juniper-oak or cypress-pine-oak associations (Wauer, 1971). Nests are built in shaded sites and concealed under grass, tree roots, or rock protuberances. Details about surface features and site selection will be addressed in a later paper.

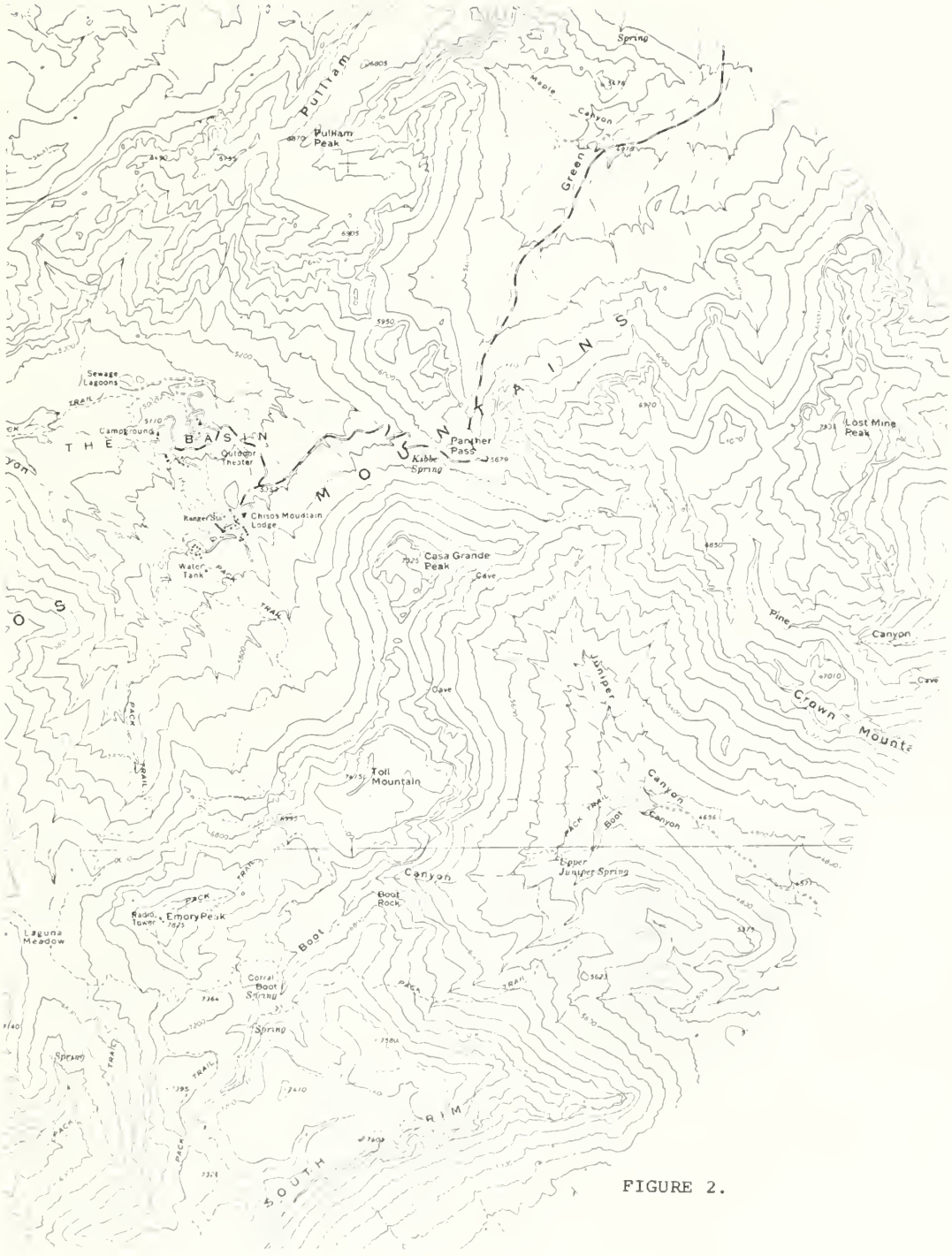

Pulliam
Pulliam Peak
Spring
Maple
Canyon
Green
MOUNTAINS
Sewage Lagoons
Campground
THE BASIN
Outdoor Theater
Ranger Sta.
Chisos Mountain Lodge
Water Tank
Panther Pass
Kibbe Spring
Lost Mine Peak
Casa Grande Peak
Cave
Pine
Canyon
Juniper
Crown
Toll Mountain
Boot
Canyon
Upper Juniper Spring
Boot Rock
Radio Tower
Emory Peak
Laguna Meadow
Corral Boot Spring
Spring
SOUTH RIM
TRAIL
PACK

FIGURE 2.

TABLE 1. Dominant territorial components in Boot Canyon.

| VEGETATION | NESTS: 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| TREES: | | | | | | | | | | |
| Pinus cembroides | x | x | x | x | x | x | x | x | x | x |
| Cupressus arizonica | x | x | | | | x | | x | x | x |
| Juniperus deppeana | x | x | x | x | x | x | x | x | | |
| Juniperus flaccida | x | x | x | x | x | x | x | x | | |
| Quercus Gravesii | x | x | x | x | x | x | x | x | x | x |
| Quercus grisea | x | x | x | x | x | x | x | x | x | x |
| Acer grandidentatus | x | x | | | | | | | x | x |
| Arbutus texana | x | x | x | x | x | x | x | x | x | x |
| SHRUBS AND OTHER WOODY PLANTS: | | | | | | | | | | |
| Nolina erumpens | x | x | x | x | x | x | x | x | x | x |
| Philadelphus microphyllus | x | x | | | | | | x | | |
| Holodiscus dumosus | | | x | | | x | x | x | | |
| Cercocarpus montanus | x | x | x | x | x | x | x | x | x | x |
| Rhamnus betulaefolia | | x | | | | | | | x | x |
| Vitis arizonica | x | x | | x | x | x | x | x | x | x |
| Garryi wrightii | x | x | x | x | x | x | x | x | x | x |
| Salvia regla | x | x | x | x | x | x | x | x | x | x |
| Xanthocephalum sphaerocephalum | x | x | x | x | x | | x | x | | |
| SUCCLENTS: | | | | | | | | | | |
| Agave Havardiana | x | x | x | x | x | | x | | | |
| Agave lecheguilla | x | x | | | | | | | | |
| Opuntia lindheimeri | x | x | x | x | x | x | x | x | x | x |
| Echinocereus triglochidiatus | x | x | x | x | x | x | x | | | |
| GRASSES: | | | | | | | | | | |
| Piptochaetium fimbriatum | x | x | x | x | x | x | x | x | x | x |
| Stipa neomexicana | | | x | x | x | x | | | x | x |
| Muhlenbergia Emersleyi | | | x | | | | x | x | | |

## HABITAT PREFERENCE

Preferred habitat was determined by the dominant territorial components within the ten 16-meter nest plots (Table 1). Twenty-four preferred plant species were selected. Ten of those occurred within all ten nest plots: Mexican pinyon (*Pinus cembroides*), Grave's oak (*Quercus gravesii*), gray oak (*Q. grisea*), Texas madrone (*Arbutus texana*), bear-grass (*Nolina erumpens*), mountain mahogany (*Cercocarpus montanus*), silktassel (*Garryi wrightii*), mountain sage (*Salvia regla*), Chisos pricklypear (*Opuntia Lindheimeri*), and pinyon-ricegrass (*Piptochaetium fimbriatum*).

Other dominant species (those found in at least 70% of the plots included, in order of abundance, Arizona grape (*Vitis arizonica*), drooping juniper (*Juniperus flaccida*), alligator bark juniper (*J. deppeana*), snakeweek (*Xanthocephalum sphaerocephalum*) and claret-cup cactus (*Echinocereus triglochidiatus*). Species found with at least 30% of the plots included, in order of abundance, Arizona cypress (*Cupressus arizonica*), Havard agave (*Agave havadiana*), finestem needlegrass (*Stripa neomexicana*), bigtooth maple (*Acer grandidentum*), bush sockspiraea (*Holodiscus dumosus*), birchleaf buck+horn (*Rhamnus betulaefolia*), mockorange (*Philadelphus microphyllus*), and bull muhly (*Muhlenbergia Emersleyi*).

Several additional plant species, although not dominant within the ten 16-meter plots, were obvious within the breeding territories. Those species were used for foraging and singing posts by Colimas, and include Emory Oak (*Q. empryii*), snow berry (*Symphoricarpos rotundifolius*), lechuguilla (*Agave leceguilla*), and goldeneye (*Virguiera dentata*).

## POPULATION DYNAMICS

The mean total Colima Warbler population of the six count years was 58.66 pairs, or 117.32 individuals. Totals of 45 pairs of Colimas were recorded in 1967, 65 pairs in 1968, 83 pairs in 1969, 59 pairs in 1974, and 52 pairs in 1976 (Table 2).

Colima Warbler populations in the Boot Canyon units exhibited good stability over all six counts. North Boot Canyon counts were 3, 3, 4, 4, 2 and 4 with a mean of 3.33. Lower Boot Canyon counts were 5, 5, 5, 6, 5, and 5, with a mean of 5.16.

Middle Boot Canyon counts were 11, 13, 20, 13, 9 and 10, with a mean of 12.66. And upper Boot Canyon counts were 4, 10, 10, 12 and 8 (a side canyon of this unit was missed in 1967), with a mean for the latter five years of 10.

Stable populations also were detected in the Laguna Meadow canyons where counts of 5, 11, 8, 6, 7 and 11 were recorded, with a mean of 8. And Toll Mountain area counts were 2, 2, 2, 4, 1 and 3, with a mean of 2.33. The mean of the six primary units is 6.75, and the mean of the annual counts for the six primary units is 38.5.

Six of the count units were found to exhibit less stable Colima Warbler populations. Two of these units--Pine and Maple Canyons--are fringe areas that are isolated away from the centralized Boot Canyon population hub by more than one mile (1.8 kilometers). Pine Canyon is located northeast of Boot Canyon and is divided into upper and lower units by a pouroff of approximately 200 feet. The upper canyon is 6,500 feet (2,133

meters) in elevation, and the lower canyon runs from 6,300 to 5,600 feet (2,067 to 1,707 meters) in elevation. Although Pine Canyon was not censused in 1967, two pairs of Colima Warblers were found in upper Pine Canyon in 1968, none in 1969 and 1970, one in 1974, and two in 1976. Also in 1976, a singing bird was recorded in lower Pine Canyon at approximately 5,700 feet (1,855 meters) elevation.

Maple Canyon was censused every year, except 1974, and only in 1976 was a singing Colima Warbler recorded there. Both canyon areas contain pine and oak woodlands similar to that within the Boot Canyon units, except for the absence of Arizona cypress in Maple Canyon.

Unstable conditions also were found in three units adjacent to the Boot Canyon population hub, in the East Rim canyons, along the South Rim Trail, and on the Emory Peak ridge. East Rim canyon counts were 9, 10, 25, 8, 6, and 3, with a mean of 4.6. And the Emory Peak ridge counts were 3, 3, 0, 2, 2, and 2, with a mean of 2.0. The mean of the six secondary units is 3.02, and the mean of the annual counts for the six secondary units is 18.5.

## SUMMARY

Analysis of count units and comparisons with stable and unstable units suggest that fringe areas are utilized extensively during years that follow high population years. High populations generally depend upon precipitation amounts during the months prior to and during the nesting season of the previous year. Precipitation recorded in the Chisos Mountains (average of Chisos Basin and Panther Junction records) during January through August in 1966 amounted to 9.55, and 45 pairs of Colima Warblers were recorded in 1967. Precipitation amounted to 10.11 inches from January through August in 1967, and 65 pairs of birds were counted in 1968. January through

TABLE 2.

| COLIMA WARBLER CENSUS UNITS | ANNUAL CENSUS TOTALS 1967 | 1968 | 1969 | 1970 | 1974 | 1976 |
|---|---|---|---|---|---|---|
| Laguna Meadow Canyons: Canyons to west and south of meadow and along Chisos Basin Trail. Elevation 1903-2133. | 5 | 11 | 8 | 6 | 7 | 11 |
| Toll Mountain: Upper slopes along the southeastern corner of the Chisos Basin. Elevation 1968-2231 | 2 | 2 | 2 | 4 | 1 | 3 |
| North Boot Canyon: Pinnacles Pass to Boot Canyon pouroff. Elevation 1903-2067 | 3 | 3 | 4 | 4 | 2 | 4 |
| Lower Boot Canyon: Along drainage from Boot Spring to pouroff. Elevation 1903-2067 | 5 | 5 | 5 | 6 | 5 | 5 |
| Middle Boot Canyon: Above Boot Spring to East Rim Trail, and canyons north of spring to Emory Peak slope. Elevation 2067-2198 | 11 | 13 | 20 | 13 | 9 | 10 |
| Upper Boot Canyon: From East Rim Trail to South Rim. Elevation 2133-2329 | 4 | 10 | 10 | 10 | 12 | 8 |
| East Rim Trail: Canyons east of Boot Canyon toward East Rim and Juniper Canyon. Elevation 2100-2329 | 9 | 10 | 25 | 8 | 6 | 3 |
| South Rim Trail: Laguna Meadow to South Rim. Elevation 1936-2362 | 3 | 6 | 9 | 6 | 3 | 2 |
| Emory Peak Ridge: Along trail from North Boot Canyon to summit. Elevation 2231-2559 | 3 | 3 | 0 | 2 | 2 | 2 |
| Pine Canyon: Drainage east of end of Lost Mine Trail. Elevation 1837-2133 | ? | 2 | 0 | 0 | 1 | 3 |
| Maple Canyon: Drainage on Green Gulch side of Pulliam Ridge. Elevation 1903-1969 | 0 | 0 | 0 | 0 | ? | 1 |
| TOTALS | 45 | 65 | 83 | 59 | 48 | 52 |

August precipitation amounted to 13.68 inches in 1968, and 83 pairs of Colimas were counted in 1969. Only 6.93 inches of precipitation were recorded during the January to August period in 1969, and 59 pairs of Colimas were recorded on the 1970 census. An average of 10.76 inches were recorded at the two stations in 1973, January through August, and 48 pairs of birds were recorded. And 12.60 inches of precipitation were recorded in 1975, and 52 pairs of Colima Warblers were recorded on the 1976 census.

Evidence from the six counts indicate that the Colima Warbler population within the Chisos Mountains is relatively stable, and, at least for the time being, does not require additional protection. Further studies, including those that relate to fire, or the lack of fires in the Boot Canyon system are presently underway. At this time, I do not recommend the designation of threatened or endangered status for the species.

## LITERATURE CITED


BLAKE, EMMET R. 1949. The nest of the Colima Warbler in Texas.

FRIEDMANN, H., L. GRISCOM, R. MOORE, and A. MILLER. 1957. Distributional checklist of the birds of Mexico. Pt. 2. Pacific Coast Avifauna.

SALVIN, OSBERT, and F. D. GODMAN. 1879-1904. Biologia Centrali-Americana, Aves. 3 vols.

SUTTON, G. M. 1935. An expedition to the Big Bend Country. Cardinal, 4:3-14.

URBAN, EMIL K. 1959. Birds of Coahuila, Mexico. University of Kansas Publ. Mus. Nat. Hist., 11, no. 8:443-516.

VAN TYNE, JOSSELYN. 1929. Notes on some birds of the Chisos Mountains of Texas. Auk, 46: 204-206.

VAN TYNE, JOSSELYN. 1936. The discovery of the nest of the Colima Warbler. Misc. Publ. Mus. Zool. Univ. Mich., no. 33:5-11.

WAUER, ROLAND H. 1971. Ecological distribution of birds of the Chisos Mountains, Texas. Southwestern Nat. 16:1-29.

WAUER, ROLAND H. 1973. Birds of Big Bend National Park and Vicinity. Univ. Texas Press, Austin.

WAUER, ROLAND H., and J. D. LIGON. (in press) Distributional relations of breeding avifauna of four southwestern mountainranges. Proceeding of the Symposium of the Biological Resources of the Chihuahuan Desert. National Park Service.

# CONCENTRATED AVIAN UTILIZATION OF AN EARLY FLOWERING CENTURY PLANT (*AGAVE HAVARDIANA*)

Robert L. Neill and Therese M. Allen[1]

## INTRODUCTION

Wauer (1971) considers the Big Bend Agave (*Agave havardiana*) a prominent member of the Sotol-Grassland Association and the Pinyon-Juniper-Oak Woodland in Big Bend National Park. The first association generally extends from an altitude of 3500 to 5500 feet and is characterized by sotol (*Dasylirion leiphyllum*), grama grasses (*Bouteloua* sp.), honey mesquite (*Prosopis glandulosa*), whitethorn acacia (*Acacia constricta*), Skeleton-leaf goldeneye (*Viguiera stenoloba*), evergreen sumac (*Rhus virens*), lechuguilla (*A. lechuguilla*) and other shrubs and grasses. The Pinyon-Juniper-Oak Woodland, the largest of the plant zones, starts at the upper limits of the Sotol-Grassland Association and extends to many of the higher peaks and mesas. Common plants in the woodland include pinyon pine (*Pinus cembroides*), drooping juniper (*Juniperus flaccida*), alligator juniper (*J. deppeana*), evergreen sumac, skunkbush sumac (*R. trilobata*), Gray's (*Quercus grisei*), Emory (*Q. emoryi*) and Grave's oak (*Q. gravesii*) and the mountain sage (*Salvia regla*). Grasses include Arizona threeawn (*Aristida arizonica*), blue grama (*Bouteloua gracilis*), bull muhly (*Muhlenbergia porteri*) and plains lovegrass (*Eragrostis intermedia*).

*Agave havardiana* grows vegetatively for eight to twenty years forming a rosette of lance-shaped leaves. At the end of the vegetative period a fifteen to twenty foot flowering stalk is produced which has from five to twenty branches, each bearing up to 300 yellow flowers per cluster. The *Agave* flowers from late April to early May in the lower elevations and into August in the higher elevations with occasional plants persisting into October. The plant dies once mature seeds are set but not until copious amounts of nectar are produced in the numerous tubular flowers. The nectar along with flower parts and associated insects, serves as the main attraction for the many species of birds in these plant associations.

In this context, then, the purpose of the study was twofold: (1) to determine nectar composition in terms of phenolics, carbohydrates and amino acids and (2) to document the concentrated avian utilization of the *Agave* that occurs at the first flowering plant of the year.

## METHODS AND MATERIALS

*Nectar analyses.* Nectar was collected from five separate flower clusters with pipettes in July 1976. The nectar was refrigerated at 5°C for future analysis. Carbohydrate tests conducted on the nectar were Barfoed's test (disaccharide), Dial's test (pentose), Seliwanoff's test (ketose) and Benedict's test (reducing sugars). To verify identity of the sugars the nectar (50λ) was spotted on Whatman 3MM chromatographic paper and cochromatographed with known sugars suggested from the previous tests. The chromatograms were developed by the descending technique in three different solvent systems: ethyl acetate, pyridine and water (12:5.4 v/v, EPW), n-butanol-acetic acid-water (63:10:27. v/v, BAW) and 6% aqueous acetic acid (6% AA). The papers were air dried and dipped in a sugar solution stain and the sugars located. The quantitative estimate of soluble carbohydrate present in *Agave* nectar was made using the anthrone reagent (Witham, Blaydes and Devlin 1971).

Amino acids in the nectar were detected by spotting 150λ on Whatman 3MM chromatographic paper. The papers were developed by the descending technique in BAW in the first dimension and 6% AA in the second dimension. Amino acids were located using a 0.2% ninhydrin reagent spray.

A routine inspection of amino acid chromatograms under UV light indicated the presence of phenolic compounds in *Agave* nectar. To characterize these substances 150λ of nectar was spotted on Whatman 3MM chromatographic papers. These were developed in BAW-6% AA and were observed under short (2537 A) and long (3360 A) UV light, the fluorescing and absorbing spots were marked and $R_f$'s determined. The papers were then dipped in diazotized sulfanilic acid, diazotized p-nitroaniline and ferric chlorise-potassium ferricyanide and examined for reacting spots (Bray et al. 1960; Smith 1960).

*Avian activity at the first flowering* Agave. From 19 to 22 May 1976, the avian activity was observed at the first flowering plant of the year. The study plant, located just south of the Basin Campground in the upper Sotol-Grassland, has three inflorescence clusters in flower with the remaining twelve branches not yet flowering. The plant was observed for a total of eighteen hours (distributed over the four day period) with 7 X 35 binoculars at a distance of 30 feet. The species, specific activity, length of visit and time of day were noted at each visit to the plant.

## RESULTS AND DISCUSSION

*Nectar analyses.* Carbohydrate analyses indicated the presence of disaccharides, reducing and ketose sugars. When unknown nectar constituents were cochromatographed with known sugars sucrose, glucose and fructose were found to be the predominant carbohydrates present. The anthrone test results indicated a concentration of 340 micrograms of soluble carbohydrate per milliliter of nectar. This concentration may be somewhat lower than originally produced by the plant due to some microbial degradation. This carbohydrate concentration of nectar does offer a substantial energy source to visiting birds and explains in part the high rate of avian activity. In addition, insects floating in the nectar offer an important potential nitrogen source to bird species with high metabolic demands and turnover rates.

The amino acids present in the nectar were in trace amounts and may have leached from pollen grains or from insects floating in the nectar rather than being produced in significant amounts by the plant.

The presence of phenolic compounds in nectar represents an unusual nectar constituent. Six different phenolic compounds were located and isolated but their identity was not determined (Table 1). The function of these compounds in nectar is not known but it is suggested that phenolics may be antimicrobial agents built into the

[1] Biology Department, The University of Texas at Arlington, Arlington, Texas 76019.

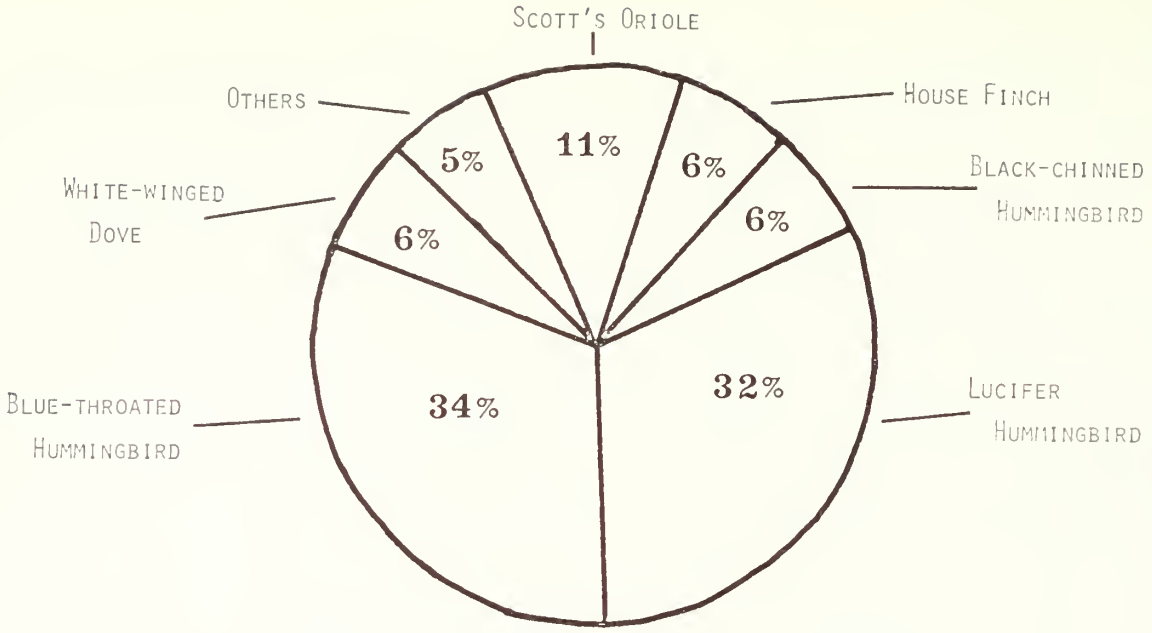
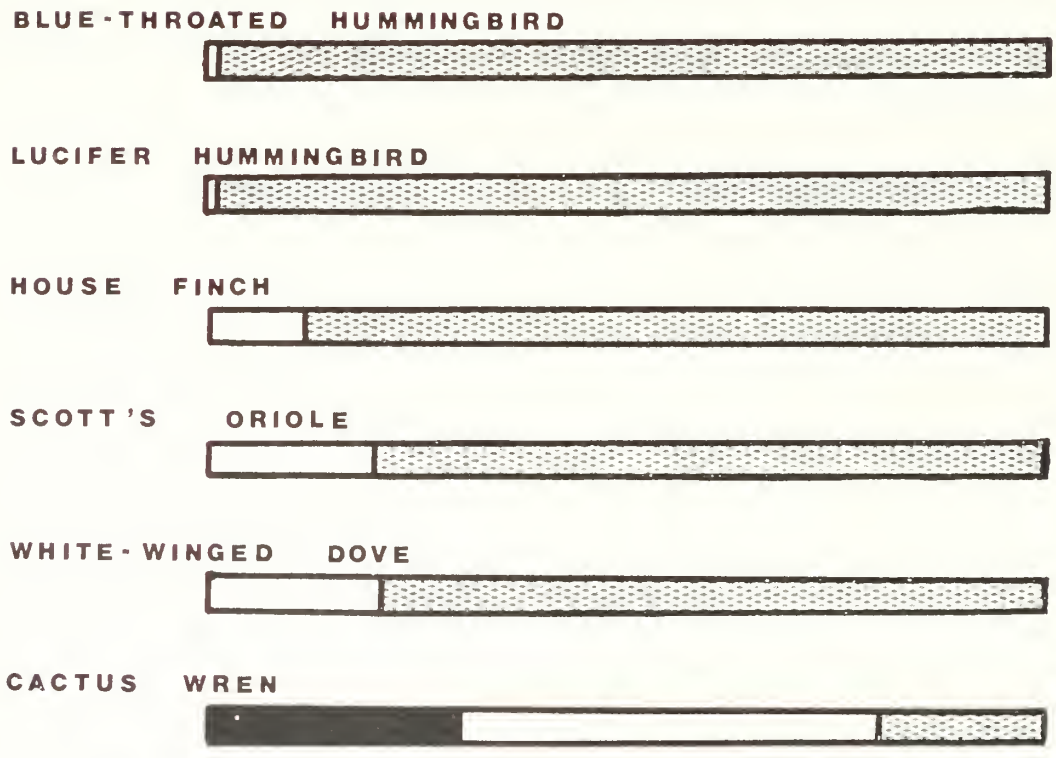



FIGURE 1. Avian utilization of *Agave havardiana*.




PERCENTAGE TIME SPENT FEEDING , PERCHING , AND SINGING
ON AGAVE HAVARDIANA TREL.

FIGURE 2.

TABLE 1. Chromatography of suspected phenolics from *A. havardiana* nectar.

| Compound | Rf's on Whatman No.3 | | Fluorescence | | Reagent colors | | |
|---|---|---|---|---|---|---|---|
| | BAW | 6% AA | Long UV | Short UV | P-Nit. | Sulfan. Acid | $FeCl_3$ $K_3Fe(CN)_6$ |
| Unknown #1 | .12 | 0 | - | - | Rose | - | - |
| Unknown #2 | .13 | .71 | Blue | Blue | - | - | Blue |
| Unknown #3 | .09 | .71 | - | - | Rose | Rose | - |
| Unknown #4 | .08 | .95 | - | - | Rose | Yellow | - |
| Unknown #5 | .09 | .80 | Blue | Blue | Rose | - | Blue |
| Unknown #6 | .18 | .77 | Blue | Blue | - | - | Blue |

plant's metabolism. Such a mechanism would insure the attractiveness of nectar to potential pollinating insect and bird species.

*Concentrated avian activity at the first flowering* Agave. Of the twenty-one avian species observed within 50 m of the *Agave*, twelve utilized the plant as a food source, territorial post or perching site (Table 2). During the observation period the Cactus Wren was the only species that used the plant as a singing perch. Ten of the twelve species utilized the *Agave* as a food source with the Brown Towhee and Varied Bunting being the exceptions.

Four hundred sixty-eight avian visits were recorded in 18 hours of observation distributed over four days. The total time spent at the plant by avian species was 20,057 seconds or 30% of the total observed time.

The predominant species active at the *Agave* based on the number of visits were the Blue-throated Hummingbird (34%), Lucifer Hummingbird (32%) and Scott's Oriole (11%) (Figure 1). Eighty percent of the total combined activity was in feeding (Figure 2). Of the six most frequent visitors to the plant only the Cactus Wren did not use the *Agave* primarily as a food source. The Lucifer Hummingbird (35%), White-winged Dove (25%), Blue-throated Hummingbird (21%) and House Finch were the major species observed feeding based on the number of seconds. Blue-throated Hummingbird (42%) and Lucifer Hummingbird (28%) accounted for more than half of the total number of feeding visits with the Blue-throat being the most aggressive hummingbird about the plant in interspecific encounters. Generally the *A. havardiana* is primarily a food source to most species that visit it.

The avian activity at the first flowering century plant is substantially greater than occurs even two weeks later when several century plants are in flower and present alternate food sources. The greatest number of visits (40) was recorded at 1400 hours which approaches the hottest part of the day (Figure 3). This activity represents a 2- to 10-fold increase in activity when compared to activity observed later in the summer.

The time spent in feeding showed peak utilization at 900 and 1700 hours when all species are considered (Figure 4). Hummingbird peak feeding periods in seconds occurred at 1400 hours with a smaller burst of feeding activity at 1800 hours. Such a feeding pattern is dissimilar to patterns later in the summer when hummingbird feeding shows three peak periods with a general increase throughout the day reaching maximum activity just before dusk. The midday feeding activity (1400) may be correlated with the low amount of nectar available per flower thus more time is required to obtain a comparable amount of nectar per hummingbird visit.

In summary, the *A. havardiana* offers a nectar rich in soluble carbohydrates for the many avian visitors. The high sugar concentration may serve as an important energy source to the birds and also be osmotically unfavorable to the establishment of microorganisms. Phenolic compounds may also be antimicrobial agents thus helping to maintain the high sugar content.

Avian activity is extremely concentrated in May when very few plants are in flower. The feeding patterns at the *Agave* differ from those observed later in the flowering season. The reduced activity at the later dates may be due to the relocation of some of the birds to other areas of the park (e.g., Blue-throated Hummingbirds to canyon areas), the passage of migrants and territorial establishment by hummingbirds. Many birds may shift feeding locations to plants where competition is less intense.

TABLE 2. Avian activity observed at *Agave havardiana*

| Species | Feeding | Perching | Singing |
|---|---|---|---|
| White-winged Dove | F | P | |
| Lucifer Hummingbird | F | P | |
| Black-chinned Hummingbird | F | | |
| Rivoli's Hummingbird | F | | |
| Blue-throated Hummingbird | F | P | |
| Ladder-backed Woodpecker | F | | |
| Cactus Wren | F | P | S |
| Scott's Oriole | F | P | |
| Summer Tanager | F | P | |
| Varied Bunting | | P | |
| House Finch | F | P | |
| Brown Towhee | | P | |

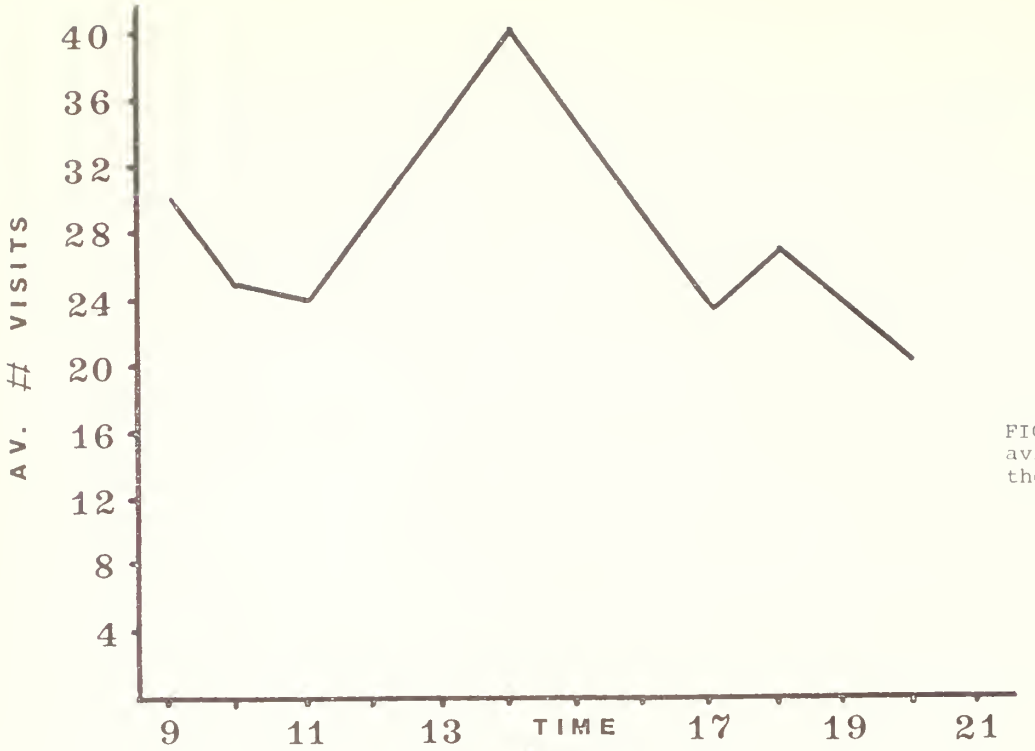



FIGURE 3. Average number of avifaunal visits vs. hour of the day.

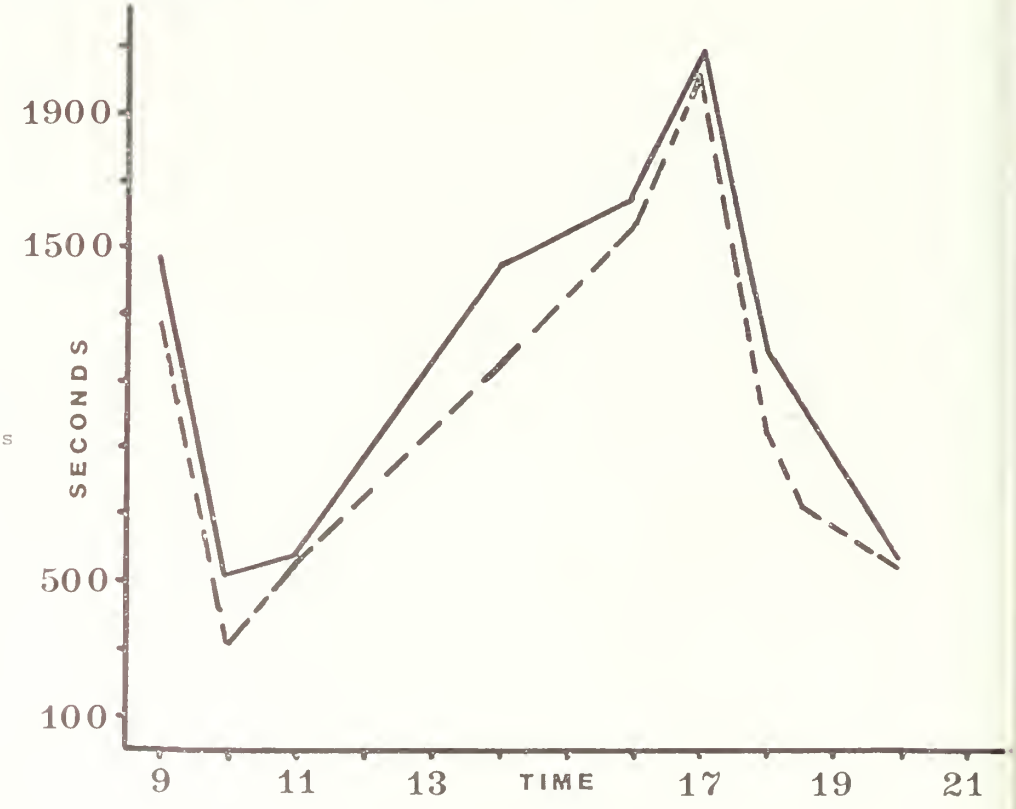



FIGURE 4. Average total avifaunal activity (———) and average total avifaunal feeding activity (----) in seconds vs. hour of the day.

LITERATURE CITED

BRAY, H. G., W. V. THORPE and K. WHITE. 1950. The fate of certain organic acids and amides in the rabbit. 10. The application of paper chromatography to metabolic studies of hydroxybenzoic acid and amides. Biochem. J., 46:271.

CORRELL, D. S. and M. C. JOHNSTON. 1970. Manual of the vascular plants of Texas. Texas Research Foundation. Renner, Texas, 1881 p.

SMITH, I. (ed.). 1960. Chromatographic and electrophoretic techniques. Vol. I. Chromatography. Interscience Publishers, Inc., New York, 617 p.

WAUER, R. H. 1971. Ecological distribution of birds of the Chisos Mountains, Texas. Southwest. Nat., 16:1-29.

WITHAM, F. H., D. F. BLAYDES and R. M. DEVLIN. 1971. Experiments in plant physiology. Van Nostrand Reinhold Co., New York.

# AVIFAUNAL ASSOCIATES OF *AGAVE HAVARDIANA* TREL., IN BIG BEND NATIONAL PARK

Therese M. Allen and Robert L. Neill[1]

## INTRODUCTION

This study of avian utilization of the Big Bend Century Plant, *Agave havardiana* Trel., is concerned primarily with the use of the plant as a food source. The Big Bend *Agave* is found is two ecological associations in Big Bend National Park: the Sotol-Grassland Association of the Chisos Mountains foothills (920-1680 m) and the Pine-Oak Association (1070-1990 m). The usual avian summer residents of the latter association include the Acorn Woodpecker, Ash-throated Flycatcher, Broad-tailed Hummingbird and the Mexican Jay. Typical among the birds of the Sotol-Grassland Association are the House Finch, Scott's Oriole, Black-chinned Hummingbird and the Ash-throated Flycatcher (Wauer 1971).

This century plant, a member of the Amaryllidaceae family, grows vegetatively for eight to twenty years as a rosette of grayish-green, broadly lance-like leaves. It then sends up a stalk, four to seven meters tall, from which alternately project branches bearing large clusters of tubular yellow flowers. Each of these fleshy flowers, 7-8cm in height, is full of sweet-smelling nectar. After flowering, usually during the period of May through August, the century plant produces fruit and then dies (Correll & Johnston, 1970).

The nectar represents a potential food source and is the major avian attraction of the century plant. The purpose of this study, then, was to clarify and identify patterns of avian utilization of *A. havardiana* during its flowering period. Bird activity about the plant was categorized, observed and timed. Such parameters as diurnal nectar production, temperature and light intensity were measured to determine their influence on the pattern of daily bird usage of the plant.

Comparatively little is known about avian utilization of a particular plant species. Some similar studies have been made in Central America. Leck (1969) briefly examined bird feeding behavior on a common tropical fruit tree. Stiles and Wolf (1970) looked at hummingbird territoriality at a tropical fruit trees. Emlen (1973)observed territorial aggression in wintering warblers at a Bahama *Agave* plant. None of these studies however touched on desert bird ecology.

## METHODS AND MATERIALS

Data were gathered over 316 hours, May through July during 1975 and 1976. A total of seven plants were studied intensively - all of the same approximate size and number of branches at elevations between 1554 and 1615m in the Basin area of the Chisos Mountains. Observations of these seven plants were made continuously for fourteen hours between 0700 and 2100 hours for nine days total and at least once at each plant. The rest of the data were taken for nine hours during peak activity periods extending from 0800 to 1300 hours and 1700 to 2100 hours. Observations were made with 7 x 35 binoculars and the information recorded on tape. Light intensity was measured in footcandles with a light meter at fifteen minute intervals while temperature was recorded at thirty minute intervals at a height of about one meter above ground level. Observations were made from a distance of nine meters from the plant - close enough for accurate identification of the hummingbirds yet far enough away to be of minimal disturbance.

To establish the diurnal nectar production pattern of *Agave havardiana*, nectar samples were extracted from ten flowers with a calibrated syringe at three hour intervals for three twenty-four hour periods between 29 June and 2 July from the same plant. Different flowers were used each twenty-four hour sampling period. Nectar was collected from interior flowers of a cluster not observed to be visited by avian species.

## RESULTS AND DISCUSSION

A total of twenty-six species were observed on *Agave havardiana* over the twenty-eight days of intensive observations during the two summers (Table 1). Another fourteen species were observed on other plants during general observation periods throughout the study and during a class project of U.T.A.'s field biology course in late June, 1974. The activity was divided into three categories - feeding, perching, and singing. Note that while only six species were observed to sing while on the plant, half the species were seen to both feed and perch.

The seven most common species as shown in Figure 1, in order of increasing total time on the plant, gives the percentage of each of the three types of avian activity for each species. The Cactus Wren used the century plant mainly as a territorial post as shown by the proportionately large amount of perching time. The hummingbirds, with their high metabolic rates, spent most of their time feeding at the plant. The seven most common species varied somewhat from 1975 to 1976. Birds common one year may be rare the next or vice versa. The Lucifer Hummingbird, the third most common bird about the *Agave* in 1976 (1768 seconds), was almost non-existent the previous year (76 seconds). In 1975, these birds not only came into the Big Bend area late but also in small numbers. Cactus Wrens were more often seen around the *Agave* in 1975, dropping from fourth to sixth most common species in 1976. shifting species data could be accounted for by different availabilities of food plants or prey, the general yearly shifting of bird populations, and a longer period of intensive study in 1976.

One conclusion that can be drawn at this point is that feeding appears to be the major avian use of the century plant. Avian feeding utilization of the century plant, when broken down by species, shows the Black-chinned Hummingbird and House Finch to be the predominant species (Figure 2). These two species were only recorded on the plant together twice however, and then they appeared unaware of each other. The House Finch was observed to eat flower parts as well as nectar while the Black-chinned and Lucifer Hummingbirds fed predominately on nectar. The White-winged Dove and Ladder-backed Woodpecker were observed to eat flower parts, flower-associated insects and to drink nectar.

[1]Biology Department, The University of Texas at Arlington, Arlington, Texas 76019.

TABLE 1. Avifaunal species list and types of activity observed on *Agave havardiana* Trel.

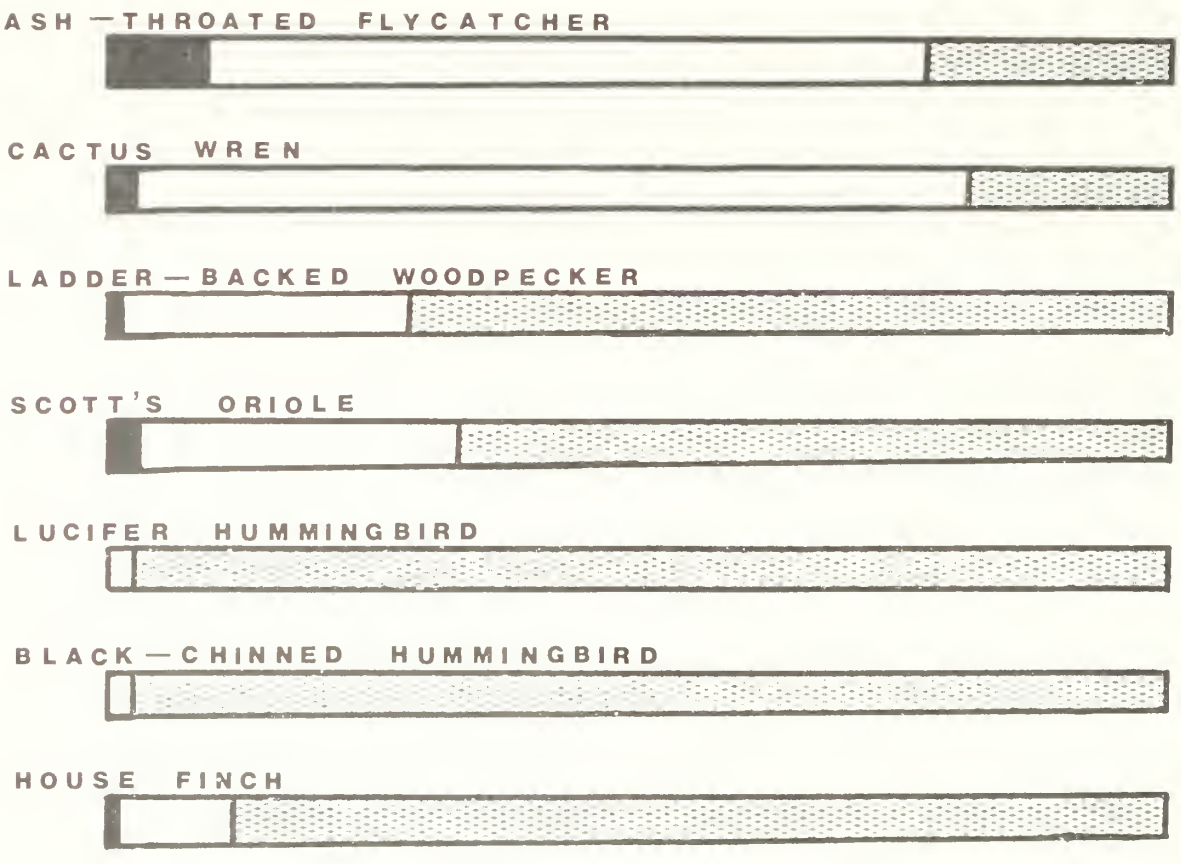
| Species | Species activity[a] | | |
|---|---|---|---|
| Band-tailed Pigeon | F | P | |
| White-winged Dove | F | P | S |
| White-thoated Swift | F | | |
| Lucifer Hummingbird | F | P | |
| Black-chinned Hummingbird | F | P | |
| Broad-tailed Hummingbird | F | | |
| Rivoli's Hummingbird | F | | |
| Blue-throated Hummingbird | F | | |
| Hummingbird sp. | F | P | |
| Ladder-backed Woodpecker | F | P | S |
| Ash-thoated Flycatcher | F | P | S |
| Say's Phoebe | F | | |
| Flycatcher sp. (small) | | P | |
| Barn Swallow | F | | |
| Common Raven | F | P | |
| Cactus Wren | F | P | S |
| Yellow-rumped Warbler | | P | |
| Scott's Oriole | F | P | S |
| Brown-headed Cowbird | | P | |
| Summer Tanager | F | P | |
| Pyrrhuloxia | | P | |
| Black-headed Grosbeak | | P | |
| Varied Bunting | F | P | |
| House Finch | F | P | S |
| Brown Towhee | | P | |
| Rufous-crowned Sparrow | | P | |

[a]F = Feeding; P = Perching; S = Singing.

The pattern of plant utilization as a function of time was recorded as was the duration o each bird's visit. However, here only the two major species will be examined.

The Black-chinned Hummingbird's mean visit tion time was eighteen seconds. However the nu ber of these visits increased significantly as day progressed (Figure 3). Linear regression d show this increase to be significant to the 0. level. The Black-chin, in general showed three major feeding peaks - 0900, 1530, and 20-2100 hours. The first peak coincides with the time sun actually rises above the rim of the Chisos the plants are in full sunlight. The second pe is immediately before the daytime high temperat and indicates that a hummingbird's high metabol rate demands nourishment more often than morni and evening. The large evening feeding burst just before sunset may be important to tide the over for the night. During the day a male Blac chin was commonly observed defending an *Agave*, his feeding territory, from other hummingbirds.

House Finches often came in pairs or group of three or four and had a mean visit time of 1 seconds. Their activity did not increase as th day progressed, but dropped off after 1800 hour Other feeding peaks occurred from 0800-0900, 11 1200, 1400 and 1600 hours. The House Finch, in addition to drinking nectar from the more inter flowers of a cluster which the hummingbirds cannot reach, were observed to eat anthers and cor las.




PERCENTAGE TIME SPENT FEEDING , PERCHING , AND SINGING
ON AGAVE HAVARDIANA TREL. - 1976

FIGURE 1.

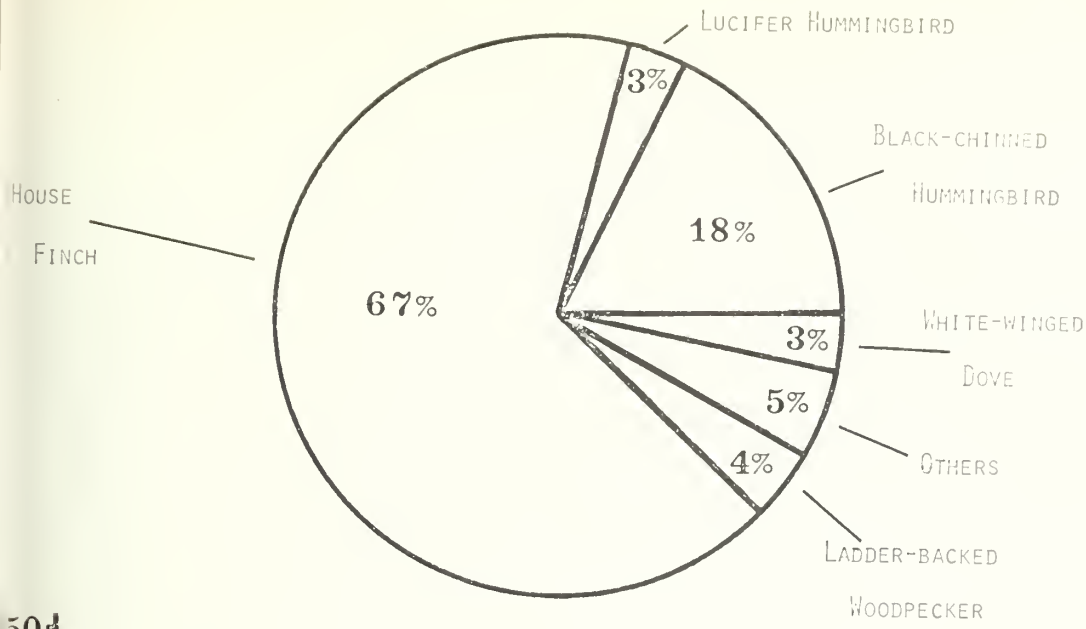



FIGURE 2. Avian feeding utilization of *Agave havardiana* Trel. (1975 and 1976).

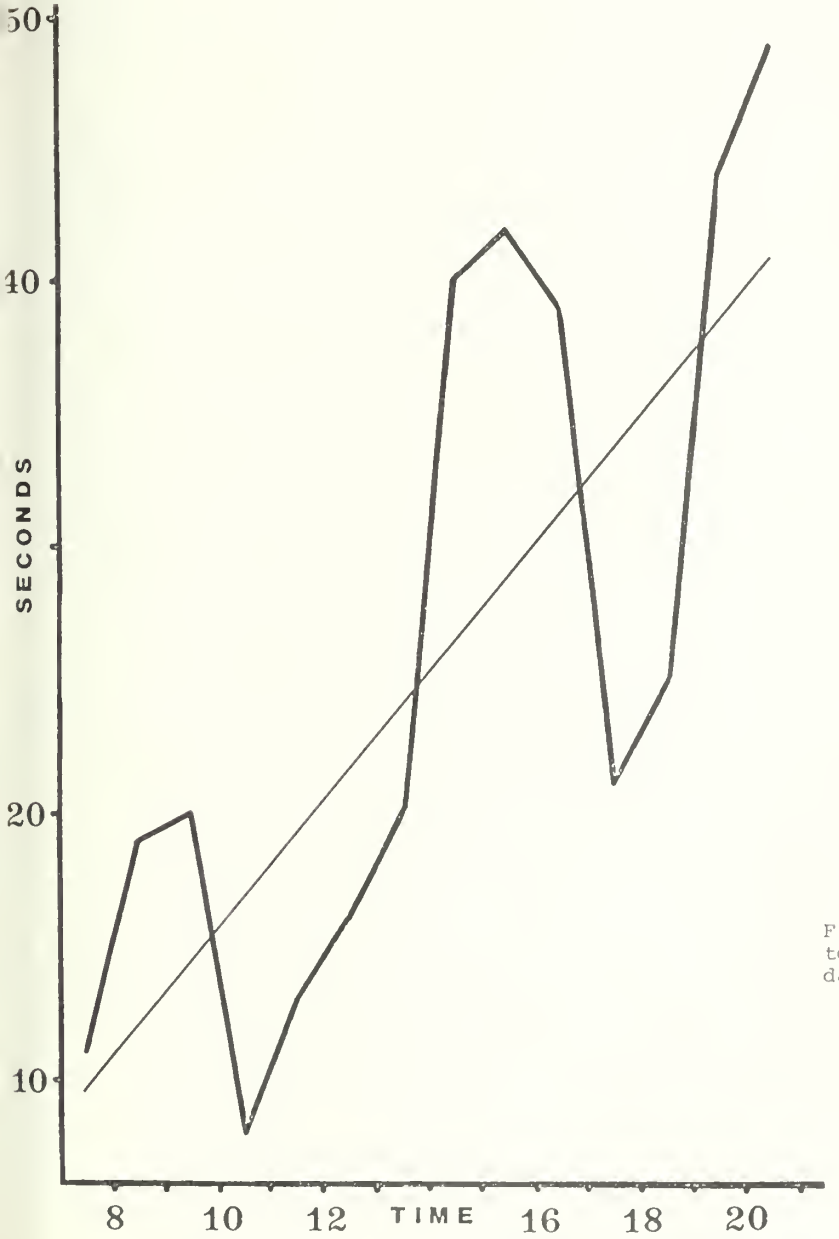



FIGURE 3. Black-chinned Hummingbird average total activity in seconds vs. hour of the day, 1976.

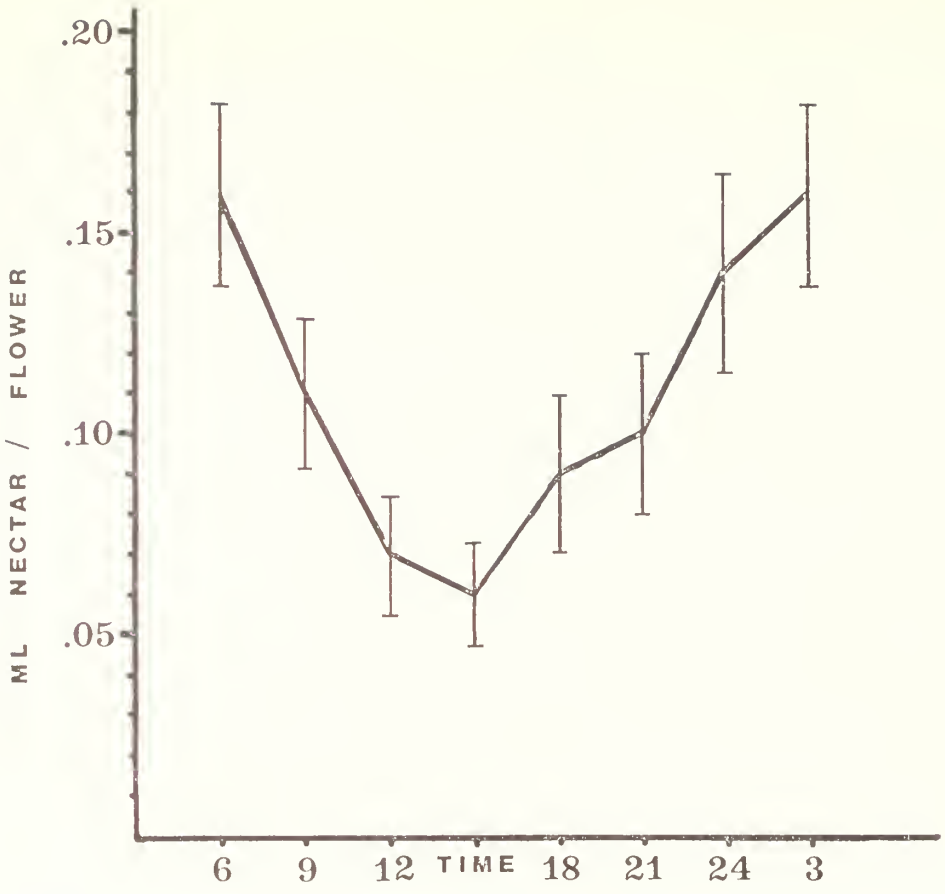



FIGURE 4. Nectar production of *Agave havardiana* Trel. vs. hour of the day.

As has been pointed out, the nectar of the Big Bend Century Plant is its main attraction as an avian food source. Rich in soluble carbohydrates up to two milliliters may accumulate per blossom. And consider that there may be up to 300 blossoms per flower cluster! Diurnal nectar production studied thus far seems to follow a pattern of high morning and nighttime nectar production with a low in midafternoon (Figure 4). The high late afternoon activity peaks of the House Finch and Black-chinned Hummingbird may represent the more frequent visits necessary to find the same amount of nectar acquired in fewer visits in the morning and evening.

Avian activity was not found to be significantly correlated with either ambient temperature or light intensity. In 1975, the influence of people on bird activity about the *Agave* was observed. Little effect was found on the bird usage pattern itself but the type of bird species were somewhat different. Avian species such as the House Finch, that seem very "people-compatible", were more numerous around campground century plants.

In conclusion, the Big Bend Century Plant was observed to provide both food and moisture to its avifaunal associates. Birds were also observed catching and eating insects which also find this *Agave* to be a suitable food source. Indeed, avian utilization of *Agave havardiana* was found to encompass a broad spectrum of avian activity.

LITERATURE CITED

CORRELL, DONOVAN S. and M. C. JOHNSTON. 1970. Manual of Vascular Plants of Texas. Texas Research Foundation, Renner, Texas. 1881 pp.

EMLEN, JOHN T. 1973. Territorial aggression in wintering warblers at Bahama *Agave* blossoms. Wilson Bull. 85:71-74.

LECK, CHARLES F. 1969. Observations of birds exploiting a Central American fruit tree. Wilson Bull. 81:264-269.

STILES, F. GARY and LARRY L. WOLF. 1970. Hummingbird territoriality at a tropical flowering tree. Auk 87:467-491.

WAUER, ROLAND H. 1971. Ecological distribution of birds of the Chisos Mountains, Texas. Southw. Natur. 16:1-29.

# WADING BIRD PRESERVATION IN EVERGLADES NATIONAL PARK

James A. Kushlan[1]

Everglades National Park was established to preserve the subtropical wilderness ecosystems of southern Florida. High among the causes for which its founders fought was the abundant bird-life of the area, especially the great population of wading birds that caught the attention and aroused the concern of the American public. These birds were not only conspicuous elements of the fauna but were also critical to the ecological functioning of their ecosystem (Kushlan 1976a). Everglades National Park (Figure 1) is a large area of several diverse but intimately related ecosystems. The management goal of this park service area is to perpetuate the natural functioning of these systems in their essential wilderness character. Thus with the park's large size and ecologically sound management goals, it should be expected that the future of its wading bird resources should be secure. Unfortunately they are not. The reasons for their ecological insecurity serve as lessons in the design and management of natural reserves.

## WADING BIRDS IN THE EVERGLADES

Southern Florida wading birds include 16 species of herons, bitterns, ibis, spoonbills and storks. Their historic nesting populations have fluctuated considerably over the past century (Figure 2). The estimated primeval populations were reduced in the 1800's because of plume hunting but made a significant recovery by the 1930's (Robertson and Kushlan 1974). Populations again fell thereafter because of habitat changes until by 1975 the nine most abundant species numbered only about 130,000 birds (Kushlan and White 1977). Population changes within the area of the park were even more drastic than those in south Florida as a whole. Under natural conditions most of the birds nested in the lower Everglades, in what is now Everglades National Park. By 1975, the populations nesting in the park had been reduced to 20% of the remaining south Florida population. These 25,400 birds represent 97% reduction from population levels in the park area during the previous century. Thus reduction of both regional and especially park populations has been severe.

To judge the causes for the decline and predict the future of park wading bird populations, it is useful to examine the responses of individual species to environmental changes. Two for which data are available include the species that is presently and was historically the most abundant wading bird in the Everglades, the white ibis (*Eudocimus albus*), and one of the most specialized species, the wood stork (*Mycteria americana*). These have been studied by Kushlan (1976a, 1976b) and Kushlan et al. (1975), respectively, and the data below draw from these studies.

The white ibis is usually the most abundant species nesting within the large inland colonies. Since 1962 it has nested in the southern Everglades of Everglades National Park only irregularly (Figure 3). This is because the species has responded to changing environmental conditions by shifting colony sites from traditional locations within the park to other areas (Figure 4). The traditional park sites are now seldom used by ibis, and its largest colonies have recently been located north of the park. Colonies are established when and where food availability becomes adequate. Thus the white ibis population appears to be persisting regionally because of its ability to move out of the park to other areas of south Florida.

The wood stork has not changed nesting sites rapidly and continues to nest near its traditional sites in Everglades National Park. The nesting population in the park has declined since 1962, yearly fluctuations now being within measurement error of available techniques (Figure 5). The traditional nesting period is November and December and nesting begun in these months was successful in about half the years (Figure 6). Before 1972 most nesting began in these months but after 1962 nesting shifted to later months and consequently nesting failed more often (Figure 6). After 1962 the timing of nesting correlated with the rate at which the Everglades dried (Figure 7). Abandonment of colonies was also related to hydrologic conditions (Table 1). Water level rises in excess of about 3 cm caused desertion of colonies. The wood stork depends on high concentrations of fish made available by rapidly falling water levels during the dry season. Rising water levels cause dispersal of these concentrating fish, decreasing their availability to nesting storks. Thus the remnant wood stork population that has remained in the park depends on specific water conditions that have not been adequate to permit successful nesting at a natural frequency.

TABLE 1. Relation of water level rises to desertion of nesting colonies by Wood Storks.

| Month of nesting | Magnitude of water level rise | |
|---|---|---|
| | <3 cm | >3 cm |
| 1 | 0%[a] (4)[b] | 100% (1) |
| 2 | 0% (1) | 100% (13) |
| 3 | 0% (1) | - (0) |

[a]Percentage of instances of desertion.

[b]Number of instances of water level rise.

There have been two aspects to the recent decline in wading bird numbers in the interior Everglades. From the 1930's to the early 1960's, a regionwide decline was associated with general loss of foraging habitat. In 1962 the levee system nearly enclosing shallow reservoirs called Water Conservation Areas (Figure 1) was completed immediately north of the park and surface water movement into park marshes was changed from a shallow, broad-fronted surface to a regulated discharge restricted to four spillways. Several changes in nesting patterns noted above correlate with the installation of these structures during 1962 and ecological processes of the Everglades depend on the volume, seasonality and spatial distribution of surface water discharge from upgradient areas, the interruption and channelization of this discharge alters the functional characteristics of the park systems dependent on it and thus the ecological viability of those systems and that of some of its component species populations.

[1]National Park Service, Everglades National Park, Homestead, Florida 33030.

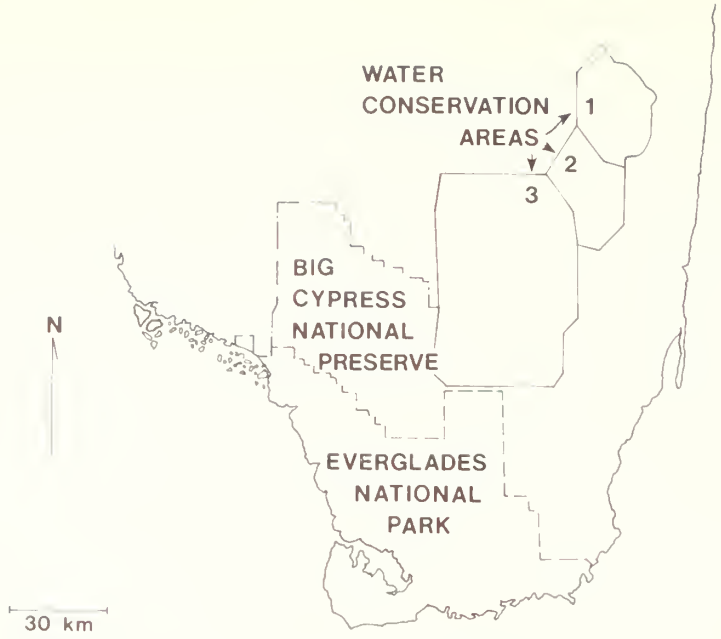



FIGURE 1. Map of southern Florida showing the contiguous preserves of Everglades National Park, Big Cypress National Preserve and three Water Conservation Areas.

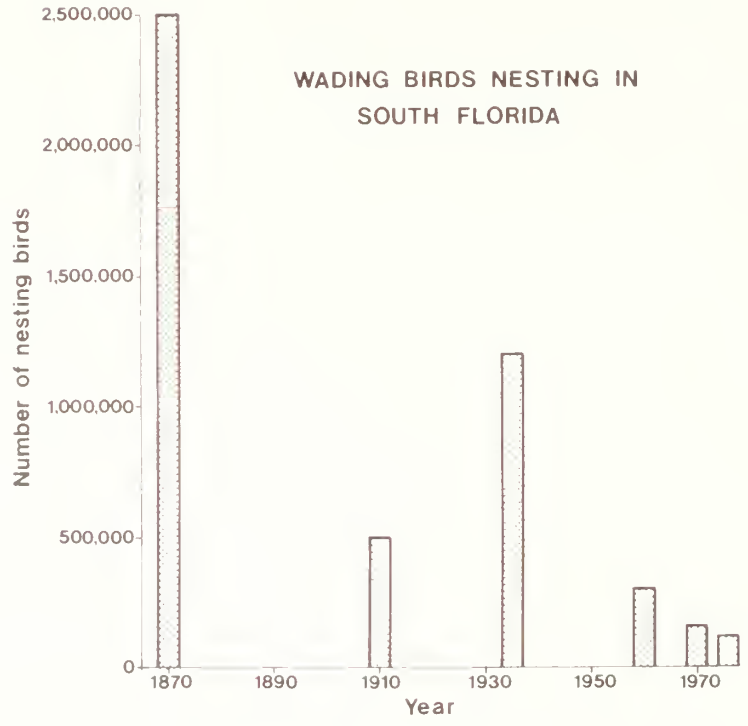



FIGURE 2. Estimated wading bird populations nesting in southern Florida. Years graphed are those for which estimates are available.

Evidence from wading bird ecology suggests that the natural ecological processes are not being perpetuated in the park. The adaptability of a generalized species such as the white ibis permits it to make range changes to accommodate changing conditions. It thus appears able to achieve an equilibrated regional population. However selecting habitats north of its traditional areas of the southern Everglades may imply that feeding habitat in the park is now relatively unsuitable. The wood stork continues to use traditional nesting sites but its low success associated with high dependence on water conditions also implies that an altered ecological system exists. Conversely, movement of wading bird colonies out of the park and lowered impact of the decreasing wood stork population deprives the system of the ecological impact of these birds and further alters the systems functional characteristics.

Thus Everglades National Park does not appear to be maintaining some populations of wading birds. Since both park site and management strategy appear beneficial to preserving these species it becomes worthwhile to examine the roles of both in the preservation of the species components of Everglades and by extension of analogous preserves.

## THE ROLE OF SIZE

Determining the role of size in the perpetuation of nature preserves has not been an easy task, especially for those preserves on continents. Application of concepts derived from biogeographical theory have been discussed at length (e.g., Terborgh 1974, 1975; Sullivan and Shaffer 1975; Diamond 1975). However, purely theoretical species-area considerations have not yet been proven useful (Preston 1962). More autoecological approaches can also be taken (Simberloff and Able 1976). Setting the size limits of continental preserves at the critical habitat requirements of extinction-prone species has been suggested (Terborgh 1974; Sullivan and Shaffer 1975).

Everglades National Park is a large preserve, containing 5670 $km^2$, 7 to 9 times larger than the minimal areas proposed for a continental preserve by Sullivan and Shaffer (1975). The fresh and estuarine marshes and swamps composed about 4250 $km^2$. However the total preserved area of southern Florida is considerably larger (Figure 1). Everglades National Park is bounded by the Big Cypress National Preserve of 2370 $km^2$ and three Water Conservation Areas of 3490 $km^2$ that extend the effective area of preserved wetlands to over 10,000 $km^2$.

The existence of large contiguous preserved areas of wetland habitat provides a means of regional persistence of some populations. It may probably also maintain nesting wading bird populations in the park at higher levels than if these areas did not exist because they provided additional habitat. They nonetheless fail to insure the preservation of natural processes in Everglades National Park because the areas are isolated from each other by levees and roads that restrict or redistribute water flow and render each segment an independently functioning isolate. Previously, different areas of the system functioned synergistically. The impact of unusual water conditions in one area was probably soon diffused to other areas by the relatively unrestricted movement of surface water. This effectively buffered the system from atypical conditions and increased the year to year predictability of environmental events, particularly the geographic pattern of food availability, and made the southern Everglades the best wading bird habitat of the region. Now the southern Florida wetland ecosystem is functionally segmented despite its large area. What size alone failed to preserve were the functional characteristics of the system, still but faintly known, that depend upon the flow and natural movement of surface water from one area to another and the predictable regionwide pattern of drying that annually occurs in the dry season. By not preserving the entire functioning unit, the functional aspects of the system cannot be preserved intact.

This aspect of size is not accounted for by species-area considerations nor by consideration of species richness vs. habitat diversity alone. When a piece of an ecosystem is set aside as a preserve, the functional characteristics of the system within the preserved area will change. The nature of the new system will depend upon what parts of the original land area are preserved and upon land use changes adjacent to the preserve. If there are not adjacent changes and the preserve is not isolated structurally or ecologically, there should be few changes. As adjacent areas change however impact will also occur in the preserve. If the preserve is completely isolated quickly, change will also occur quickly. The consolidation of a new ecological system in a demarcated continental preserve will usually require time and will not be entirely achieved until changes in nearby land areas cease having additional impact. Only at such time, at a new level of organiization, does a continental preserve become sufficiently like an island preserve to exhibit an island-like self containment. At that point, in a stabilized ecosystem, species may still be lost because of size constraints. In such a new system these will be the least adundant and probably therefore the least critical species and the loss of such relatively rare species may bring about minimal additional change in the isolated system. In comparison with the initial system however the difference will be profound.

## MANAGEMENT STRATEGIES

Many management strategies exist for mature preserves. One often proposed is that of preserving organic diversity. Because of the key role of species richness in island biogeographic theory, applying such concepts to nature preserves is premised on accepting the management goal of preserving maximum species richness (Wilson and Willis 1974; Terborgh 1974; Sullivan and Shaffer 1975). This is generally, but not always (Wilson and Willis 1974), meant to be the richness of naturally occurring species. It is generally proposed that the preservation of ecosystem processes or of entire biological communities is necessary for species preservation. Preserving ecosystem processes is the management goal of many preserves including natural areas of the U.S. National Park Service (NPS 1975). Other acceptable management goals range to single species management. When natural habitats no longer support a critical population level, a preserve may be actively manipulated to conserve a species with the remainder of the ecosystem being altered and total species diversity reduced. Management calling for ecosystem perpetuation may also in practice be inimical to preservation of natural species richness. This is because ecosystem perpetuation may be approached but not achieved in many continental preserves as described above for Everglades National Park.

There undoubtedly exist management options yet to be elaborated that may result in achieving a closer approximation of natural processes in Everglades National Park albeit not a return to its natural ecologic state. If we assume that these exist and that implementation occurs, we may then project possible effects on species richness. In nesting wading birds, we can predict that white ibis will probably maintain a regional population that may or may not return in numbers to the park.

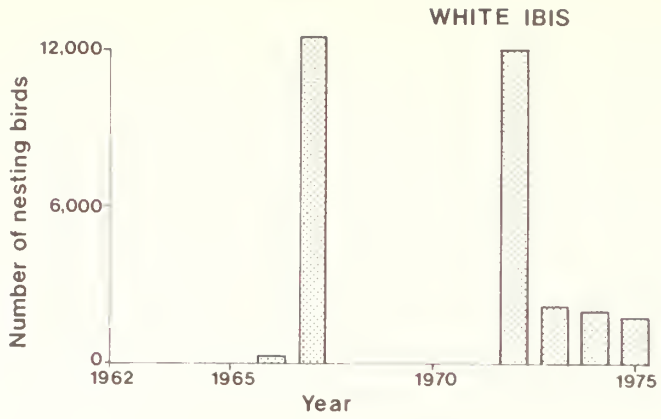



FIGURE 3. Number of white ibis nesting in interior Everglades National Park. No ibis nested in years for which there is no bar.

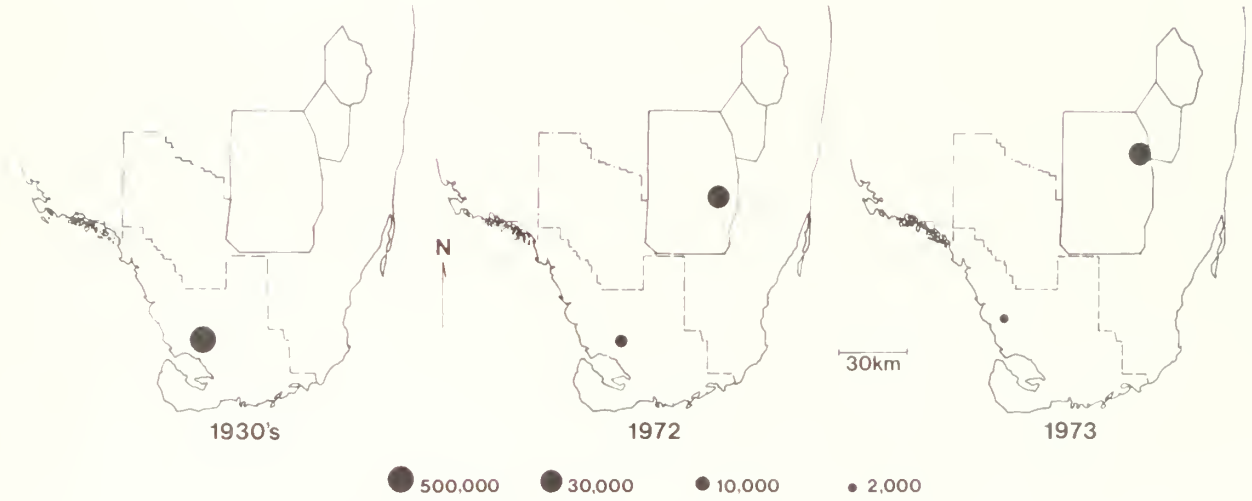



FIGURE 4. Location of white ibis nesting colonies in interior southern Florida. Size of dot indicates approximate magnitude of the nesting population.

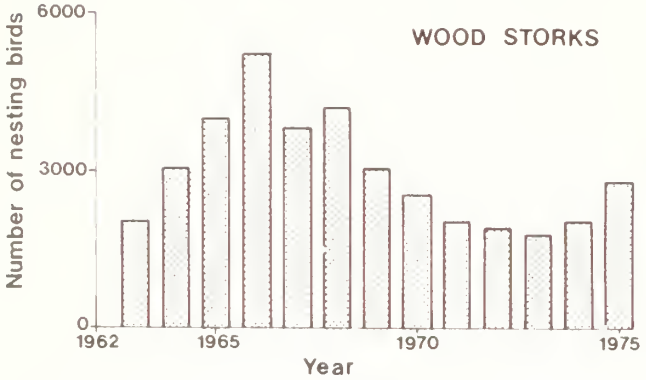



FIGURE 5. Number of wood storks nesting in interior Everglades National Park.

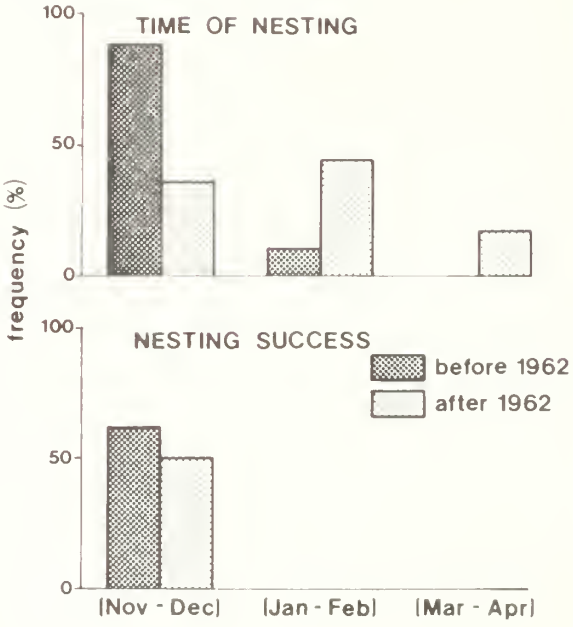



FIGURE 6. Timing and success of wood stork nesting in Everglades National Park before and after 1962. Time of nesting is expressed as a percentage of the total nesting attempts for two periods, 1953-61 and 1963-73. Nesting success is the percentage of the attempts made in each period that were successful.

►

Although we cannot predict its equilibrium population level, we can predict its probable continual occurrence at some level in the park. The wood stork may or may not be perpetuated in the park. Environmental conditions surrounding the park and changed equilibrium populations of associated species suggest that even the best management strategy may not be sufficient to perpetuate the wood stork in the park.

Thus a management dilemma is faced. The closest approach to maintaining most of the natural processes within the park may not be sufficient for maintaining natural species richness. In fact the relatively early truncation of the larger, more specialized members of ecological guilds is predictable in demarcated preserves. However on a management level important decisions must be made in the face of regional, or perhaps, continental extirpation of a species. Should the management strategy of a preserve attempting to perpetuate natural processes be altered for the benefit of that highly endangered species? In the case of the wood stork this might mean management accelerating drying rates or provisioning of artificial fish ponds. Or should a preserve attempt to achieve the closest approximation of natural conditions for most components of the system realizing the probable loss of species? The best may be a combined strategy. Large parks could be managed to preserve ecological processes and therefore preserve the vast majority of their biota, but may lose species. Additional preserves would be managed for the perpetuation of a particular endangered species. Recognizing the inevitability of extirpation in no way countermands the necessity to attempt to maintain all species as part of their naturally functioning ecosystem. Nor does it reduce necessity to maintain the worldwide rate of species extinction at a natural level. It does however pose the possibility of failure within limited areas and require the formulation of alternative strategies that do not disrupt the management of large preserves.

Such alternate strategies for managing an endangered species may pose a conflict in American preserves. The legal ability to manage for ecosystems at the expense of an extremely specialized species runs counter to endangered species regulations whereby an agency may undertake no action, including no action, that would further reduce critical populations of an endangered species. Perhaps providing in some areas for specific, highly manipulative management for individual species preservation and permitting in others management to approach as close as possible the maintenance of natural ecosystem processes despite some species loss may be the strategy that preserves as much as possible of the natural world.

## LITERATURE CITED


DIAMOND, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of nature reserves. Biol. Conserv. 7:129-146.

KUSHLAN, J. A. 1976a. Wading bird predation in a seasonally fluctuating pond. Auk 93:464-476.

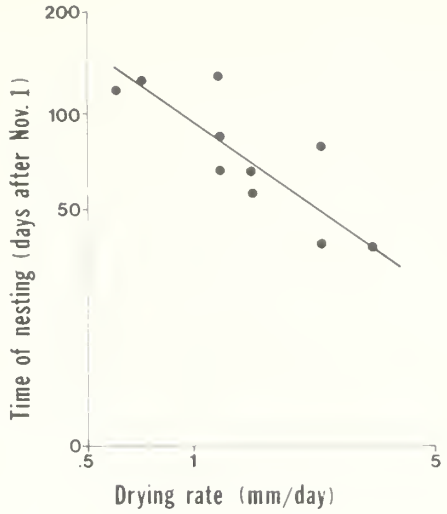




FIGURE 7. Relation between time of nesting of wood storks and the rate of drying in the southern Everglades.


KUSHLAN, J. A. 1976b. Site selection for nesting colonies by the American white ibis *Eudocimus albus* in Florida. Ibis 119:590-593.

KUSHLAN, J. A., J. C. OGDEN, and A. L. HIGER. 1975. Relation of water level and fish availability to wood stork reproduction in the southern Everglades, Florida. Openfile Rep. 75-434. U.S. Geological Survey, Tallahassee, Florida 56 pp.

KUSHLAN, J. A., and D. A. WHITE. 1977. Nesting wading bird populations in southern Florida. Fla. Sci. in press.

NATIONAL PARK SERVICE. 1975. Management objectives of the National Park Service. U.S. Dept. Interior, Washington, D. C. 155 pp.

PRESTON, F. W. 1962. The canonical distribution of commonness and rarity: Part II. Ecology 43: 410-432.

ROBERTSON, W. B., JR. and J. A. KUSHLAN. 1974. The southern Florida avifauna. *In* P. J. Gleason (ed.), Environments of south Florida: present and past. Mem. Miami Geol. Soc. 2: 414-452.

SIMBERLOFF, D. S., and L. G. ABLE. 1976. Island biogeography theory and conservation practice. Science 191:285-286.

SULLIVAN, A. L., and M. L. SHAFFER. 1975. Biogeography of the megazoo. Science 189:13-17.

TERBORGH, J. 1974. Preservation of natural diversity: The problem of extinction prone species. BioScience 24:715-722.

TERBORGH, J. 1975. Faunal equilibria and the design of wildlife preserves. pp. 369-380. Tropical Ecological Systems, Ecological Studies Vol. 11, Springer-Verlag.

WILSON, E. O., and E. O. WILLIS. 1974. Applied biogeography. pp. 522-534. *In* M. L. Cody and J. M. Diamond (eds.). Ecology and evolution of communities. Belknap Press, Cambridge, Mass.

# WHITE PELICAN REPRODUCTIVE FAILURES IN THE MOLLY ISLANDS BREEDING COLONY IN YELLOWSTONE NATIONAL PARK[1]

Kenneth L. Diem[2]

Surveys of white pelicans (*Pelicanus erythrorhynchos*) populations in North American suggest extensive changes have taken place since the early 1900's (Lies and Behle 1966; Vermeer 1970b). Colonies have disappeared, size of colonies has fluctuated, nesting locations have changed and new colonies have been established. Also, Vermeer and Reynolds (1970) and Anderson and Hickey (1972) report physiological disturbances associated with chemical pollutants which can produce changes in white pelican reproductive success. Decreases in reproductive success and general population declines in some fish-eating birds have been reported by Keith et al. (1970), Henny (1972), and Anderson and Anderson (1976). Considering these conditions, this paper updates the status of the white pelican Molly Islands colony in Yellowstone National Park from that reported by Diem and Condon (1967).

In relation to the size of other North American white pelican breeding colonies, the Molly Islands Colony is a minor colony consisting of ±450 adults (Lies and Behle 1966; Diem and Condon 1967). Despite its small size, the colony is unique for these reasons: (a) it is the only white pelican breeding colony in a national park; (b) the location of the colony at an elevation of 7,733 ft (2,357 m) is the highest recorded for any colony of the species; (c) discovered in 1890, the colony has had variable surveillance since 1917, with relatively intense monitoring since 1965; (d) the breeding population is composed of birds from both coasts of North America; and (e) the colony's nesting sites on the two Molly Islands change frequently with no predictable pattern.

The two Molly Islands are located approximately 0.25 mile (0.4 km) apart and 0.5 mile (0.8 km) from the southern shore of the Southeast Arm of Yellowstone Lake. Depending on seasonal fluctuations of the lake water level, Rocky Island has a central rocky knoll which may project 6-9 ft (1.8-2.7 m) above the lake's surface. Sandy Island is a flat, sand and silt covered island which projects 2.5 ft (0.6-1.5 m) above the water surface. With fluctuations of the lake water levels, the combined surface acreage of the islands carried between 0.75 and 1.25 a (0.3 and 0.5 ha).

A vigorous climate prevails on the Molly Islands. Annual precipitation of 20-30 in (51-77 cm) is uniformly dispersed throughout the year. Snow may fall in any month. Killing frosts occur up to early July and after the middle of August. Average July temperatures are in the mid-50 F (+ 10C) range with maximum temperatures reaching the mid-90 F (+ 32 C) range.

## METHODS

The small size of the islands and the unavoidable disturbance which would result from humans landing on the island, required that all nesting and fledging censuses be conducted from a boat 100-200 ft (31-61 m) from shore. As a result, some error in the nest counts probably occurred and the collection of clutch data was impossible. Censuses of young about to fledge were considered to be very accurate. The majority of the counts were made by the author with assistance from Park personnel in late June or early July and in August. On several occasions, counts were conducted solely by Park personnel.

Between 1972-74 attempts were made to use super 8 mm and 35 mm remote sensing cameras, described by Diem et al. (1973), to monitor human disturbance on the islands.

In 1971 and 1973, eggs from flooded pelican nests were collected to determine the amount and kind of organochlorine residues present. Analyses for PCB, DDT and its metabolites were conducted by the Denver Wildlife Research Center, U.S. Fish and Wildlife Service, using pooled samples. Thickness indices of the eggshells were calculated using Ratcliffe's (1967) formula of the weight of the shell divided by the product of the shell length and breadth in millimeters.

Climatological data were taken from the U.S. Department of Commerce (1961-75). Surface water data were taken from the U.S. Department of the Interior (1961-75) when they first established a water surface gauge on Yellowstone Lake at the Lake Hotel boat dock.

## RESULTS AND DISCUSSION

The reproductive success of the Molly Islands pelican colony from 1966 to the present is summarized in Figure 1. Even though a few young were produced in 1970, 1971, and 1974, those years are considered to have had total reproductive failure for these reasons: (a) the three surviving young in 1970 were only 50-60% developed on August 22 and no adults were observed to be present for the care of these young; (b) the four surviving young in 1971 had four adults nearby but the young were less than 50% of the way to fledging which left their survival in doubt; and (c) no young was seen in or around three nests remaining active on July 22, 1974, which again precludes any successful fledging in the Yellowstone fall environment.

Significantly, prior to 1970, total reproductive failure in the colony had never been recorded. No single factor has been identified as the cause of the 1970, 1971, and 1974 failures. Instead, these reproductive failures appear to have been

[1]Many individuals have contributed time and effort to this project and I am most appreciative for their invaluable assistance. Two individuals deserve particular recognition for their outstanding assistance and logistic support: Dale Nuss, District Ranger, and John Good, former Chief Park Naturalist. For her critical reading and preparation of the manuscript, I am indebted to my wife. I am grateful to the Denver Wildlife Research Center, U.S. Fish and Wildlife Service, for their analytical assistance. Financial and logistic support was received from the National Park Service, Yellowstone National Park, and the University of Wyoming.

[2]Department of Zoology and Physiology, University of Wyoming, Laramie.

caused by a complex interaction between energy supplies and demands and body burdens of sub-lethal chemical pollutants.

The white pelicans arrive at Yellowstone Park as early as April 19 and no later than May 23. Nest building and egg laying in the first nests begin in early May, 20-30 days before the ice cover on Yellowstone Lake disappears. These nesting pelicans arrange themselves into distinct colony subunits. One explanation for these discrete groupings of nests may be the expected variation in the states of physiological readiness for breeding in arriving pelicans. These variations could easily result from different (a) ages of the pelicans; (b) energy supply and demand conditions on the wintering grounds; (c) distances of migration; and (d) energy supply and demand conditions during migration. Prevailing environmental conditions on Yellowstone Lake following the birds' arrival could further modify that state of physiological readiness and influence the number of nesting groups formed.

A summary of the distribution of nests and nesting groups on the Molly Islands is presented in Table 1. Pelican preference for a nesting site appears to favor the Sandy Island. Varying degrees of snow cover or ice jams may play a role in this selection. Disturbances from coyotes may be another factor in these unexplained shifts between islands. Blokpoel (1971) and Vermeer (1970a) have described how mammalian predators caused reproductive failures in white pelicans in Saskatchewan and Alberta. No specific data on the pattern of ice melt around the Molly Islands is available. However, the difference in position of the islands and differences in water depths surrounding them could permit coyotes to travel over ice to one island and not the other. The timing and duration of coyote disturbance may also influence the total number of nests or renesting attempt.

Nesting shifts have even extended to an area outside Yellowstone Lake. In 1962, G. Schaller (pers. comm.) observed where pelicans had attempted their first nests on the shores of Heart Lake before abandoning the site in favor of the Molly Islands. Regardless of the cause, if nest site shifts take place after nesting has once commenced or is about to commence, there is an undesirable increased energy cost to the birds.

In the Yellowstone Lake environment, pelicans arriving in April and May have variable exposures to lake ice, shoreline snow cover and ambient air temperatures falling below 20 F (-6.7 C). The magnitude and duration of these exposures in relation to production of young pelicans between 1961 and the present are depicted in Figure 1. This figure does not incorporate the important matter of timing as indicated by the following: (a) a 12 in (30.7 cm) snowfall on May 13, 1962; (b) a 16 in (41 cm) snowfall on May 24, 1965; (c) a 0.5 in (1.3 cm) freezing or near freezing rainfall on May 21, 1970 and on May 31, 1971; and (d) a 7 in (18 cm) snowfall on May 20, 1974. It would appear that the foregoing climatic phenomena of the Yellowstone Lake area have played major roles in increasing or decreasing physiological stress in the breeding birds which in turn significantly influences (a) the number of nests built; (b) the quantity and quality of eggs laid; (c) nest attentiveness and "broodiness" of the adults; and (d) the hatching success of the eggs.

Also shown in Figure 1 is the pattern of snowmelt runoff entering Yellowstone Lake. Expression of the amount and duration of that snowmelt appears to be best stated as the number of days when snowmelt runoff has raised the level of Yellowstone Lake 4 ft (1.2 m) or more. The magnitude of the surface water curve in Figure 1 has been strongl influenced by runoff levels which exceeded 7 ft (2.1 m) in 1971 and 1974 and 6 ft (1.8 m) in 196 1967, 1970, 1971, 1972, 1974, and 1975.

While snowmelt runoff is often associated wit flooding problems, 60-70% of the Molly Islands colony nests are situated above the flooding zon More importantly, the sudden water depth increas of Yellowstone Lake, sometimes being 2.5-3 in (6 - 7.7 cm)/24 hrs, create serious energy problems f the pelicans. Like drought conditions, this seasonal runoff appears to force the white pelic s to change feeding sites. In July and August 197 Davenport (1974) observed 44% of the pelicans on the waters of Yellowstone lake's southern arms a 56% on the open water shorelines of the lake. I 1974, during the same months, she observed 100% of the birds on the waters of the southern arms.

Adult pelicans require about 2 lbs (0.9Kg) of fish/day for general maintenance conditions (Davenport 1974). Feeding zone changes precipitated by water depth changes will require increased expenditures of time and energy by the pelican in search of food. Further decreases in energy intake are likely since pelican captures fish in deeper waters can be proportionately les successful than in shallower waters. Anderson and Anderson (1976) have described the direct relationship of food fish availability to fluctu tions in Pacific Coast pelican numbers and to th diversity and numbers of California Coast seabir in general. In Yellowstone, the degree of impac of a shortage of food fish is greatly dependent on timing and duration of high water. Besides the influence on the adults' general physical we being, an early runoff creating a food fish shor age could affect nesting in the same manner described earlier for climatic influences. Late o extended snowmelt runoff, also creating forage fish shortages, can indirectly place severe phys logical stress on the unfledged white pelicans. These juveniles are completely dependent on the adults for the 100 lb (45.4 Kg) of fish needed t reach the fledgling stage of development (Davenport 1974).

A variety of complex interactions appear to have created perturbation in the reproduction of young pelicans in Figure 1. In 1962, a heavy late snowfall on May 13 was offset by a snowmelt runoff that never exceeded 5 ft (1.5 m), result in a fair production of young. Production of young in 1965 was depressed further than in 1962 by a heavy snowfall on May 24 and snowmelt runof that reached 6 ft (1.8 m) by mid-June and a 5 ft (1.5 m) level that extended to August 7. In 196 the runoff never exceeded 4 ft (1.2 m) and declined after June 30 with the result that the nu ber of young fledged nearly equaled the number of active nests.

In 1967, deep ground snow cover, cold air temperatures and a snowmelt runoff exceeding the 6 f (1.8 m) level appear to have combined to depress the production of young pelicans to the lowest level recorded since 1949. The disparity betwee nests and young fledged indicates losses resulte from late nest abandonment and/or losses of young after hatching. These losses of young cou be the result of a direct food shortage or it could be the result of parental inattentiveness. Hunt (1972) has described how parental occupatio with increased foraging effort resulted in highe losses of herring gull (*Larus argentatus*) chicks.

The features of Figure 1 offer no explanation for the decline of nests and production of young pelicans in 1968. However, the ice cover of Yellowstone Lake has usually disappeared by 18-2 May. In 1968, it was not melted until June 16. That condition would have limited the forage fis

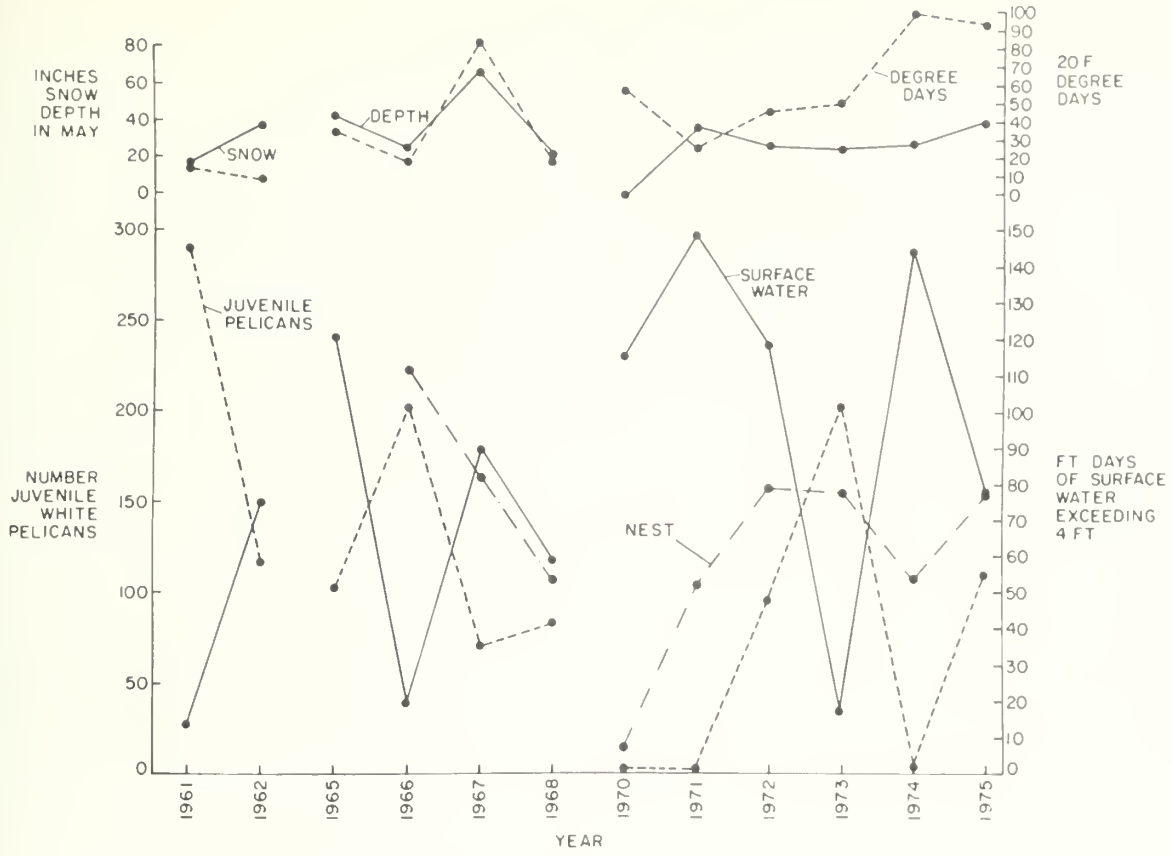



FIGURE 1. Comparisons of numbers of Molly Islands white pelicans fledged with numbers of pelican nests, foot days of snowmelt runoff at or above 4 ft, depth of snow cover and 20 F degree days, 1961-75.

TABLE 1. Distribution of white pelican nests and nesting groups on the Molly Islands, 1966-68 and 1970-75.

| Survey Date | Rocky Island | | Sandy Island | |
|---|---|---|---|---|
| | No. Nests | No. Groups | No. Nests | No. Groups |
| June 24, 1966 | 28 | 2 | 193 | 7 |
| June 26, 1967 | 158 | 7 | 9 | 1 |
| July 5, 1968 | 86 | 5 | 23 | 2 |
| July 3, 1970 | 2 | 1 | 11 | 1 |
| June 24, 1971 | 0 | 0 | 76 | 1 |
| June 22, 1972 | 29 | 2 | 128 | 4 |
| July 21, 1973 | 66 | 2 | 108 | 3 |
| June 16, 1974 | 109 | 3 | 0 | 0 |
| June 25, 1975 | 7 | 1 | 145 | 4 |

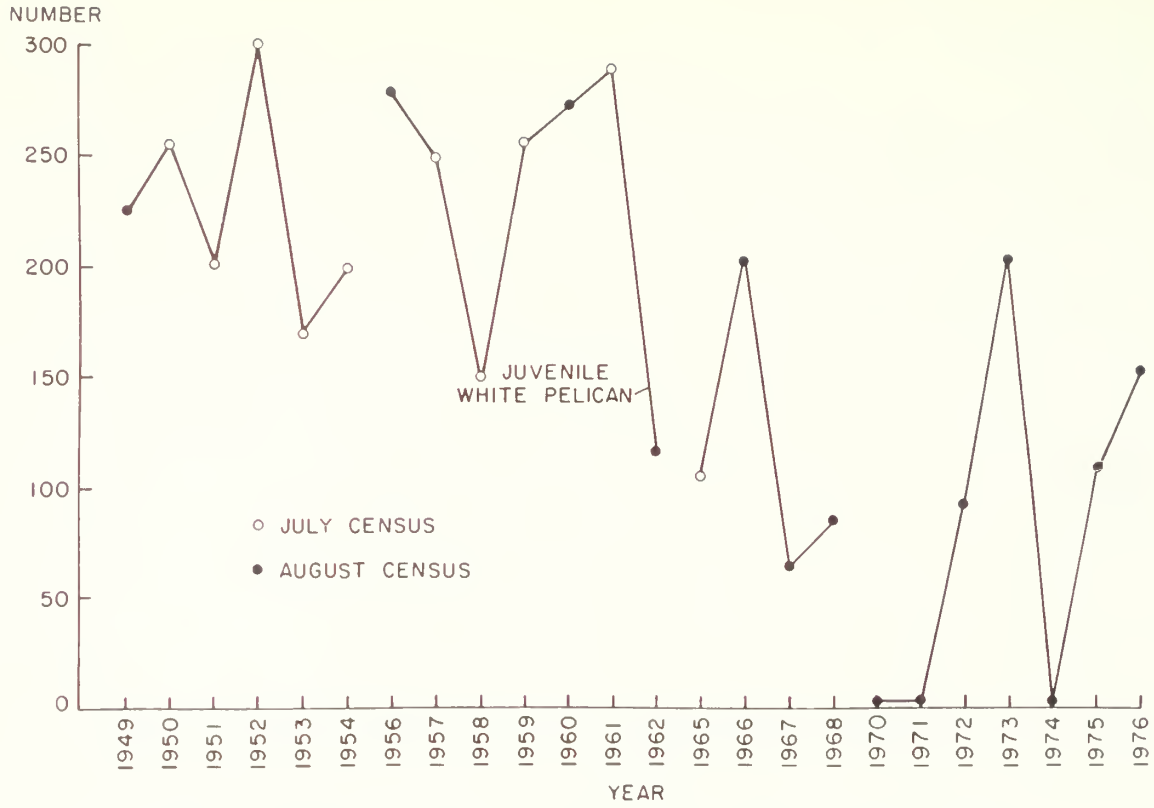



FIGURE 2. Numbers of Molly Islands while pelicans fledged, 1949-76.

TABLE 2. Wet weight in ppm of organochlorine residues in white pelican eggs.

| Location | Year | n | Composite Sampling | DDE | Dieldrin | PCB |
|---|---|---|---|---|---|---|
| Molly Islands | 1971 | 12 | 13299[2] | 3.90 | 0.0 | 5.0[5] |
| | | | 13330[2] | 4.00 | 0.0 | 5.0[5] |
| | 1973 | 7 | 16191[3] | 0.66 | 0.50 | 5.0[6] |
| | | | 16192[3] | 2.30 | 0.42 | 2.0[6] |
| Canadian Prairie Provinces | 1968-69 | 160 | 16 | 1.81[4] (0.83-4.76) | 0.13[4] (0.05-0.38) | |

[2]Aliquot sample numbers of a 12 egg composite.

[3]Aliquot sample numbers of a 7 egg composite.

[4]Mean and range of 16 10-egg composite samples.

[5]Arochlor 1254 standard.

[6]Arochlor 1260 standard.

[7]Vermeer and Reynolds (1970).

TABLE 3. Shell weight and shell thickness indices of white pelican eggs.

| Location | Year | n | Shell Weight $\bar{x}$ (Range) | Shell Thickness Index $\bar{x}$ (Range) |
|---|---|---|---|---|
| Molly Islands | 1971 | 12 | 13.65 (10.21-15.46) | 2.86 (2.33-3.22) |
| | 1973 | 7 | 13.94 (11.24-16.18) | 2.90 (2.45-3.15) |
| Western U.S.[8] | pre'47 | 268 | 15.70 | 3.26 |
| Interior N. Amer.[8] | pre'47 | 94 | 16.56 | 3.33 |
| Saskatchewan[8] | 1949 | 5 | 16.79 | 3.45 |
| Nevada[8] | 1968 | 25 | 14.24 | 2.87 |
| Alta, Man. Sask, N.D.[8] | 1965-68 | 34 | 14.99 | 3.07 |

[8]Anderson and Hickey (1972).

TABLE 4. Computed annual life cycle of Molly Islands white pelican population, using average natality, population structure and mortality, 1957-62 and 1965-76.

| | 1957-62 | 1965-76 |
|---|---|---|
| Adult Breeding Population | 500 | 450 |
| Average No. of Young Fledged | 182 | 92 |
| Fall Population | 682 | 542 |
| Average Annual Mortality (32%)[9] | 218 | 173 |
| Net Population | 464 | 369 |
| Percent Population Change | -7 | -18 |

[9]Based on banding returns for 1957-62 (Diem and Condon 1967).

availability for the pelicans with a resultant short supply of energy for nesting, egg laying and incubation. Two severe hail storms added insult to injury on August 15 and August 23. Twenty young pelicans or 19% of the young produced died as a result of those two storms.

In 1970, the 0.5 in (1.3 cm) of freezing rain on May 21 and cold air temperatures marked the beginning of a disastrous season. The 5 ft (1.5m) snowmelt runoff level was reached on June 19 and the 6 ft (1.8 m) level occurred 10 days later. Energy stress was high and nesting was practically eliminated. In 1971, conditions initially were favorable for nesting. However, the 5 ft (1.5 m) level of snowmelt runoff occurred 5 days earlier than in 1970 and reached the 7 ft (2.1 m) level on June 29. In addition to the greater depth, the duration of the 5 ft (1.5 m) level extended to August 6. The disparity between nests and young produced was even greater than in 1967.

Initially, the 1972 nesting season received a poor start from cold air temperatures and a snowmelt runoff which reached the 5 ft (1.5 m) level as early as June 9 and 6 ft (1.8 m) level on June 15, 7 days earlier than in 1971. However, while the runoff was initially intense, it slowed rapidly and was below 5ft (1.5 m) by July 22, facilitating a fair production of young. During 1973, a relatively uneventful spring fostered a nesting effort nearly identical with 1972. However, this time the snowmelt runoff never reached 5 ft (1.5 m) and lasted only from June 15 to July 15 and pelican production was the highest since 1961.

Another total reproduction failure resulted in 1974 when very cold air temperatures and a 7 in (18 cm) snowfall on 20 May coincided with a prolonged snowmelt runoff which exceeded the 7ft (2.1 m) level. The 109 nests being incubated on June 16 declined to 3 nests attended by 9 adults by July 22. The outlook for 1975 was grim considering the cold air temperatures and mid-June disappearance of the ice cover on Yellowstone Lake. The entire season was delayed 3 weeks. Fortunately, the stressful late spring-early summer period changed abruptly into a favorable breeding season producing a fair number of young pelicans.

Historically, several years prior to 1949 had climatological and snowmelt runoff characteristics which potentially should have suppressed white pelican production. However, no marked white pelican population decline was evident until the early 1950's. The date coincides with the initiation of the general decline of the Pacific Coast brown pelican and the presence of environmental chemical pollution described by Anderson and Anderson (1976). Analysis results for organochlorine residues in the Molly Islands white pelican eggs are given in Table 2. Interpretation of the Molly Islands results is difficult because of: (a) interference during analysis between PCB and DDE; (b) sampling error in the two aliquots because of wide variations in pesticide residues in individual eggs of the pooled sample; and (c) variations induced by different analytical machines and/or technicians operating them. Variations of residues in individual eggs could easily occur as a result of the diverse conditions each pelican could encounter during migration or on the wintering grounds. Erratic as the concentrations are, the range of variability is comparable to that of the Canadian pelicans which average about three times less DDE and dieldrin.

Anderson and Hickey (1972)have summarized the thinning effects of DDE on the eggshells of birds. The level of DDE in the Molly Islands eggs is very close to or slightly over the lower concentration level where changes in the eggshell can be expected. Collapsed eggshells from thinning have never been observed in the Molly Islands colony. Comparison of eggshell characteristics presented in Table 3 with pre-1947 white pelican values from Anderson and Hickey (1972) indicates the Molly Islan eggshell weights have decreased 15% since 1949 and the shell thickness index has decreased 13% However, natural variations of these characteristics between individual eggs may range betwee 10-12% (Ohlendorf, pers. comm.) Considering th implication of this variable and the potential collector bias inherent in pre-1947 museum egg collections, the actual decline in the shell weight and shell thickness index of the Molly Islands pelican eggs since 1949 may be more rea istic at 3-5%.

The more serious chemical pollutant concentra d in the Molly Islands pelican eggs is dieldrin. - sides being 14 times more toxic than DDT (DeWit et al. 1960) dieldrin was found to reduce bobwh quail reproduction by 40% with 1 mg/kg in their diet (Dewitt and George 1960). Dieldrin also appears to be more concentrated in fish-eating birds (Vermeer and Reynolds 1970). The majorit of research indicates it does not cause eggshel thinning (Blus et al. 1971; Anderson and Hickey 1972). The exact concentration of dieldrin in the Molly Islands eggs is not a firm level because of the PCB interference. Future analyses should be able to provide greater reliability.

The PCB levels are equally difficult to asses for the same reason of interference with dieldri Also, an analysis should be conducted for the very toxic polychlorinated dibenzofurans (PCDF's found as an impurity in a wide range of manufactured PCB's (Kaiser 1976). The lack of PCDF information clouds an interpretation on the spec fic role of PCB's in inhibiting reproduction.

Gress (1970) observed aberrant reproduction b havior in the brown pelicans on Anacapa Island and associated these behavioral changes with pesticide influences. I have observed what appe - ed to be similar changes in the behavior of whit pelicans on the Molly Islands. In every year of extreme stress from climatic and snowmelt runoff influences since 1967, nest attachments and pare - chick bonds appeared to be very weak. For exam , very weak nest bonds were particularly observed in 1967 and in 1974. In 1970 and 1971, the few young that were produced were late hatched birds. In 1970, the adults had abandoned the young peli ns by August 22, several weeks before fledging. In 1971, all but four adults appeared to have abandoned the surviving young by August 12.

Contrary to the circumstances in many other w te pelican colonies (Lies and Behle 1966; Vermeer 1970b) human disturbance on the Molly Islands ha been negligible since 1967. Limited camera data taken in 1972 and 1973 and general observations by Park personnel and myself confirm this. Mark increases of canoeists in the future may require establishment of a closure zone around the islan during June, July and early August.

The simultaneous decline of the Molly Islands white pelican population, beginning in the early 1950's, and the large scale accumulation of chem ical pollution in the environment, suggest that the chemical pollutants acquired by the pelicans have served to amplify the influence of the Yellowstone environmental stress factors on peli ns after 1950.

The complex interactions of all the foregoing influences have had a detrimental cumulative and additive effect on the Yellowstone white pelican population. Unfortunately prior to 1949, Yellow stone pelican population data are of limited val for comparison purposes. The bulk of those obse - tions were from the 1920's and early 1930's when an unknown degree of killing of white pelicans b

Park personnel seriously biases those data (Diem and Condon 1967). The general decline of the production of young pelicans since 1949 is evident in Figure 2. This trend if further supported by computations of the white pelican annual life cycle presented in Table 4.

Several important considerations related to Table 4 are: (a) annual mortality derived from banding data for 1957-62 was 7.5% higher than for 1949-54 (Diem and Condon 1967); (b) maintenance of a stable population during the period 1965-76 would have required the production of 0.94 young/breeding pair; however in 1957-62, 0.73 young/breeding pair were produced and in 1965-76 that number decreased to 0.41 young/breeding pair; and (c) Henny (1972) reported that the California brown pelican declined at a rate of 17% over a 10 year period while the South Carolina brown pelican declined at a rate of 16%. From the foregoing data, it is easy to understand why the future of the white pelican in Yellowstone is a matter for concern.

A clear understanding of this decline in white pelican is further hampered by the simultaneous establishment of a new breeding colony outside of Yellowstone National Park. At Riverside, Colorado, R. A. Ryder (pers. comm.) has been studying a white pelican colony which has only existed for 15 years and is now producing 300 young/year. This raises the legitimate question about whether the decline in adults from 500 to 450 represented a real loss of birds or merely a shift in the distribution of birds. However, the general situation for North American white pelicans as reported by Lies and Behle (1966) and Vermeer (1970b) support the contention that while some new colonies have been established, losses or declines in the total numbers of colonies and numbers of birds within the colonies far exceeds those new starts.

## CONCLUSIONS AND RECOMMENDATIONS

Since 1949, the Molly Islands white pelican colony has experienced a declining reproductive success. Complex interactions between severe natural climatic and hydrologic phenomena and chemical pollutants carried by the pelicans appear to be the major modifiers of the white pelican reproduction. Total reproductive failures have occurred in three nesting seasons since 1970 without eggshell collapse observed in other fish-eating birds having poor reproductive success. Observations since 1967 suggest that the sublethal levels of pesticides are exerting a subtle, but important catalytic influence. That influence serves to amplify the degree of stress beyond that stress level which might normally be produced by severe natural climatic and hydrologic events. Despite the prolonged nature of the decline since 1949, the three total reproductive failures emphasize how quickly a breeding colony could be lost through a set of uncontrollable circumstances.

Recognizing that the Molly Islands white pelicans spend 7 months every year outside of the Park being exposed to hazards of environmental pollution, habitat destruction, migration accidents and human disturbance, the Park Administration should still have a very deep concern for the welfare of that colony. Management plans should include provisions for monitoring, protecting and maintaining an environment conducive to successful reproduction in the historical and sole white pelican breeding colony in a national park. Implementation of the recent guidelines formulated by Buckley and Buckley (1976) is particularly appropriate for the Molly Islands colony.

On the basis of what is now known, a reasonable forecast of pelican reproductive success can be developed from the climatic and snowmelt runoff data in this report, with modifications for one or more special environmental events which occur. Such gross forecasts should in no way substitute for nesting and fledging surveys. Greater financial and manpower support should be devoted to assure complete climatic and hydrologic data for the Yellowstone Lake area on a daily basis during May through August.

Every effort should be made to collect and preserve all pelican eggs, from nests lost to flooding or abandonment, for a thorough pesticide analysis. Particular emphasis should be given to screening for DDE, dieldrin and the toxic polychlorinated dibenzofurans (PCDF) associated with many PCB products. Measurements of eggshell characteristics should be continued.

A carefully controlled color leg band marking program of juveniles about to fledge would be necessary to clarify the function of the nesting groups. Specifically, this would contribute to an understanding of the annual composition of the nesting groups in relation to age of the birds, wintering areas occupied and shifting of nesting sites within and between islands. This type of banding would also assist in determining if chemical pollutants are restricted to specific subunits of the population and/or to specific individuals as determined by their wintering areas and/or routes of migration.

In addition, research should address several topics related to the unique features associated with the dynamics of the Molly Islands white pelican population. First, the Molly Islands pelican population has historically been very near to the natural environmental limit for long-term maintenance of the colony. Can one then generalize that DDE, dieldrin and other chemical pollutants in sublethal concentrations exert their greatest and frequently most subtle detrimental influences on those avian populations which are at the margins of their historic ranges? If this is true, can we or should we identify some of those marginal populations as "threatened" or "endangered" populations even though the general population of the species may not be clearly in those categories?

Second, to what minimum population level can an aggregation of breeding white pelicans be reduced without detroying the "coloniality" which serves to stimulate and synchronize courtship behavior and promote successful group feeding and the maintenance of new energy levels adequate for the production and recruitment of flying young to the population?

Third, are the chronic body levels of pesticides strongly selective, under stressful environmental condition, against the younger less experienced birds during their first breeding season? If so, to what extent are these chemicals postponing the successful breeding age of those maturing birds and what affect is this having on the population?

Fourth, is there a level of pesticides, singly or in various combinations, that can be accommodated within the pelicans without detrimentally modifying their behavior under periods of natural environmental stress?

## LITERATURE CITED

ANDERSON, D. W. and I. T. ANDERSON. 1976. [illegible] tribution and status of brown pelicans in the California Current. Amer. Birds [illegible]:
ANDERSON, D. W. and J. J. HICKEY. 1972. [illegible] changes in certain North American birds. Proc. Internatl. Ornith. Congress 15: 514-44[illegible].

BLOKPOEL, H. 1971. Fox predation on a bird island. Blue Jay 29(1):32-34.

BLUS, L. J., R. G. HEATH, C. D. GISH, A. A. BELISLE and R. M. PROUTY. 1971. Eggshell thinning in the brown pelican: implication of DDE. BioScience 21(24):1213-1215.

BUCKLEY, P. A. and F. G. BUCKLEY. 1976. Guidelines for the protection and management of colonially nesting waterbirds. North Atlantic Regional Office, U.S. Natl. Park Ser., Boston, Mass.

DAVENPORT, M. B. 1974. Piscivorous avifauna on Yellowstone Lake, Yellowstone National Park. Completion Report to Yellowstone Natl. Park. Mimeo. 62 p.

DEWITT, J. B. and J. L. GEORGE. 1960. Bureau of Sport Fisheries and Wildlife, pesticide-wildlife review: 1959. Fish and Wildlife Circular No. 84, Revised. U.S. Dept. Interior, Wash. D.C.

DEWITT, J. B., C. M. MENZIE, V. A. ADOMAITIS and W. L. REICHEL. 1960. Pesticidal residues in animal tissues. Trans. Twenty-fifth North Amer. Wildl. Conf. p. 277-285.

DIEM, K. L. and D. D. CONDON. 1967. Banding studies of water birds on the Molly Islands, Yellowstone Lake, Wyoming. Yellowstone Library and Museum Assoc., Yellowstone Park, Wyo. 41 p.

DIEM, K. L., A. L. WARD, and J. J. CUPAL. Cameras as remote sensors of animal activities. Proc. XV Internatl. Congress of Game Biol., Stockholm, Sweden. p. 503-509.

GRESS, F. 1970. Reproductive status of the California brown pelican in 1970, with notes on breeding biology and natural history. Wildl. Manage. Branch Admin. Rept. No. 70-6. Calif. Dept. of Fish and Game, Sacramento. 21 p.

HENNY, C. J. 1972. An analysis of the population dynamics of selected avian species, with special reference to changes during the modern pesticide era. Wildl. Res. Rept. 1, Bur. Sport Fisheries and Wildl., U.S. Dept. of Interior, Wash. D.C. 99 p.

HUNT, G. L., JR. 1972. Influence of food distribution and human disturbance on the reproductive success of herring gulls. Ecol. 53(6 1051-1061.

KAISER, K. L. 1976. PCB's: How Toxic? Scienc 192:612-614.

KEITH, J. O., L. A. WOODS JR. and E. G. HUNT. Reproductive failure in brown pelicans on the Pacific Coast. Trans. Thirty-fifth North Amer. Wildl. and Nat. Resources Conf. p. 56-64.

LIES, M. F. and W. H. BEHLE. 1966. Status of the white pelican in the United States and Canada through 1964. Condor, 68:279-292.

RATCLIFFE, D. A. 1967. Decrease in eggshell weight in certain birds of prey. Nature 215:208-210.

U.S. DEPT. COMMERCE. 1961-75. Climatological data-Wyoming Section. 71-84 (5-8).

U.S. DEPT. OF INTERIOR. 1961-75. Water resourc data for Wyoming, Part 1. Surface water records. Geol. Survey.

VERMEER, K. 1970a. A study of Canada geese, *Branta canadensis*, nesting on islands in southeastern Alberta. Can. J. Zool. 48:235-240.

VERMEER, K. 1970b. Distribution and size of colonies of white pelicans, *Pelicanus erythrorhynchos*, in Canada. Can. J. Zool. 28:(5): 1029-1032.

VERMEER, K. and L. M. REYNOLDS. 1970. Organochlorine residues in aquatic birds in the Canadian Prairie Provinces. Can. Field-Natur. 84(2):117-130.

# THE COLUMBIAN SHARPTAILED GROUSE: WITH SPECIAL REFERENCE TO THEIR POTENTIAL REINTRODUCTION TO LAVA BEDS NATIONAL MONUMENT

E. E. Starkey & R. A. Schnoes[1]

## INTRODUCTION

In 1963, the Advisory Board on Wildlife Management in the National Parks, chaired by Dr. A. Starker Leopold, recommended that a primary goal of park management should be the maintenance or recreation of biotic associations "as nearly as possible in the condition that prevailed when the area was first visited by the white man" and that "a national park should represent a vignette of primitive America." In keeping with this philosophy, we are presently conducting research to ascertain the nature of the primeval ecosystem at Lava Beds National Monument in Modoc County near Tule Lake, California, as well as the changes resulting from exploitation by European man. This research includes investigations on the plant communities of the Monument, with special reference to fire history and ecology (Martin and Johnson, 1976), as well as native wildlife species. A major project has been the reintroduction of California bighorn sheep, which have been absent since approximately the turn of the century. Although the project is not yet complete, and the ultimate outcome is still uncertain, we remain cautiously optimistic.

In addition to the bighorn project, we are presently considering the reintroduction of another native wildlife species, the Columbian sharptailed grouse (*Pediocetes phasianellus columbianus*).

The Columbian sharptail is one of six subspecies of sharptailed grouse found in North America and is the only sharptail subspecies native to the Pacific Northwest.

The Columbian sharptailed grouse was discovered by Lewis and Clark along the plains of the Columbia River in 1805, and was named by Ord in 1815 (Bent, 1932). Skeletal remains of sharptailed grouse discovered in Oregon date back to the late Pleistocene epoch (American Ornithologists Union, 1957).

Today I would like to present the process which we are following in determining the feasibility of reintroducing sharptails to Lava Beds, as well as make some general comments concerning the current status of Columbian sharptails in the United States including management and research recommendations.

## SPECIES HISTORY

The first step in our process has been to review all information available on the past and present status of the subspecies. The objective of this phase has been to determine whether Columbian sharptails were present primevally in the Lava Beds area, and their present nationwide distribution and population trends. The importance of the first objective is obvious since we are primarily interested in native species. The second objective is also important in that it provides us with a perspective on the "health" of the entire subspecies. Clearly, our priorities and management practices would be different from a species or subspecies which was nationally endangered than for one which was only extirpated locally.

## PAST AND PRESENT DISTRIBUTION

At the time of settlement by European man, the distribution of Columbian sharptails included much of the inland Pacific Northwest, as well as locations in western Colorado, northern Utah, northern New Mexico, western Montana, and western Wyoming. Major Bendire (1892) stated that "it is one of the most abundant and best known game birds of the Northwest, inhabiting the prairie country to be found along the foothills of the numerous mountain chains intersecting its range; seldom venturing into wooded portions for any distance, and then only during the winter months, when it is partially migratory in certain sections. The Columbian sharptail breeds more frequently in the sheltered and sunny slopes of the grass-covered foothills of the mountains than in the lower valleys and creek bottoms."

Early settlers in eastern Washington found the Columbian sharptailed grouse to be the most abundant and best known game bird in the area (Yocom, 1952). These grouse inhabited the steppes of eastern Washington and the ecotonal areas between forests and grasslands. By 1897, sharptails had declined sharply, and the Washington legislature approved restrictive hunting seasons. Most farmers in southeastern Washington reported seeing sharptails for the last time between 1910 and 1929 (Buss and Dziedzic, 1955). No reliable census information is available but the Washington Department of Game estimates spring populations to be from 2,000 to 5,000 birds.

Prior to extensive settlement, the sharptail was also abundant in Idaho. Although sharptails were extremely abundant when settlers arrived, by 1917 their populations were rapidly declining (Rust, 1917). Murray (1938) stated that "probably not more than a thousand birds of this species remain in Idaho at this time, and it is possible that an actual count would reveal less than half this number."

Small relict populations remain in the west and southeastern portions Of Idaho. The largest populations exist on the Curlew National Grasslands in Oneida County and in Fremont County. Population estimates are not available but Parker (1970) stated that "either a low point in a cyclic pattern of population fluctuations is being approached, or that the population is generally declining."

The primitive range of the Columbian sharptail also included the valleys of central and northern Utah, where these birds were present by the thousands (Lee, 1936). Joel Ricks, an early pioneer of Cache Valley, Utah, stated that "in the summer, the prairie chicken (sharptailed grouse) came to the river bottoms on the west of the valley for shade. There were tens of thousands of these chickens until about 1875 when they began to dwindle." Also, Warden William

[1]Cooperative Park Studies Unit, Oregon State University, Corvallis.

Anderson of Weber County reported that the grouse were so thick that they "darkened the sun when they flew up." Hart et al. (1950) estimated the statewide population of sharptails to be about fifteen hundred individuals.

Sharptails were never abundant in Nevada, and were only common in northern Nevada prior to 1900. Declines in their population began around 1900, and by 1930 only remnant populations remained. The subspecies is probably no longer present in Nevada.

Columbian sharptails were also probably never abundant in Colorado. However, little is known about the historical abundance, largely because of the use of common names in reports. Early explorers and settlers wrote of partridges, sharptails, prairie chickens, prairie hens, sage chickens, and willow grouse. The similarity among tetraonid species, and the use of these common names, has made it impossible to precisely determine the primeval distribution of sharptails in Colorado (Rogers, 1969).

Currently, Columbian sharptailed grouse are present in nine western counties and may be present in six additional counties of Colorado. Existing populations may be declining, although census data are not available.

Columbian sharptails were formerly found throughout most of eastern Oregon. As in other northwestern states, their number declined rapidly. By 1905, Columbian sharptails were rare in the southcentral portion of the state. The last sighting of sharptails in Oregon was made by Baker District Bureau of Land Management personnel in Baker County, in northeastern Oregon, about 1968 or 1969 (Olsen, 1976). The subspecies is in all probability absent from the state at the present time. However, it is classified as endangered by the State of Oregon (Marshall, 1969).

Sharptailed grouse were formerly common in portions of northeast California, including the Modoc region where Lava Beds is located. In 1974 sharptails were found by Dr. Newberry to be abundant northeast of present day Redding and about the Klamath Lakes and in the Des Chutes Basin of Oregon as far as The Dalles (Baird et al., 1974). H. W. Henshaw (1880) wrote that "about camp Bidwell (Modoc County), California, the 'sharptails' are sufficiently numerous to afford excellent shooting, and good bags may be made there." Mr. W.S. Criss of Lookout, Modoc County, California, reported that in 1916 there were many "little brown prairie chickens" on his ranch up to about fifteen years previously. He claimed they were at one time "so thick one could not walk through the fields without scaring up several bunches."

By 1918, Grinnel et al. considered that the Columbian sharptailed grouse was "nearly or quite extinct within the state." However, rumors of sharptails persisted throughout the 1920's although no sightings were confirmed. The Lava Beds superintendent's annual report for 1920 refers to a group of "long tailed" grouse seen in the vicinity of the Monument. These were most likely sharptails but no other information is available. Mailliard (1927) states that he had heard reports of one or two bands being seen in Modoc County during 1921 to 1924.

## U.S. POPULATION ESTIMATES

Because of the lack of information on contemporary Columbian sharptailed populations, it is difficult to establish a reasonable nationwide estimate of populations. However, using data available, either from state game departments or old reports in the literature (Table 1), it would appear that total U.S. populations would be very unlikely to exceed 15,000 - 20,000 individuals.

Presently, the Columbian sharptail is classified as "status undetermined" by the U.S. Fish and Wildlife Service. This means that not enough information is available to classify the subspecies as threatened or endangered.

A comparison of our rather crude population estimate with estimates for a number of threatened and endangered avian species indicates that the Columbian sharptail may well be a strong candidate for the threatened species list (Table 2), particularly since their present numbers are at best stable and very likely declining.

## CAUSES OF POPULATION DECLINES

A number of reasons have been suggested for the decline of Columbian sharptail populations throughout the Northwest. Perhaps the most common hypothesis is that overgrazing and intensive cultivation altered the sharptail's habitat.

Another possible cause may have been hunting by early settlers. Grinnel et al. (1918) states that in northern California "... the disappearance of this bird can be attributed to no other cause than to its incessant pursuit by man. As long as a single bird remained hunting persisted." Apparently they were an easy species to hunt.

While overgrazing, cultivation and hunting could readily have had significant impacts on populations, many western ranges are in better condition now than they were at the turn of the century (Chohlis, 1952; Daubenmire, 1970), and restrictions or closed hunting seasons have been enacted throughout most of the Columbian sharptails' primeval range. However, populations have continued to decline.

Cultivation of land had increased in intensity during the last 75 years, particularly with the completion of large scale irrigation projects, and the development of new technology such as circular sprinkler systems. While such agricultural practices no doubt are responsible for low or non-existent sharptail populations in many areas of the Pacific Northwest, large portions of the primeval range of the subspecies are not under cultivation of any kind.

It is unlikely that any single factor caused the decline of the Columbian sharptail. It is also possible that the initial limiting factors have been replaced by others. A likely hypothesis is that hunting and overgrazing around the turn of the century caused initial declines, followed by habitat changes resulting from fire suppression as well as continued overgrazing and cultivation in some areas.

## HABITAT ANALYSIS

The principal objectives of this phase were the location of potentially suitable habitat within the Monument and the formulation of habitat improvement recommendations.

As with most species of wildlife, habitat requirements vary with season and stage of the

TABLE 1. Current population estimates of Columbian Sharptailed Grouse in the United States.

| State | Population |
|---|---|
| Washington | 5,000 individuals |
| Idaho | 2,000 |
| Utah | 2,000 |
| Colorado[a] | - |
| Montana[b] | - |
| Nevada | 0 |
| California | 0 |
| Oregon | 0 |
| Wyoming | 0 |

[a]The subspecies is present in western Colorado in unknown numbers.

[b]Remnant populations remain in western Montana.

sharptail life cycle (Marshall and Jensen, 1937). Grassy openings are important during the spring and summer, and are used as dancing grounds and brood-rearing areas. Maximum use in southeastern Idaho occurred in locations with approximately 70% grass cover (Parker, 1970). However, although open grassland was the most important cover type for brood rearing, considerable use was also made of areas with mixtures of shrubs and grasses. During the winter months, sharptails depended much more heavily on brushy cover.

Unfortunately, a difficulty in determining what constitutes optimum habitat results from the possibility that remnant populations may only be present in suboptimum locations. This may be a reasonable possibility because Columbian sharptailed grouse populations are generally either declining or, at best, stable.

However, historical accounts indicate that at the turn of the century the subspecies occupied habitat roughly similar to that occupied now. Unfortunately, such generalized descriptions give no insight concerning relative species composition and density.

The northern two-thirds of Lava Beds supports a shrub-steppe plant community. Common shrubs include big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* spp.), and grasses are generally bluebunch wheatgrass (*Agropyron spicatum*), cheatgrass (*Bromus tectorum*) and squirreltail (*Sitanion hystrix*). The southern one-third consists of dense shrub communities containing mountain mahogany (*Cercocarpus ledifolius*) and bitterbrush (*Purshia tridentata*). Idaho fescue (*Festuca idahoenis*) is a common grass. Juniper (*Juniperus occidentalis*) is scattered throughout the Monument, and ponderosa pine (*Pinus ponderosa*) forests are found along the southern and southeastern boundaries. This vegetation is different from that present primevally, and changes have been documented by Martin and Johnson (1976).

Potential and present vegetation of Lava Beds will be sampled extensively and mapped, starting in the spring of 1977. This study, combined with previous research by Martin and Johnson (1976) should provide considerable insight into the primeval vegetation of Lava Beds.

It appears that optimum habitat consists of a mosaic of grass and various shrub and hrub/grass communities. Parker (1970) states "The areas still inhabited by sharptails are those which have retained a mixture of native grasses and brush." Pure stands of any single community do not seem optimum.

TABLE 2. Population estimates of selected avian species classified as threatened in 1973[a]

| Species | Population |
|---|---|
| Northern greater prairie chicken | 8000,000-1,000,000 |
| Lesser prairie chicken | 12,000- 80,000 |
| California brown[b] pelican | 100,000+ |
| Eastern brown[b] pelican | 8,500 breeding pairs |
| Hawaiian duck[b] | 3,500 |
| Mexican duck[b] | 15,000 |

[a]Estimates from Threatened Wildlife of the United States. Resources Publication 114. March 1973. Bureau of Sport Fisheries and Wildlife, USDI.

[b]Included in United States list of endangered fauna, May 1974. Fish and Wildlife Service, USDI.

We are presently developing recommendations for burning to improve sharptail habitat. For example, it may be advisable to burn first in those areas which supported perennial grasslands most recently. A 1936 vegetation map indicates that at least two areas were still dominated by bunchgrass communities at that time. The probability of restoring the grassland component of the ecosystem would seem higher there than for areas which have been dominated by shrubs for longer periods of time, or may never have been grassland.

## FEASIBILITY ANALYSIS

This phase has actually been initiated concurrently with habitat analysis. The primary objectives are to locate a source of reintroduction stock and assess the difficulties likely to be involved in obtaining and transporting birds. We have not yet located a source of stock, but will soon contact Idaho, Washington and British Columbia.

We anticipate substantial difficulty in trapping birds. While males can be readily obtained on dancing grounds, females are less available.

Therefore we will very seriously consider a captive propagation program. Prairie sharptails have been propagated in captivity in a number of places, so we believe such a program to be reasonable. However, it will be expensive and time-consuming.

Regardless of our ultimate source of birds, a number of important questions remain to be answered. Timing of the reintroduction, sex ratios and group sizes may all be critical. The sharptail is a behaviorally complex species and relatively little is known about requirements for successful transplants.

## CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

1. Serious consideration should be given to reclassifying the Columbian sharptail from "status undetermined" to "threatened."

2. Preservation and expansion of existing populations should be a multi-agency responsibility. Essentially all federal and state land managing agencies in the Pacific Northwest and Intermountain west had large populations on their lands primevally. Therefore, they should share the task of restoring them, or at least preserving remnant populations.

3. The National Park Service should take a position of leadership in preserving and expanding the range of the subspecies. As long as Columbian sharptails remain classified as "status undetermined" the U.S. Fish and Wildlife Service is not likely to expend significant funds for habitat preservation or improvement. The nonmigratory nature of the subspecies also places it outside the Fish and Wildlife Service's jurisdiction. Exceptions would be various Wildlife Refuges, and the National Bison Range, in western Montana.

Game agencies in states where populations are low or nonexistent are not likely to support sharptail research and management projects either. There are not large enough populations to represent significant resources for sport hunting and sharptails generally cannot compete with deer, elk, salmon, and trout for research and management support. Fortunately some states are increasing their funding for nongame species, and some of this may find its way to sharptail projects. However, the National Park Service has a policy of reintroducing extirpated natives and could therefore act as a catalyst.

4. Research should be supported which would develop an optimum habitat model for Columbian sharptails. This would require study of habitats in a number of areas where the subspecies persists, in an attempt to identify similarities, as well as differences.

5. The Columbian sharptail should be reintroduced to Lava Beds since it was apparently present primevally. This must follow habitat manipulation by fire, and it is quite likely that captive propagation will be required to provide suitable quantities and sex ratios of reintroduction stocks.

In conclusion, I believe that if the above recommendations are followed, the Columbian sharptailed grouse populations can be restored to states where they are now absent, and existing populations can be expanded. It is unlikely that they will ever be abundant, because of wide spread land-use practices, but at least we will not have lost another native.

## LITERATURE CITED


AMERICAN ORNITHOLOGISTS UNION. 1957. Checklist of North American Birds. Fifth Edition. Baltimore: Lord Baltimore Press. 691 pp.

BAIRD, S. F., T. M. BREWER and R. RIDGWAY. 1874. A History of North American Birds: Land Birds. Boston: Little, Brown and Co. 560 pp.

BENDIRE, C. E. 1892. Life Histories of North American Birds. U.S. Nat. Mus. Spec. Bull. 1(1), 446 pp. Quoted in Bent (1963).

BENT, A. C. 1932. Life Histories of North American Gallinaceous Birds. Reprinted in 1963. New York: Dover Publications. 490 pp.

BUSS, I. O. and E. S. DZIEDZIC. 1955. Relation of cultivation to the disappearance of the Columbian sharp-tailed grouse from southeaster Washington. Condor 57:185-187.

CHOLIS, G. J. 1952. Range conditions in eastern Washington fifty years ago and now. J. Range Mgmt. 5(3):129-134.

DAUBENMIRE, R. 1970. Steppe Vegetation of Washington. Wash. Agric. Exp. Stn. Tech. Bull 62, 131 pp.

GRINNEL, JOSEPH, HAROLD CHILD BRYANT, and TRACY IRWIN STORER. 1918. The Game Birds of California. Berkeley: University of California Press. pp. 558-564.

HART, C. M., O. S. LEE and J. B. LOW. 1950. The Sharp-tailed Grouse in Utah, Its Life History, Status, and Management. Utah State Dept. of Fish and Game, Publ. 3 79 pp.

HENSHAW, H. W. 1880. Ornithological report from observations and collections made in portions of California, Nevada, and Oregon. Appendix L. Appendix oo. Annual Report of Capt. George M. Wheeler, Corps. of Engineers, U.S.A. for 1879.

LEE, ORVILLE S. 1936. The Life History of the Columbian Sharptailed Grouse in Utah. Unpublished M.S. Thesis. Utah State Univ. 86 pp.

MAILLIARD, JOSEPH. 1927. The Birds and Mammals of Modoc County, California. Proc. Calif. Acad. Sci. XVI (10):261-359.

MARSHALL, D. B. 1969. Endangered Plants and Animals of Oregon. III. Birds. Special Report 278, Agricultural Experiment Station, Oregon State University. 23 pp.

MARSHALL, W. H. and M. S. JENSEN. 1937. Winter and spring studies of the sharp-tailed grouse in Utah. J. Wild. Mgmt. 1(3-4):87-99.

MARTIN, R. E. and A. F. JOHNSON. 1976. Fire ecology and management of Lava Beds National Monument. Proceedings of the First Conference on Scientific Research in the National Parks.

MURRAY, T. B. 1938. Upland game birds in Idaho and their future. Univ. Idaho Bull. 33(22)55-66. Quoted in Parker (1970).

OLSON, BILL. 1976. Status report: Columbian sharptailed grouse. Oregon Wildlife 31(4):10.

PARKER, THOMAS L. 1970. On the ecology of the Sharp-tailed Grouse in Southeastern Idaho. Unpublished M. S. Thesis, Idaho State Univer-SITY. 140 pp.

ROGERS, GLENN E. 1969. The Sharp-tailed Grouse in Colorado. Tech. Publ. No. 23, Colorado Division of Game, Fish and Parks.

RUST, H. J. 1917. An annotated list of the bird of Fremont County, Idaho, as observed during the summer of 1916. Condor 19:29-43.

YOCOM, C. F. 1952. Columbian sharp-tailed grouse *(Pediocetes phasianellus columbianus)* in the state of Washington. Amer. Midl. Naturalist 48(1):185-192.

# HISTORICAL SURVEY OF PEREGRINE FALCON EYRIES IN NATIONAL PARK SERVICE LANDS BORDERING LAKE SUPERIOR[1]

Frank B. Isaacs and Norman F. Sloan[2]

## INTRODUCTION

Since the late 1940's the endangered American peregrine falcon (*Falco peregrinus anatum* Bonaparte) has all but disappeared as a breeding bird in North America. This decline was the result of impaired reproduction caused by certain persistent pesticides and industrial pollutants, habitat destruction and human harassment (Snow, 1972). A 1965 Conference on Peregrine Falcon Populations held at Madison, Wisconsin (Hickey, 1969) focused attention on the plight of the peregrine and was the stimulus for current efforts to reintroduce captive bred peregrines into abandoned historic nest sites. The ultimate goal of this program is to rebuild the peregrine population in eastern North America to 50 percent of the numbers estimated for the 1940's or to a level the present environment will support. This will be accomplished by reintroducing a strain of pen-reared peregrines more adapted to present conditions (Eastern Peregrine Falcon Recovery Team, 1976).

In December of 1974 the National Park Service began providing funds for a study of the history, current status and possibilities for reintroduction of the peregrine falcon into areas in Isle Royale National Park, Pictured Rocks National Lakeshore and the Apostle Islands National Lakeshore (Figure 1). This report presents the results of that study.

## STUDY AREAS

The Apostle Islands National Lakeshore is located at the northernmost tip of Wisconsin Figure 1). Twenty of the 22 Apostle Islands are included within the park and contain approximately 39,500 acres (15,985 hectares) (Matteson *et al.*, 1973). The mainland portion of the park includes 12 miles (19.3 kilometers) of shoreline stretching from Sand Bay to Squaw Bay on the northwest side of the Bayfield Peninsula. The region lies within the hemlock (*Tsuga* sp.) - white pine (*Pinus strobus* Linnaeus) - northern hardwoods vegetation type. Summer climate is cool with a mean July temperature of 65°F (18.3°C) (Beals, 1960).

Isle Royale National Park is a 210 square mile (54,390 hectare) archipelago located in northwestern Lake Superior (Figure 1). The main island is 45 miles (72.5 kilometers) long by eight miles (12.9 kilometers) wide and is surrounded by approximately 200 smaller islands and numerous rock outcroppings. Climate is typified by cool summers and severe winters with snow depths normally two feet (.61 meters), but occasionally exceeding three feet (.91 meters). Sugar maple (*Acer saccharum* Marsh.) - yellow birch (*Betula alleghaniensis* Britton) and spruce (*Picea* sp.) - fir (*Abies* sp.) - white birch (*Betula papyrifera* Marsh.) are the two basic climax forest types found on the island (Krefting *et al.*, 1966).

The Pictured Rocks National Lakeshore is located in east-central Upper Michigan and stretches for approximately 42 miles (67.6 kilometers) along the Lake Superior shoreline (Figure 1). The park contains about 27,500 acres (11,129 hectares) of federally owned land and an additional 39,000-acre (15,783 hectare) buffer zone that remains in private ownership but is managed under an agreement with the National Park Service (Feil, *et al.*, 1968). The Pictured Rocks escarpment which rises abruptly as much as 200 feet (61 meters) above Lake Superior extends for 15 miles (24 kilometers) along the lakeshore. The forest on top of the Pictured Rocks escarpment is beech (*Fagus grandifolia* Ehrh.) - sugar maple mesic forest (Read, 1975).

## METHODS

The first step in the analysis of the possibilities of reintroducing the peregrine falcon into Upper Michigan and northern Wisconsin was to define its past history in this area. An extensive literature search and communications with appropriate individuals, museums and organizations established an historical basis for the study. The information on past peregrine nestings along the south shore of Lake Superior suggested localities in the three study areas that might have peregrine reintroduction potential.

The 1975 and 1976 summer field seasons were devoted to searching each study area for current peregrine falcon activity and investigating the reintroduction potential of areas with a history of peregrine activity. Photographic and written records were kept throughout the study.

Sites with reintroduction potential were described using criteria outlined by the Federal Peregrine Falcon Recovery Team. Site descriptions of four areas were forwarded to the Recovery Team in the fall of 1975.

During 1976, surveys of possible prey or competitor species were made at five sites with peregrine falcon reintroduction potential. Each survey was conducted over a ten-hour period beginning at approximately 0800 hours Eastern Daylight Time. The investigator was positioned above each site at a point that offered an extensive view of the surrounding territory. All species moving past the point during the ten-hour survey period were tallied. Special note was made of colonial nesting birds and raptors.

Information on human use was collected during 1976. Overall use data for each park were provided by the respective park superintendents. Human activity near each of the five described sites was noted during the ten-hour species survey. Requests for information on Lake Superior water

[1]Thanks are extended to the National Park Service for providing funds and logistic support throughout this project and for providing the assistance of Christopher York during the 1975 field season. Superintendents John Morehead, Isle Royale National Park, Robert L. Burns, Pictured Rocks National Lakeshore and Pat Miller, Apostle Islands National Lakeshore, and their respective staffs must be recognized for the cooperation and interest instrumental in making this study a success.

[2]Forestry Department, Michigan Technological University, Houghton 49931.

quality, especially pesticide or industrial pollutant levels in water, fish or fish-eating birds, were sent to appropriate agencies.

## RESULTS

### *Peregrine Falcon Nesting History in Upper Michigan and Northern Wisconsin*

Development of an accurate history of peregrine falcon nesting activity in Upper Michigan and northern Wisconsin is important in defining use patterns (Table 1).

#### *The Apostle Islands National Lakeshore*

Verch (1976) reported that "Peregrine Falcons occur each year in the vicinity of the islands during the migratory period." Lound and Bratley (1976) reported that peregrines nested somewhere along the sandstone cliffs on Bark Point, 6 miles (9.7 km) west of the west boundary of the Lakeshore. Warren E. Bielenberg (1976, pers. comm.) recorded a pair of peregrines active near a beaver pond on 12, 14, and 15 May 1972. These few records of peregrine activity are a complete listing of historical data available on peregrines in the Apostle Island National Lakeshore area. Beals (1958, 1960, 1967) studied the summer bird life of the Apostle Islands and found no evidence of peregrine falcons. Harris and Matteson (1975) studied nesting gulls and terns in the Apostle Island area in 1974 and also found no indication of peregrine falcon activity (James T. Harris 1976, pers. comm.). In addition, Bill Feeney (1976, pers. comm.) who has been an active hawk bander for many years and claims to know the Apostle Islands area as well as anyone, noted that he had never seen peregrines in the area although he had searched the Islands quite extensively. The survey conducted for this study verified the fact that there is no evidence of current or historic peregrine falcon nesting in the Apostle Islands National Lakeshore area.

The mainland and island shorelines are 50 percent red clay bluffs and approximately 40 percent low red sandstone cliffs that occasionally reach 50 feet (15.2 meters). The remainder is gravel or sand beach.

Visitor use was estimated by Bielenberg (pers. comm.) as being 15,000 to 20,000 days per year for Rocky and Stockton Islands and 75,000 total days for the entire Park. The majority of this use is concentrated in one day visits by persons taking the tour boats through the Islands. Sport fishing and sailing are also popular, but no statistics are available.

#### *Isle Royale National Park*

Peregrine falcons have been recorded 20 times in Isle Royale National Park (Table 2). Nesting pairs were reported in 1890 and 1955. Nine of the 37 areas surveyed in 1975 were used by peregrines and were in the vicinity of possible suitable nesting habitat. The remaining 28 acres were visited because topographic features indicated possible peregrine habitat. Three sites with reintroduction potential: the Palisades, Passage Island and Feldtmann Ridge were described and the information was submitted to the Federal Peregrine Falcon Recovery Team.

The Palisades were described in detail and photographed in 1975. On 15 August 1976 a species survey was conducted from the top of the cliff and human use throughout the ten-hour survey was noted. Since there are no foot trails near the site, the only human activity at the Palisades was boat traffic below the cliffs.

The Passage Island lighthouse cliff was described in 1975. The cliff was photographed and a species survey was conducted in 1976. Human activity during the 17 August survey was limited to three passes directly beneath the west end of the cliff by a National Park Concessions charter fishing boat.

The Feldtmann Ridge site was described and photographed in 1975. The species survey was completed on 20 August 1976 at the Feldtmann Ridge site. Human activity during the survey period was limited to one hiker moving east on the trail that runs along the top of the ridge. Visitation and use data supplied by Isle Royale National Park were too generalized to be of any value in this report.

#### *Pictured Rocks National Lakeshore*

Peregrine falcon acitivity has been reported from the Pictured Rocks National Lakeshore area five times (Table 3). Nesting was noted on Grand Island in 1906. Nestings along the Pictured rocks are recorded for 1927 and 1961 or 1962.

Surveys of all cliff areas in Pictured Rocks National Lakeshore were completed during 1975 and 1976. Between Sand Point and Chapel Beach, the sandstone cliffs rise directly from Lake Superior with the vertical face reaching a height of 200 feet (61 meters) in the area of Grand Portal Point. From Sand Point to the Mosquito River the cliffs are basically smooth, sheer, slightly concave faces with very little ledge structure. The cliff from Mosquito River to Chapel Beach show more variability with vertical and horizontal configurations increasing in frequency.

At Grand Portal Point ledge structure reaches a maximum. During the 11 August 1975 survey by boat, the site of a suspected abandoned peregrine eyrie on the northeast side of Grand Portal Point was located. The site was then rated for its potential for reintroduction.

In 1976 the sandstone cliffs from Chapel Beach to 12-Mile Beach were surveyed. Ledge structure diminishes east of Grand Portal Point.

Peregrine falcon nesting habitat is concentrated at Grand Portal Point because of suitable ledge structure. The Grand Portal Point area is actually two formations. Indianhead Rock forms the west side of the point and the actual Grand Portal point forms the east side. Approximately one mile (1.61 kilometers) separates the two structures.

A possible abandoned peregrine nesting ledge was located on the west side of Indianhead Rock in 1976. During the 1976 survey both the Grand Portal Point ledge and the Indianhead Rock ledges were photographed.

Species surveys were completed for each site, and a climb to the Indianhead rock ledge was made in 1976. On 30 June 1976 the climb was made to the Indianhead Rock ledge. No evidence of past peregrine occupation was found. Three young herring gulls were on the ledge at the time of the climb.

A herring gull colony was found to extend for approximately one-half mile (.8 kilometer) on each side of Grand Portal Point. The major concentration of nests coincided with the abundance of ledge structure and beaches or rubble piles at the base of the escarpment providing nesting substrate. The nesting colony was therefore concentrated in the area with maximum




FIGURE 1. Study area locations within the Lake Superior Basin.

peregrine nesting potential. An estimate of 200 herring gulls and 75 - 100 nests in this colony would not be unreasonable.

Human activity was again recorded during both species surveys in Pictured Rocks National Lakeshore. From Grand Portal Point tour boats were counted passing directly beneath the ledge four times, and seven hikers used the trail on top of the escarpment. At Indianhead Rock, tour boats passed directly beneath the ledge twice, private boats came within one-half mile of the cliff 11 times and one passed by over one-half mile from the cliff. No hikers were tallied during the Indianhead survey.

The major hiking trail in the Pictured Rocks National Lakeshore runs directly on top of the escarpment through the Indianhead Rock and Grand Portal Point regions. Thus, nearly all backcountry visitors to the Park could conceivably be a source of human interference. Backcountry permits issued by the Park may give an indication of what the extent of this interference could be (Table 4).

### *Residue Levels in Lake Superior Bald Eagle and Herring Gull Eggs*

Analysis of residue levels in eggs of bald eagles and herring gulls nesting on Lake Superior show high concentrations of polychlorinated biphenyls (PCB's) and chlorinated hydrocarbons (DDT, DDE, DDD, Dieldrin). Postupalsky (1971) sampled eggshell parameters and residue levels in bald eagle eggs collected along the north shore of Lake Superior. He found the following mean residue levels (parts per million wet weight); DDT-0.89, DDE-56.6, DDD-0.69, Dieldrin-1.11, and estimated PCB's-27.8. Eggshell thinning in this declining, non-reproducing eagle population was 21 - 24 percent. Ryder (1974) sampled 1973 herring gull eggs along the north shore of Lake Superior and found 15.9 to 33.9 parts per million (ppm) wet weight DDE and from 40.6 to 64.1 ppm PCB's.

In 1976 the Michigan State Department of Natural Resources (Lawrence D. Fay, pers. comm.) collected herring gull eggs feom two sites along the south shore of Lake Superior. Colonies on Round Island, Chippewa County and Williams Island, Alger County were sampled. The results of that analysis are included in Table 5.

## DISCUSSION AND CONCLUSIONS

Twenty-two peregrine falcon nestings have been recorded from 12 locations in Upper Michigan and northern Wisconsin (Table 1). The fact that very few ornithological records are published for this sparsely populated region suggests that these figures represent a minimum for the region.

Historical data (Table 1) show that the peregrine falcon once bred on Isle Royale National Park and along the sandstone cliffs of the Pictured Rocks National Lakeshore and was absent as a breeding species in the Apostle Islands National Lakeshore. In the Apostle Islands National Lakeshore, the sandstone cliffs offer the only possible peregrine falcon habitat. Because these cliffs are low, their value as protective nesting cover or as suitable hunting platforms is lacking when compared to traditional peregrine nest sites in eastern North America (Hickey, 1942). Site restrictions, plus the lack of historical peregrine activity, give this area little value as a possible peregrine reintroduction site.

Four possible peregrine falcon reintroduction areas were described during this study. Three of these areas are located in Isle Royale National Park and one is in the Pictured Rocks National Lakeshore. Of the three Isle Royale sites, only one, the Palisades has a history of peregrine nesting (Table 2). Within the Pictured Rocks, Grand Portal Point reintroduction area are two sites that may have been used by breeding peregrines.

TABLE 1. Peregrine falcon nesting history in Upper Michigan and northern Wisconsin 1876-1961 or 1962.

| Date | Location | Source |
|---|---|---|
| 14 April 1876 | Michigammi | Wood 1951 |
| 26 May 1890 | Gull Rocks | Daggett 1890 |
| July 1906 | Grand Island | Doolittle 1906 |
| July 1927 | Pictured Rocks | Wood 1951 |
| 1936 | Huron Islands | Manville 1942 |
| 1937 | Huron Islands | Hickey[a] |
| 20 June 1937 | Marquette County | (Ibid.) |
| 13, 14 June 1938 | Marquette County (2 nests) | (Ibid.) |
| 25 June 1939 | Marquette County | Wood 1951 |
| Before 1939 | Huron Mountain Club | Hickey[a] |
| 20 June 1939 | South Fox Island | Hatt et al. 1948 |
| 19 July 1939 | Mackinac Island | Wood 1951 |
| N.D. | Bark Point | Lound and Bratley 1976 |
| 27 June 1949 | Delta County[b] | Black 1950 |
| 14 April 1950 | Delta County[b] | Wickstrom, N.D. |
| Summer 1954 | Delta County (2 nests)[b] | Black 1955 |
| 1955 | Isle Royale | Janke[c] |
| 1956 | Delta County[b] | Berger and Mueller 1969 |
| 1957 | Delta County[b] | (Ibid.) |
| 1961 or 1962 | Pictured Rocks | Taylor[d] |

[a]Joseph J. Hickey. 1975. Pers. comm. Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706.

[b]Personal communications with Feeney, Marcus, and Taylor indicate that these nests may have all been located in the Burnt Bluff area of the Garden Peninsula.

[c]Robert A. Janke. 1975. Pers. comm. Department of Biological Sciences, Michigan Technological University. Houghton, Michigan 49931.

[d]William Taylor. 1975. Pers. comm. U.S. Forest Service, Hiawatha National Forest, Escanaba, Michigan 49826.

TABLE 2. History of the peregrine falcon in Isle Royale National Park, 189-1975.

| Data | Date | Observation | Source |
|---|---|---|---|
| 1. | 26 May 1890 | Nest on gull rocks, pair present | Daggett 1890 |
| 2. | 15 Sept. 1929 | Immature female collected by Albert Brown on Passage Island | Wood 1951 |
| 3. | 2-26 May 1948 | Sightings reported on Passage Island | Krefting et al. 1966 |
| 4. | 1955 | Nest reported on the Palisades | Janke[a] |
| 5. | 22 Sept. 1961 | Sightings on Passage Island and Merritt Lane | Krefting et al. 1966 |
| 6. | 15 March 1962 | Sighting between Moskey Basin and Lake Richie | (Ibid.) |
| 7. | 10 Oct. 1962 | Sighting on McCargoe Cove | (Ibid.) |
| 8. | 5 July 1963 | Male sighted on Amygdaloid Island | Stauber 1963 |
| 9. | 14 July 1963 | Male sighted in the Palisades, flew toward Passage Island | (Ibid.) |
| 10. | 8 Aug, 1963 | Sighting near Lake Ojibway | (Ibid.) |
| 11. | 30 Aug. 1963 | Two sighted on northshore of Passage Island | (Ibid.) |
| 12. | 8 July 1964 | Sighting at Duncan Bay | Stauber 1964 |
| 13. | 24 Sept. 1965 | Sighting one-half mile northeast of Mott Island | Zakis[b] |
| 14. | 4 Aug. 1971 | Sighting along Greenstone trail two miles from Windigo | (Ibid.) |
| 15. | 14 Aug. 1971 | Sighting on Mount Siskiwit | (Ibid.) |
| 16. | 30 Sept. 1971 | Sighting on Greenstone Beach | (Ibid.) |
| 17. | 31 Sept. 1971(?) | Questionable sighting in Chippewa Harbor, pari of birds | (Ibid.) |
| 18. | 22 Aug. 1972 | Sighting near Feldtmann tower | (Ibid.) |
| 19. | 15 Sept. 1972. | Questionable sighting near old Feldtmann tower site | (Ibid.) |
| 20. | 23 July 1974 | Questionable sighting near Feldtmann tower | (Ibid.) |

[a]Robert A. Janke. 1975. Pers. comm. Biology Department, Michigan Technological University, Houghton, Michigan 49931.

[b]Aivars Zakis. 1975. Pers. comm. 7421 Portland Avenue South, Richfield, Minnesota 55423.

TABLE 3. History of the peregrine falcon in the Pictured Rocks National Lakeshore area, 1906-75.

| Date | Observation | Source |
|---|---|---|
| July 1906 | Nest with full fledged young on Grand Island | Doolittle 1906 |
| July 1927 | Nest with young photographed along Pictured Rocks | Wood 1951 |
| Summer 1938 | Adult sighted in pictured Rocks area | Hickey[a] |
| 1961 or 1962 | Young taken from a nest by falconers on Pictured Rocks area | Taylor[b] |
| 18 April 1963 | Sighting at Beaver Basin | Cuthbert 1964 |

[a]Joseph J. Hickey. 1975. Pers. comm. Department of Wildlife Ecology, 226 Russell Laboratories, University of Wisconsin, Madison, Wisconsin 53706.

[b]William Taylor. 1975. Pers. comm. U.S. Forest Service, Hiawatha National Forest, Escanaba, Michigan 49829.

TABLE 4. Backcountry permits issued by Pictured Rocks National Lakeshore personnel April-August, 1973-75.

| | 1973 | 1974 | 1975 |
|---|---|---|---|
| April | 25[1/] | 25 | 10 |
| May | 132 | 20 | 80 |
| June | 32 | 104 | 344 |
| July | 74 | 180 | 998 |
| August | 340 | 490 | 1229 |

1/ - Figures are in people-days.

Table compiled from data in the Pictured Rocks National Lakeshore files.

TABLE 5. Results of residue analysis of herring gull eggs collected from two southern Lake Superior nesting colonies in 1976.

| | | Round Island Chippewa County | | Williams Island Alger County | |
|---|---|---|---|---|---|
| Residue | | Sample Number 1 | 2 | Sample Number 1 | 2 |
| DDT | | 7.97[1/] | 5.08 | 7.81 | 9.22 |
| DDD | | <0.02 | <0.02 | <0.02 | <0.02 |
| DDE | | 18.60 | 12.20 | 22.00 | 23.90 |
| Dieldrin | | 0.59 | 0.42 | 0.35 | 0.55 |
| Estimated PCB's | 1254 | 64.80 | 38.30 | 64.80 | 75.80 |
| | 1260 | 40.60 | 25.80 | 39.10 | 46.90 |

1/ - All values are in parts per million.

Bent (1961) describes the peregrine's diet as being primarily birds ranging in size from mallard ducks (*Anas platyrhynchos* Linnaeus) to warblers. Cade et al. (1968), Bond (1946), and Hunt et al. (1975) have all looked at peregrine prey species. The long list of documented prey species suggests that food availability is seldom a limiting factor in peregrine nesting success.

Species list compiled during the ten-hour survey from each proposed reintroduction site seems to indicate that food supply is sufficient in each area to support breeding peregrines. At all sites, except the Isle Royale, Feldtmann Ridge site, herring gulls (*Larus argentatus smithsonianus* Coues) were especially abundant, and nearby breeding colonies of this species would supply enough food for peregrines to successfully raise young.

The activities of man, either directly or indirectly, have always been the greatest threat to peregrine falcon survival (Hickey, 1942; Ratcliffe, 1969; Hickey and Anderson, 1969; Snow, 1972). Human disturbance is a problem at each proposed reintroduction site, but could be eliminated with cooperation between researchers and Park Service personnel.

Failures in reproductive success as the result of environmental pollutants have been a major cause of the decline in peregrine falcon populations (Hickey and Roelle, 1969; Hodson, 1971). Peregrines suffer reproductive failure when DDE, a breakdown product of DDT, levels reach 20 parts per million (ppm) in their eggs. Reproductive success of ducks and herring gulls is not affected until levels reach 100 ppm (Zimmerman, 1975). PCB's have similar effects on reproductive success (Hickey, 1969).

The peregrine falcon is a top predator in its ecosystem. Persistent pesticides and PCB's tend to concentrate as they are passed from prey to predator through the food chain. Cade et al. (1968) found residues of these chemicals to be 10 to 100 times more concentrated in peregrine eggs and chicks than in prey species.

Pesticides and PCB levels in Lake Superior eagle and herring gull eggs (Table 5) are at a level that indicates contamination of the ecosystem in excess of levels that would cause peregrine reproductive failure. Until these residue levels drop to a point where reproductive success is not affected, no reintroduction attempts should be made into areas bordering Lake Superior. D. B. Peakall (pers. comm. 1976), Sergej Postupalsky (pers. comm. 1976) and Richard Powers (pers. comm. 1976) all agree with this conclusion.

## SUMMARY

A study of peregrine falcon history, current status and reintroduction possibilities in the Apostle Islands National Lakeshore, Isle Royale National Park and Pictured Rocks Lakeshore was conducted. A survey of peregrine history in Upper Michigan and northern Wisconsin revealed 20 nest records at 12 localities. Two eyries were documented in both Isle Royale National Park and Pictured Rocks National Lakeshore. No record of peregrines nesting in the Apostle Islands National Lakeshore was found.

Three areas of Isle Royale National Park; the Palisades, Passage Island and Feldtmann Ridge, were described in detail and the information was submitted to the Federal Peregrine Falcon Recovery Team. The Grand Portal Point area of Pictured Rocks National Lakeshore was identified as an abandoned eyrie and was also submitted for consideration as a possible reintroduction site.

The data presented on chemical pollutants indicate that difficulty may exist in establishing a breeding population of peregrines at the present time. However, we do not wish to imply that an experimental release should not be attempted. There is much useful information that could be obtained from such a release. We need to know more about the problems that may arise from more northern releases. Will the birds become highly migratory or will they try to stay in the area?

It would also be useful to study the sociological problems that may develop from the sudden closure of a trail system or the forcing of a tour boat away from a traditionally visited site. Is the general public willing to accept use restrictions on National Park lands for a bird?

We also have a safe release site in the Voyageur's National Park in northern Minnesota where birds could be released and still be a part of the Lake Superior basin.

## LITERATURE CITED

BEALS, EDWARD. 1958. Notes on the summer birds of the Apostle Islands. Passenger Pigeon 20:151-160.

_____. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bul. 72(2):156-181.

_____. 1967. Notes on the summer birds of the Apostle Islands, II. Passenger Pigeon 29:17-18.

BENT, A. C. 1961. Life histories of North American birds of prey. Part 2: Orders *Falconiformes* and *strigiformes*. Dover Pub., Inc., New York. x + 466 p.

BERGER, D. D. and H. C. MUELLER. 1969. Nesting peregrine falcons in Wisconsin and adjacent areas. Pages 155-122 *in* J. J. Hickey (ed.), Peregrine falcon populations: their biology and decline. Univ. Wisc. Press, Madison.

BLACK, C. T. (ed.). 1950. Seasonal records of Michigan birds - breeding season, 1949. Jack-Pine Warbler 28(2):31-38+.

_____. (ed.). 1955. Michigan bird survey, summer and fall, 1954. Jack-Pine Warbler 33(1):19-32.

BOND, R. M. 1946. The peregrine population of western North America. Condor 48(3):101-116.

CADE, T. J., C. M. WHITE and J. R. HAUGH. 1968. Peregrines and pesticides in Alaska. Condor 70:170-178.

CUTHBERT, N. L. 1964. Michigan bird survey, Spring 1963. Jack-Pine Warbler 42(1):195-227.

DAGGETT, FRANK S. 1890. Isle Royale. Ornithologist and Oologist 15(7):99-100.

DOOLITTLE, E. A. 1906. The summer birds of Grand Island. No. 7067 in Marquette Co. Hist. Soc. manuscript file. 13 p.

EASTERN PEREGRINE FALCON RECOVERY TEAM. 1976. Eastern peregrine falcon recovery plan: preliminary draft recovery plan. 130 p.

FEIL, A. G., JR. et al. 1968. Pictured Rocks National Lakeshore, Michigan Master Plan. U. S. Dept. Int., Nat. Park Service. 22 p.

HARRIS, J. T. and S. W. MATTESON. 1975. Gulls and terns as indicators of man's impact upon Lake Superior. Inst. for Environ. Studies, Univ. Wisc. Sea Grant Coll. Pro. Tech. Rept. No. 227. v + 45 p.

HATT, R. T., J. VANTYNE, L. C. STUART, C. H. POPE, A. B. GROBMAN. 1948. Island life: a study of the land vertebrates of the islands of eastern Lake Michigan. Cranbrook Institute of Science Bull. No. 27. xi + 179 p.

HICKEY, J. J. 1942. Eastern population of the duck hawk. Auk 59:176-204.
_____ 1969. Peregrine falcon populations: their biology and decline. Univ. Wisc. Press, Madison. xxii + 596 p.
_____ and D. W. ANDERSON. 1969. The peregrine falcon: life history and population literature. Pages 3-42 *in* J. J. Hickey (ed.), Peregrine falcon populations: their biology and decline. Univ. Wisc. Press, Madison.
_____ and J. E. ROELLE. 1969. Conference summary and conclusions. Pages 553-567 *in* J. J. Hickey (ed.), Peregrine falcon populations: their biology and decline. Univ. Wisc. Press, Madison.
HODSON, K. 1971. Research planning conference on peregrines and other birds of prey. Raptor Res. News 5(4):123-131.
HUNT, W. G., R. R. ROGERS, and D. J. SLOWE. 1975. Migratory and foraging behavior of peregrine falcons on the Texas coast. Can. Field-Nat. 89(2):111-123.
KREFTING, L. W., F. B. LEE, P. C. SHELTON and K. T. GILBERT. 1966. Birds of Isle Royale in Lake Superior. U. S. Dept. Int., Fish and Wildl. Service, Special Report - Wildl. No. 94. 56 p.
LOUND, R. H. and D. BRATLEY. 1976. Port Wing: Bayfield County. Pages 81-84 *in* D. D. Tessen (ed.), Wisconsin's favorite bird haunts. Wisc. Soc. for Orni., Inc. 132 p.
MANVILLE, R. H. 1942. Report on wildlife studies at Huron Mountain Club., 1939-42. vii + 165 p.
MATTESON, R. E., J. L. O'LEARY, T. G. SQUIRE, L. STADNYK and C. E. TWING. 1973. The impact of the Apostle Islands National Lakeshore on Bayfield County. Sigure Olson Inst. of Environ. Studies, Ashland. 121 p.
POSTUPALSKY, S. 1971. Toxic chemicals and declining bald eagles and cormorants in Ontario. Can. Wildl. Service, Pesticide Section Manuscript Report No. 20. 42 p.
RATCLIFFE, D. A. 1969. Population trends of the peregrine falcon in Great Britain. Pages 239-269 *in* J. J. Hickey, ed. Peregrine falcon populations: their biology and decline. Univ. Wisc. Press, Madison.
READ, R. H. 1975. Vascular plants of Pictured Rocks National Lakeshore, Alger County, Michigan. Reprinted from: The Michigan Botanist Vol. 14. 44 p.
RYDER, J. P. 1974. Organochlorine and mercury residues in gulls' eggs from western Ontario. Can. Field-Nat. 88:349-352.
SNOW, C. 1972. Habitat management series for endangered species, Report No. 1, American peregrine falcon, *Falco peregrinus anatum* and Arctic peregrine falcon, *Falco peregrinus tundrius*. Bureau of Land Mgmt., U. S. Dept. Int., Tech., Note 6601. 35 p.
STAUBER, E. 1963. The birds of prey of Isle Royale. Special report, Dept. of Forestry and Cons., Purdue Univ. Oct. 7, 1963. Mimeo. in Isle Royale Nat. Park files. 29 pgs + 6 pgs of maps.
_____. 1964. Birds of prey on Isle Royale National Park II. Dept. of Forestry and Cons., Purdue Univ. Mimeo in Isle Royale Nat. Park files. 17 pgs. + 1 map.
VERCH, R. 1976. Ashland County, Pages 90-94 *in* D. D. Tessen (ed.), Wisconsin's favorite bird haunts. Wisc. Soc. for Orni., Inc. 132 p.
WICKSTROM, G. ND. Seasonal records of Michigan birds, Spring 1950. Jack-Pine Warbler.
WOOD, N. A. 1951. The birds of Michigan. Misc. Publ., Univ. Mich. Mus. Zoology, No. 75. Univ. Mich. Press, Ann Arbor. 559 p.
ZIMMERMAN, D. R. 1975. That the peregrine shall live. Audubon Magazine. Nov. 1975. Pages 38-49.

# FOREST FIRES AND THE TREE-HOLE NESTING CYCLE IN GRAND TETON AND YELLOWSTONE NATIONAL PARKS[1]

Dale L. Taylor[2]

Natural, or lightning-caused, forest fires have been allowed to burn in zoned areas of several national parks (Kilgore, 1974). The purpose of natural fire-vegetation management is to perpetuate indigenous plant and animal associations. Without fire, marked changes will occur in patterns of vegetation and associated animal species (Taylor, 1973b; Loope and Gruell, 1973; Agee, 1974). Fire-vegetation management plans have been in effect in Yellowstone and Grand Teton National Parks since 1972 (Sellers and Despain, 1974; Loope and Wood, 1974).

As a part of ongoing research on fire ecology and in response to public interest in the Waterfalls Canyon forest fire, long-term studies were initiated in Grand Teton National Park in 1974. Similar studies had been previously conducted in Yellowstone (Taylor, 1969, 1973a, 1973b, and 1974). This paper examines the tree-hole nesting cycle and shows that at least three bird species, the northern three-toed woodpecker (*Picoides tridactylus*), black-backed - three-toed woodpecker (*Picoides arcticus*) and mountain bluebird (*Sialia currucoides*) are fire-associated species in northwestern Wyoming. Three-toed woodpeckers depend upon forest fires to create favorable habitat, and mountain bluebirds depend upon three-toed woodpeckers and hairy woodpeckers (*Dendrocopus villosus*) for nesting sites. Without forest fires, populations of the three species will be reduced or possibly eliminated from the parks.

## STUDY AREAS

*Yellowstone National Park.* All seven study areas were severely burned, were 40 acres or larger, and were between 8,000 and 8,200 feet elevation. Post-burn vegetation was primarily lodgepole pine (*Pinus contorta*). Forest canopy closure occurred about 40 years post-fire. Detailed descriptions of each area are in Taylor (1969).

Censuses from 1966 through 1973 provided density estimates of breeding birds for 5, 7, 11, 13, 17, 19, 25, 29, 57, 111, and 300 years post-fire.

*Grand Teton National Park.* The Waterfalls Canyon natural fire of 1974 burned 3,492 acres in forest dominated by Engelmann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*). Three study areas were selected:

1. Severe burn. More than 90% of the trees were killed, usually by crown fire. The area covered 89 acres (36 ha).

2. Moderate burn. Most of the overstory (40% or more) was alive one year post-fire. Fire created a complex mosaic of burned and unburned vegetation. The study area was 116 acres (47 ha).

3. Unburned. In 1975, this 42-acre (17 ha) site was dominated by old growth Engelmann spruce and subalpine fir.

A 100-acre (40.5 ha) area severely burned in 1932 (43 years post-fire) was also studied. The pre-fire spruce-fir forest was probably uniform, however, post-fire vegetation varied from open grassland - forb - shrub to dense lodgepole pine forest.

All four study areas were located at 6,770 feet (2,065 m) elevation. Barmore, *et al.* (1976) provides a description of each area.

## CENSUS METHODS

Bird density was estimated by the transect survey method (Haapanen, 1965; Kendeigh, 1944). Breeding birds were considered to be those within a 75-foot (22.9 m) wide belt on each side of a 1,000 yard (914 m) paced transect (census area = 10.3 acres (4.2 ha). Some census strips in Yellowstone were 12.4 acres (5.1 ha).

## RESULTS AND DISCUSSION

Northern three-toed woodpeckers (listed as rare in Grand Teton National Park, Follett, 1976) concentrated on the severe burn and to a lesser extent on the moderate burn one year post-fire. Black-backed three-toed woodpeckers also nested on the severe and moderate burns, but were not observed on other sites (Table 1). This species is not listed for Grand Teton National Park (Follett, 1976), although Salt (1957) recorded 0.7 breeding pairs per 100 acres (41 ha) in spruce-fir forest west of String Lake.

In Yellowstone neither northern or black-backed three-toed woodpeckers were observed on any of the study areas, but one nest of the former species was found on the 13-year post-fire area. Follett (1976) lists these two woodpeckers as occasional and rare, respectively.

Three-toed woodpeckers apparently concentrate on newly burned areas, remain for possibly four to at most five years, and then leave (Table 1; Figure 1). Prodigious numbers of round headed wood borers (*Monochamus* sp. and *Xylotrechus longitarsis*: Cerambycidae) occur under bark of fire-killed trees one year post-fire. Woodpeckers feed on these borers. Woodpecker densities decline the second year post-fire when few wood borers are present.

Somewhat lower but more stable three-toed woodpecker densities occurred on moderate burns (Table 1). Three-toed woodpeckers were observed in old growth spruce-fir forests, but not until the second post-fire year. This indicates food was reduced in severely burned areas the second year post-fire and birds moved into nearby unburned forests to feed.

Hairy woodpeckers were not observed on the severely burned area one year post-fire (Table 1). An increase to 10 pairs per 100 acres the second year was associated with more than a 50% decline in three-toed woodpeckers. Hairy woodpeckers were present on the moderate burn, 43-year post-fire lodgepole pine, and unburned

[1]I thank William J. Barmore, Research Biologist, Grand Teton National Park, for advice and support during this study.

[2]Sterling College, Sterling, Kansas.

TABLE 1. Density of woodpeckers and mountain bluebirds in Grand Teton National Park. Areas were censused 1 and 2 years post-fire. P = present, but not in census transects.

GRAND TETON NATIONAL PARK

MEAN BREEDING PAIRS/100A.

| | Severe years Post-Fire | | Moderate years Post-Fire | | 43 years Post-Fire | | Spruce-Fir | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 |
| Hairy Woodpecker | | 10 | 5 | 2 | 2 | 0 | 2 | |
| Northern Three-toed Woodpecker | 34 | 15 | 7 | 10 | | | P | |
| Black-backed Three-toed Woodpecker | 5 | P | 2 | 5 | | | | 2 |
| Mountain Bluebird | P | 15 | | | | | | |

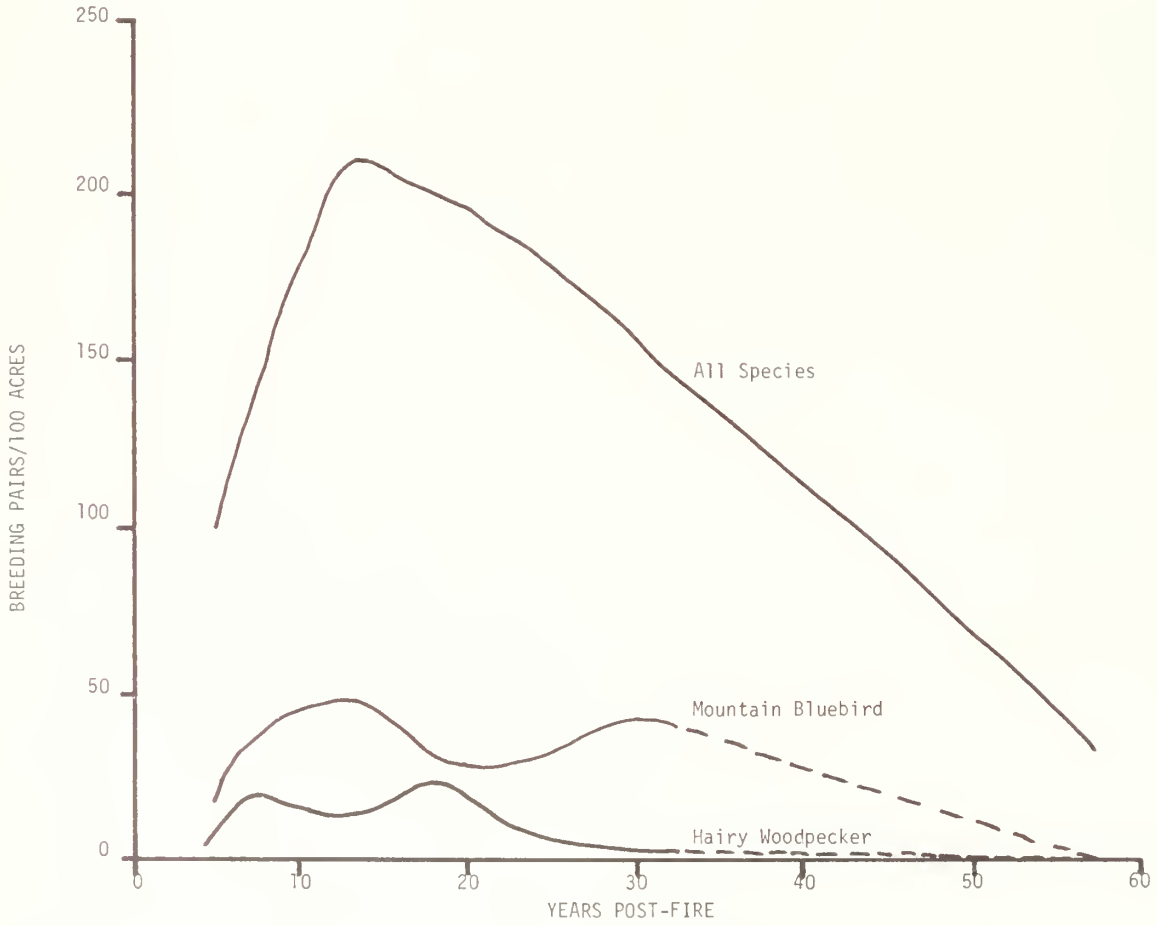



FIGURE 1. Density of mountain bluenirds, hairy woodpeckers, and all species of birds occurring in post-fire lodgepole pine stands in Yellowstone National Park.

spruce-fir areas, but density declined in all areas the second year post-fire. Hairy woodpeckers apparently moved from surrounding unburned forests to severely burned areas. In Yellowstone, hairy woodpeckers were present five years post-fire, increased until about 25 years post-fire, and then declined to zero by about 50 years post-fire (Figure 1).

Mountain bluebirds were present on the severe burn one year post-fire, but they were never observed nesting. They increased to 15 pairs per 100 acres the second year and nested in nest holes made and utilized by northern three-toed woodpeckers the previous year. Mountain bluebirds were never observed on the moderate burn, the 43-year post-fire area, or unburned spruce-fir.

In Yellowstone, mountain bluebird density increased until about 29 years post-fire, then declined to zero by about 50 years post-fire (Figure 1). No areas were censused between 29 and 57 years post-fire, so the exact time when densities of hairy woodpeckers and mountain bluebirds actually reached zero is not known.

I previously described (Taylor, 1973a), a "tree-hole cycle" initiated by forest fires. Woodpeckers concentrate on burned areas to nest in standing, fire-killed trees and to feed on insect larvae that attack them. Mountain bluebirds, tree swallows (*Iridoprocne bicolor*), and other birds nest in holes made by woodpeckers. I believed the hairy woodpecker initiated the nest hole cycle in Yellowstone Park, but the youngest stand I examined was five years post-fire. McLaren (1962) described a flicker (*Colaptes auratus*) nest hole cycle in British Columbia.

It now appears that the nest hole cycle is initiated by northern and black-backed three-toed woodpeckers in northwest Wyoming. The two species apparently disperse from burned areas four to five years post-fire. Hairy woodpeckers contribute nest holes from the second year until the end of the cycle when all snags topple. Mountain bluebirds and other species have nesting sites available that otherwise would not be present. About 50 years post-fire, when the forest canopy has closed, all tree hole nesting species will vanish even though a few snags may remain. Feeding and nesting habitat have become so changed by lack of snags and increased height and density of new trees as to render the area unsuitable for tree-hole nesting species.

Trees killed by mountain pine beetles (*Dendroctonus ponderosae*) do not provide food and nesting habitat comparable to burned areas. Klein, *et al.* (1972) state that most lodgepole pine stands in the Grand Teton Park area have been vulnerable to beetle attack which killed 10-45% of the trees over 5 in. (13 dm) diameter breast height. Hairy woodpecker density was less than one pair/100 acres in two areas (Beaver Creek and Signal Mountain) containing high densities of beetle-killed lodgepole pine. No three-toed woodpeckers or woodpecker nest holes were observed (Taylor, unpubl. data).

Balda (no date) recommends determining minimum number of dead and dying snags required to support populations of secondary cavity nesting birds at a level where normal density and diversity of species is maintained in ponderosa pine (*Pinus ponderosa*). This study indicates that burned areas no more than five years post-fire are required to maintain habitat for northern three-toed woodpeckers, black-backed three-toed woodpeckers, and mountain bluebirds in coniferous forests of northwestern Wyoming.

## LITERATURE CITED


AGEE, J. K. 1974. Environmental impacts from fire management alternatives. Report to the National Park Service, Western Regional Office, San Francisco, California. 92 pp. mimeo.

BALDA, RUSSELL P. (no date). The relationship of secondary cavity nesters to snag densities in western coniferous forests. U.S. Forest Service, Albuquerque, New Mexico. 37 pp. mimeo.

BARMORE, WILLIAM J., DALE L. TAYLOR, and PETER HAYDEN. 1976. Ecological effects and biotic succession following the 1974 Waterfalls Canyon Fire in Grand Teton National Park. Research Progress Report. Grand Teton National Park. 99 pp. mimeo.

FOLLETT, RICHARD. 1976. Birds of Yellowstone and Grand Teton National Parks. Yellowstone Library and Museum Association, Yellowstone Park, Wyoming. 73 p.

HAAPANEN. A. 1965. Bird Fauna of Finish forests in relation to forest succession. I. Annales Zoologica Finnici 2:153-196.

KENDEIGH, S. C. 1944. Measurement of bird populations. Ecol. Monog. 14:67-106.

KILGORE, BRUCE M. 1974. Fire Management in the National Parks: An Overview. Tall Timbers Fire Ecology Conference, No. 14, pp. 45-57.

KLEIN, W. H., STIPE, L. E., and FRANDSEN, L. V. 1972. How damaging is a mountain pine beetle infestation? U.S.D.A., Forest Service, Division of Timber Management, Ogden, Utah.

LOOPE, LLOYD and G. E. GRUELL. 1973. The ecological role of fire in the Jackson Hole area of northwestern Wyoming. Quaternary Research 3(3):425-443.

LOOPE, LLOYD and ROBERT P. WOOD. 1974. Fire Management in Grand Teton National Park. Tall Timbers Fire Ecology Conference, No. 14. pp. 87-98.

MCLAREN, W. D., 1962. A Preliminary study of nest site competition in a group of hole nesting birds. M.S. Thesis. University of British Columbia, Vancouver.

SALT, GEORGE. 1957. An analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. Condor 59(6):373-393.

SELLERS, ROBERT and DON G. DESPAIN. 1974. Fire Management in Yellowstone National Park. Tall Timbers Fire Ecology Conference, No. 14, pp. 99-113.

TAYLOR, DALE L. 1969. Biotic succession of lodgepole pine forests of fire origin in Yellowstone National Park. Ph.D. Dissertation. University of Wyoming. 320 p.

_____. 1973a. Competitive exclusion between tree swallows and mountain bluebirds in Yellowstone National Park. Reprot to the National Geographic Society, Washinton, D.C.

_____. 1973b. Some ecological effects of forest fire control in Yellowstone National Park. Ecology 54(6):1394-1396.

_____. 1974. Forest Fires in Yellowstone National Park. J. Forest History. 18(3):68-77.

# COMPARATIVE ECOLOGY OF TWO AVIAN PREDATOR GUILDS: A DISCUSSION ON THE USE OF ADAPTIVE SYNDROMES IN STUDIES OF PREDATION

Robert C. Eckhardt[1]

## INTRODUCTION

Every predatory species, indeed, every species, has a unique way of life. While we frequently are impressed by the differences in the life styles of very closely related species, the similarities can often be equally striking and important. In this paper, using insectivorous birds as an example, I show how predators can be viewed in terms of their fundamental similarities, regardless of taxonomic distances. Through the use of the concepts of guild and adaptive syndrome, these similarities can be exploited to enhance our understanding of predators and the process of predation.

A guild is a group of species that exploits the same resource in a similar way. For example, in Root's (1973) examination of the insect herbivores utilizing the foliage of collard plants, he found three distinct classes of feeders: the pit feeding guild, whose member species rasp small pits from leaf surfaces; the strip feeding guild, whose members chew holes throughout the foliage; and the sap feeding guild, whose members probe into the plant and suck its juices. Similarly, in avian insectivores, we can enumerate a number of different guilds: foliage-gleaners, such as warblers; flycatchers; sweepers, such as swifts and swallows; woodpeckers; probers, such as creepers and nuthatches; and so forth.

Guilds identify the basic functional roles played by the species of a particular trophic level within a community. Because of the similarity of modes of life in species comprising a guild, we expect competitive interactions to be most intense within a guild and less intense between members of different guilds. Guild structure, and the interactions of the members of a guild, are not, of course, unchanging. As Root (1973) has shown with the collard fauna, the abundance, even the presence, of a particular species may vary relative to its individualistic response to location, weather, or other factors.

Organisms can be arranged in guilds because every species displays a particular manner of resource utilization. Each species has a set of characteristics, or adaptations, that are associated with its method of resource utilization. This coordinated set of characteristics is called an adaptive syndrome (Root and Chaplin, 1976). To date, the concept of adaptive syndromes has been applied only to individual species. Root and Chaplin (1976), for example, distinguish between the adaptive syndromes of two closely related species of *Oncopeltus*, the milkweed bug. Of course, species of a single guild, whether or not they are closely related taxonomically, have similar life styles, and consequently, similar adaptive syndromes. To return to the above example, the two species of *Oncopeltus* are strikingly similar in terms of time budgets on their host plant, despite the fact that it is the differences between the two species that are dwelled upon by the authors.

Although all species of a local guild must be different in some way (the principle of competitive exclusion states that two species cannot occupy the same niche), they are certainly more similar, one to another, than to the species of any other guild. For this reason, I have proposed (Eckhardt, 1977) that the concept of adaptive syndromes be expanded to include the idea that every guild can be described by a unique, characteristic adaptive syndrome only slightly less specific than the syndromes of its member species. In the remainder of this paper I will illustrate this idea in two guilds of insectivorous birds, and discuss how its use may be helpful in the study of predators and predation.

## METHODS

During the summers of 1973 to 1975, I studied the foraging ecology of eight locally sympatric species of warblers and flycatchers. The birds breed at an elevation of 2658 m, in a willow floodplain bordered by lodgepole pines, on the west side of Rocky Mountain National Park, Colorado. Three species of warblers make up the gleaning guild: Wilson's Warbler, *Wilsonia pusilla*; Yellow Warbler, *Dendroica petechia*; and Yellowthroat, *Geothlypis trichas*. These species are what I call active searchers, or actively searching predators (often termed "searchers" or "widely foraging" predators elsewhere). Five species of flycatchers make up the flycatching guild: Dusky Flycatcher, *Empidonax oberholseri*; Willow Flycatcher, *E. traillii*; Western-Flycatcher, *E. difficilis*; Western Wood Pewee, *Contopus sordidulus*; and Olive-sided Flycatcher, *Nuttallornis borealis*. These species are what I call passive searchers, or passively searching predators (often termed "pursuers" or "sit-and-wait" predators elsewhere).

The foraging behavior, ecology, and breeding biology of the birds were observed in the field during the breeding season. All observations were made with the aid of 7 x 35 binoculars, and each observation was timed with a stopwatch. Information concerning the bird and its location, a description of the perch and perch plant, and numerous aspects of behavior and foraging that occurred during the observation period were recorded in a personal shorthand on data sheets in the field. This information was transcribed daily to a permanent record for each species. A more detailed account of methods and the data taken during observations can be found in Eckhardt (1977).

## RESULTS: THE FORAGING CHARACTERISTICS OF WARBLERS AND FLYCATCHERS

I examined a wide variety of characteristics of the foraging strategies exhibited by these eight species. There are two ways of looking at the results. One is to ask how different are the syndromes of the species within each guild. This is the approach commonly used in ascertaining the methods of resource division in closely competing species. Another way of looking at the results is to contrast the characteristics of the members of different guilds as a whole and ask how similar

[1]Assistant Professor of Zoology, University of Maine, Orono, Me. 04473.

are the members of each guild. In this way it is possible to evaluate the extent to which guilds are discrete entities with definitive characteristics, that is, the extent to which each guild exhibits a unique adaptive syndrome. In the paragraphs that follow, I discuss some of the more significant aspects of the foraging behavior of the eight species, with the objective of illustrating the degree to which the two guilds can be distinguished by their adaptive syndromes.

One of the most significant aspects of a bird's biology is the way in which it captures its prey. Warblers and flycatchers employ four major foraging maneuvers: gleaning, which is taking a prey item from a substrate while the predator is perched; hovering, or taking a prey from a substrate while the predator is in flight; sallying (sometimes called hawking), or taking airborne prey on the wing; and pouncing, a specialized form of sallying, in which the prey is on the ground and the predator alights only long enough to take it. Figure 1 gives the foraging repertoire of each species, showing the percentage of attacks of each type performed by each species. Warblers glean 75% of the time or more. Flycatchers, on the other hand, predominantly sally, although in some species hovering constitutes a significant fraction. In all flycatcher species, the total of hovers and sallies makes up 90% or more of all attacks. Thus it can be seen that in their foraging repertoire the two guilds are distinctly different.

The foraging repertoire could be considered an indicator of "activeness of pursuit," for while gleaning requires little more than an extra jab of the bill, hovering and sallying require far larger expenditures of energy. Two other characteristics could be thought of as indicators of "activeness of search." One of these is what I call velocity, the average number of perches visited per minute (Table 1, column A). In warblers, velocity is high, ranging from 10 to over 33. Flycatchers, on the other hand, visit a distinctly smaller number of perches per minute, from a high of 3.8 to a low of 0.6.

While velocity measures the *absolute* rate of search (in terms of the frequency of perch changes per unit time), search intensity, defined as the average number of perches visited per attack, measures the *relative* rate of search (the frequency of perch changes with regard to the foraging rate). Once again, the two guilds are distinctly different, with warblers having the larger values (Table 1, column B). Warblers have search intensities ranging from 9.7 to 5.0; for flycatchers the values vary from 3.4 to 1.2. To summarize to this point, then, gleaners are active searchers (they look for prey difficult to find) but passive pursuers (they attack prey easy to catch). Flycatchers, on the other hand, are passive searchers (they wait for prey easy to find) but active pursuers (they attack prey difficult to catch).

Foraging intensity measures the rate of attack in attacks per minute. By this measure, although the two guilds do have distinctly different ranges, there is a slight overlap between them (Table 1, column C). In warblers, foraging intensity is high and ranges from 4.6 to 1.7. In flycatchers, values are generally lower, ranging from 1.8 to 0.2.

A direct consequence of the foraging repertoire of each species is the type of attack substrate utilized. (An attack substrate is the substrate of a prey item toward which an attack is directed.) Figure 2 illustrates the percentage of each common attack substrate utilized by each species. For warblers, which are primarily gleaners of deciduous foliage, willow predominates. On the other hand, flycatchers are predominantly salliers, and thus their prey are usually aerial, although the *Empidonax* species (whose foraging repertoire includes a significant amount of hovering) also utilize a substantial percentage of a variety of different solid substrates.

The foraging repertoire also influences the average distance travelled from perch to prey. This distance is the attack radius, and these are illustrated for all species in Figure 3. Attack radii among warblers are small, ranging from hardly more than zero to 1.1 ft. Flycatchers tend to have longer radii which range from 3.8 to 26.1 ft.

Just as attack radii are relatively small in warblers, the size of what I call the foraging space is also relatively small in warblers. There are several ways of measuring foraging space -- fortunately, all of them suggest the same conclusions. Perhaps the simplest way of illustrating the differences in foraging space is by comparing the diversities of the utilization of different dimensions of foraging space: the height of the perch; the height of attack; and the distance of the attack from the perch. Diversities were calculated by dividing heights and distances into 5 ft intervals, determining the proportion of attacks in each interval, and applying these figures to the Shannon diversity measure,

$$H' = -\sum_{i=1}^{n} p_i \cdot \log p_i,$$

where $p_i$ is the proportion in the i-th category. The results (Figure 4) show that in all three dimensions warblers have lower diversities and hence a smaller overall foraging space than flycatchers.

Finally, size relationships are different in the two groups of birds. Two indicators of size -- body weight and wing length -- will serve to illustrate this comparison. Schoener (1965) has defined small (i.e., not ecologically significant) differences as those in which the ratio of the larger to the smaller is less than 1.14. Ecologically significant differences generally have ratios of over 1.14. These ratios for the two guilds are given in Table 2. (Western Flycatcher have been excluded because they nest in a slightly different habitat than the others.) Gleaners all have ratios of less than 1.14. Except for the *Empidonax* sibling species pair, which are similar in size and hence have low ratios, flycatcher values exceed the 1.14 value. In general, then, warblers are ecologically similar while flycatchers are ecologically different in body size.

## DISCUSSION

It is clear from the preceding results that as one might expect, each species has a unique combination of characteristics and adaptations. More significant to the present discussion, however, is the fact that guilds can be distinguished one from another by the general range of characteristics displayed by their members. Thus a guild could be said to have an adaptive syndrome characteristic of it and distinct from those of all other guilds. We could take the idea one step further and say that the identification and classification of distinct guilds is contingent upon the description of a unique adaptive syndrome

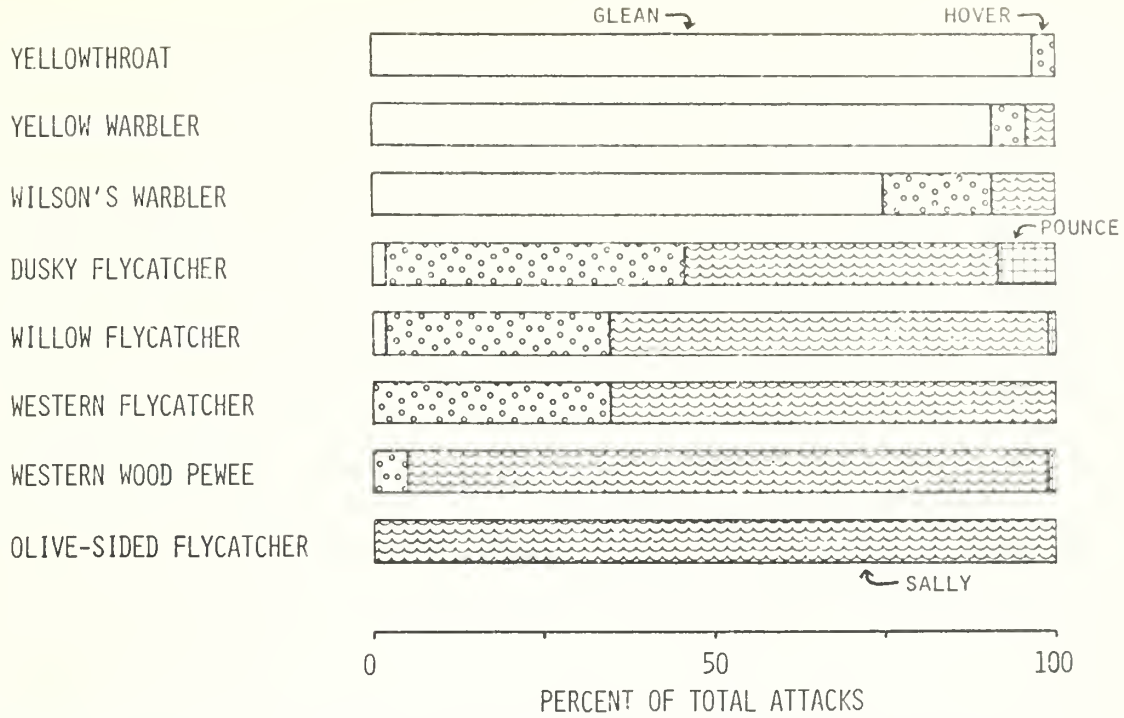



FIGURE 1. Foraging repertoires in Warblers and Flycatchers. Illustrated are the percentages of each attack mode utilized in the total number of attacks made by each species.

TABLE 1. Velocity, search intensity, and foraging intensity in Warblers and Flycatchers.

| | A | B | C |
|---|---|---|---|
| Species | Velocity (perches visited/minute) | Search Intensity (perches visited/attack) | Foraging Intensity (attacks/minute) |
| Wilson's Warbler | 33.3 | 9.7 | 3.1 |
| Yellow Warbler | 25.0 | 5.0 | 4.6 |
| Yellowthroat | 10.0 | 5.7 | 1.7 |
| Western Flycatcher | 3.8 | 3.1 | 1.2 |
| Willow Flycatcher | 2.9 | 3.4 | 0.8 |
| Dusky Flycatcher | 2.6 | 2.7 | 1.0 |
| Western Wood Pewee | 2.2 | 1.2 | 1.8 |
| Olive-sided Flycatcher | 0.6 | 2.1 | 0.2 |

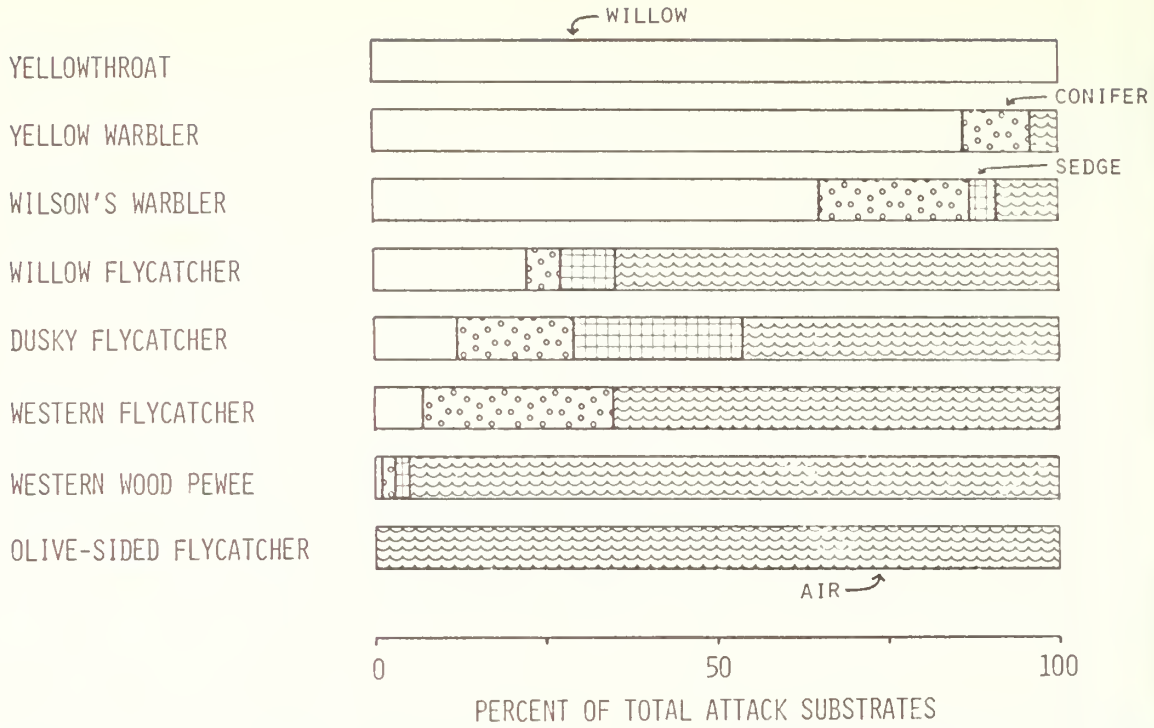



FIGURE 2. Attack substrates in Warblers and Flycatchers. Attack substrate is defined as the substrat of a prey item which is the object of an attack. Illustrated are the percentages of each attack substrate utilized in the total number of attacks made by each species.

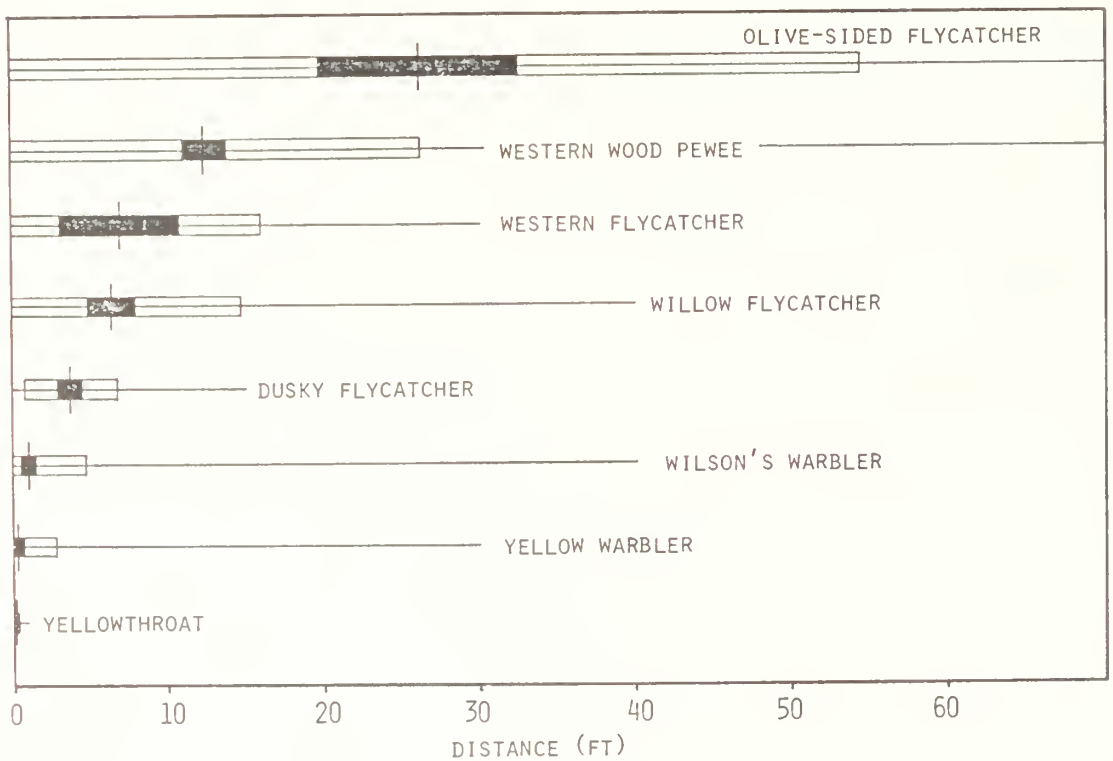



FIGURE 3. Attack radius in Warblers and Flycatchers. Attack radius is defined as the distance traveled from perch to prey. Horizontal lines indicate the range of observed values, vertical lines designate the mean. Open rectabgles enclose one standard deviation above and below the mean, solid rectangles enclose the 95% confidence interval.

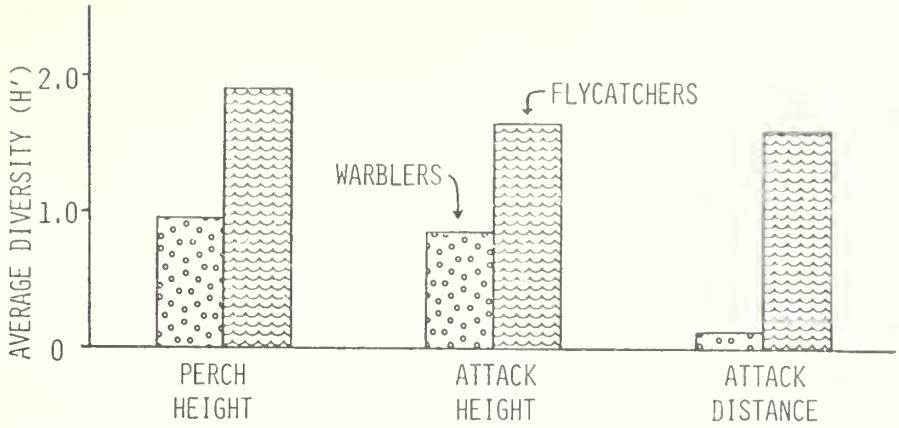



FIGURE 4. Average diversity of three dimensions of foraging space in Warblers and Flycatchers. Diversity is measured as an average of the species in each guild, using the Shannon Index, H', with 5 ft interval classes.

TABLE 2. Difference ratios. Given in ascending size sequence, ratios of larger to smaller Western Flycatcher not included.

| Guild | Weight | Wing length |
|---|---|---|
| Gleaners | 1.09 | 1.04 |
| | 1.09 | 1.09 |
| Flycatchers | 1.06 | 1.03 |
| | 1.26 | 1.25 |
| | 2.20 | 1.24 |

Elsewhere (Eckhardt, 1977), I have suggested that there are a small number of adaptations, "core adaptations," that are basic to and identify each adaptive syndrome. Evolutionarily, these are the most important of the species' characteristics -- they are the major adaptive traits. They came first in the evolution of the species, and the complete set of characteristics that make up the species' adaptive syndrome is the result of an accumulation of optimal adaptive responses to these few traits. It is for this reason that we can speak of an adaptive syndrome as a coordinated set of characteristics. Through the study of the interrelations of different adaptive syndromes and their core adaptations, we can gain an understanding of the complex processes involved in predation.

The identification of an adaptive syndrome or a guild is simplified by the use of core adaptations. Because every adaptive syndrome possesses a unique set of core adaptations, we can predict which syndrome a species possesses simply by observing which core adaptations it displays. It

TABLE 3. An outline of the adaptive syndromes of active and passive searchers.

| Active Searchers | Passive Searchers |
|---|---|
| Comparable in some ways to what have been called "searchers" or "widely-foraging" predators. | Comparable in some ways to what have been called "pursuers" or "sit-and-wait" predators. |
| CORE ADAPTATIONS | |
| 1. Foraging repertoire associated with "passive prey," which are hard to find, easy to catch. | 1. Foraging repertoire associated with "active prey", which are easy to find, hard to catch. |
| 2. High velocity (perches/minute). | 2. Low velocity. |
| 3. High search intensity (perches/attack). | 3. Low search intensity |
| OTHER ADAPTATIONS | |
| 4. High foraging intensity (attacks/minute). | 4. Low foraging intensity. |
| 5. Attack radius small. | 5. Attack radius large. |
| 6. Size of foraging space (structural diversity of foraging microhabitat) small. | 6. Size of foraging space (structural diversity of foraging microhabitat) large. |
| 7. Species usually differ in critical morphological dimensions (wing, weight) by ratios less than 1.14. | 7. Species usually differ in critical morphological dimensions (wing, weight) by ratios greater than 1.14. |

## CONCLUSION

Adaptive syndromes are not simply theoretical constructs. They are a particularly useful way of studying predators and the process of predation. They provide an alternative approach to the study of predation, an alternative to the optimal foraging theories that have become widespread in recent studies of predation. They have the advantage that they are easy to use and test in the field; their applicability can thus be readily confirmed or denied. Adaptive syndromes identify the critical adaptations (i.e., the core adaptations) of different types of predators -- the most basic and least plastic aspects of their behavioral ecology. Only through an understanding of these critical adaptations and adaptive syndromes will we elucidate the relationships between different predators, and predators and their prey. And, as further study identifies the major adaptive syndromes of predatory species, be they mammals, birds, insects, or whatever, ecologists will gain a better understanding of what it is we actually see functioning in parks and other natural areas.

Many will attest to the fact that predators and predation create some of the most serious problems faced in parks today. Predators are often the first to disappear in an area, and are among the most difficult animals to manage well. The use of the concepts of the guild and the adaptive syndrome in future studies can help us to gain a should be possible, then, to predict the whole set of a species' characteristics simply from the knowledge of a few. I can illustrate this with the summary of the adaptive syndromes of active searchers (warblers) and passive searchers (flycatchers) found in Table 3. Species exhibiting one of these adaptive syndromes can be identified readily by the types of attack modes they employ, their velocity, and their search intensity (lines 1 through 3). These are the core adaptations--they provide the clearest picture of the differences between the two groups, and together they are the most reliable defining qualities for the two syndromes. Also, they appear to have the greatest potential for distinguishing these from other adaptive syndromes. The remainder of the Table (lines 4 through 7) lists additional characteristics which reflect other areas of contrast between active and passive searchers. Presumably these came later in the evolution of the species and its behavior, are secondary to the core adaptations, and can be predicted from a knowledge of the core adaptations.

better understanding of predation as a universal process, and ultimately help to ameliorate these management problems. Finally, on the most general level, it is the relationship of the different adaptive syndromes of *all* guilds that best reveal the structure of a community. And only with an understanding of community structure can we succeed in the difficult tasks of management, preservation, and restoration of whole ecosystems.

## SUMMARY

The use of the concepts of guilds and adaptive syndromes in the study of predation is explored. It is suggested that every guild has a unique and characteristic adaptive syndrome and that guilds can be distinguished one from another by the general range of the characteristics displayed by their syndromes. The foraging syndromes of warblers and flycatchers inhabiting a willow floodplain in Rocky Mountain National Park are used as an illustration. The usefulness of the idea of adaptive syndromes to the understanding of predators and predation is discussed.

## LITERATURE CITED

ECKHARDT, R. C. 1977. Foraging strategies in two guilds of insectivorous birds in the Colorado Rocky Mountains. (in prep.)

ROOT, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards *(Brassica oleracea)*. Ecol. Monogr. 43:95-124.

ROOT, R. B. and S. J. CHAPLIN. 1976. The life-styles of tropical milkweed bugs, *Oncopeltus* (Hemiptera: lygaeidae), utilizing the same hours. Ecology 57:132-140.

SCHOENER, T. W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. Ecolution 19:189-312.

# THE INFLUENCE OF FOX PREDATION ON RING-BILLED AND HERRING GULL NESTING SUCCESS

William E. Southern, Francesca J. Cuthbert and Stephen R. Patton[1]

Sleeping Bear Dunes National Lakeshore in Michigan's Lower Peninsula (Leelanau County) includes two of Lake Michigan's largest islands, North and South Manitou. The smaller of the two, South Manitou, encompasses about 5,260 acres of woodland, meadow, dune and beach habitats. A sandy peninsula extending eastward from the northern end of the island contributes to the formation of one of the finest natural harbors on the Great Lakes. The peninsula historically has been a nesting place for Herring Gulls (*Larus argentatus*) and possibly Ring-billed Gulls (*L. delawarensis*).

The earliest reports of gull colonies on the peninsula were provided by retired U.S. Coast Guard personnel who operated the island's lighthouse during 1926 and 1927 (F.J. Looze, pers. comm.). Although these men could not identify the gulls involved to species, their descriptions of nests and nest distribution led me to suspect that both species were nesting at this site. If this is correct, it places South Manitou among those few islands in the Great Lakes that were used by Ring-billed Gulls for nesting purposes during the first quarter of the Twentieth Century. Prior to about 1923, Ring-billed Gulls were absent from most of the Great Lakes as a breeding species, apparently as a result of heavy depredation by humans. Their return to abundance was slow and came in response to (a) legislated protection that prohibited egging and commercial sale of feathers, (b) changes in availability of nesting habitat caused by periodic fluctuations in water levels, and (c) fish introductions and other human endeavors that influenced food supply.

Very little information about the number of gulls using the Manitou colony-sites was collected before the mid-1960's. From 1966 through 1969, Scharf (1970, Inland Bird Banding News 42:6-9) provided estimates of the breeding populations; Scharf and Shugart (pers. comm.) did similarly for 1970 through 1974; and during 1975 and 1976 we made direct counts of nests present in both colonies. In 1966, Scharf reported that 6,000 pairs of Ring-billed Gulls nested on the island but figures were not provided for Herring Gulls. Thereafter colony size was reported to decrease consistently and by 1969 only 2,500 pairs apparently remained (Scharf 1970). There was a corresponding decline in the amount of nesting space used by Ring-billed Gulls, from 18,288 square meters in 1966 to only 6,401 square meters in 1973 (Shugart, pers. comm.).

High juvenile mortality was noted in 1969, and Scharf (1970) counted 656 dead chicks in about 5,486 square meters of the colony. He concluded that this represented a 33 to 50 percent rate of juvenile mortality. Scharf attributed the high death rate to parental neglect associated with all-terrain vehicles (ATV's) having entered the colony on several occasions. He also suggested that pesticides or botulism might have been involved in the deaths.

Some recovery was noted in the early 1970's, and the number of breeding pairs increased somewhat. This probably was associated with gulls being forced to move from previously used colony-sites by rising Great Lakes water levels. Many islands were either submerged or greatly reduced in size as the cyclic level of lakes Michigan and Huron rose to an all-time high during the early 1970's. During these years, juvenile mortality remained high, the death rate for breeding adults was unusually high, and the number of breeding pairs using the sites fluctuated significantly from year to year.

## OBJECTIVES AND PROCEDURES

This period in the 1970's when Ring-billed and Herring Gull breeding populations were unstable and productivity was low happened to coincide with the approximate time that the National Park Service began land acquisition for the National Lakeshore. Being cognizant of the apparent problem in the gull colonies, Max Holden, then a Regional Biologist for the National Park Service, encouraged support of an investigation to determine what decimating factors were at work in the gull colonies.

When we were planning our 2-year investigation in 1974, consensus of opinion within the Park Service seemed to be that human visitors to the island were entering the colonies indiscriminately and creating disturbances that increased mortality rates. The possibility also was raised that procedures used by recent scientific investigators may have contributed to problems in the colony and the Park Service was prepared to place the colonies off limit to all human activities. Our objectives, therefore, were to monitor the (a) possible effect of mammalian predators; (b) nature and extent of human disturbances; (c) effect of climatic factors; (d) rate of and causes for nest desertion, egg loss, and adult and juvenile mortality; and, (e) habitat characteristics of colony areas having different nest densities. Information stemming from investigation of these topics in 1975 was to serve as the basis for a preliminary management plan that would be implemented and tested during the subsequent nesting season (1976).

During the 1975 and 1976 breeding seasons (10 May - 15 July) our research team lived on the island and censused the breeding population of both species, determined clutch sizes and hatching rates, monitored rates of adult and chick mortality, and identified the primary causes of diurnal and nocturnal disturbances that increased mortality. The breeding success of Ring-billed Gulls at the Calcite Colony (Rogers City, Presque Isle County, Michigan) on Lake Huron also was monitored by a resident staff and served as a control.

Colonies were censused on about the same date (20-22 May) each year. This was accomplished by the direct-count method wherein each nest and its respective contents were recorded. This method has an accuracy of about 98 percent when performed by experienced personnel and probably represents the best available procedure although it is very time-consuming. Although nest counts were made after incubation had peaked, ar increase of about 7 percent in nest

[1]Department of Biology, Northern Illinois University, DeKalb.

number may have occurred as the season progressed. The additional nests were produced by late arrivals, renesters, or birds asynchronous for various reasons (e.g. nesting as subadults).

## RESULTS

### *Data on Reproductive Potential and Realized Breeding Success*

*Ring-billed Gulls.* -- On 20 May 1975, there were 5,175 Ring-billed Gull nests at South Manitou that contained eggs. The mean clutch size was 2.74 which compared favorably with the mean of 2.82 at the control colony. The number of eggs per nest ranged from 1 to 6 at Manitou and the control. The mean area available per pair within the Manitou colony boundaries was 2.74 square meters.

Existing data for the Calcite Colony indicate that a minimum hatching rate of about 75% can be expected and at least 80% of the chicks hatched should survive to the time of departure from the colony. Application of these multipliers to the number of eggs produced in the Manitou colony suggests that a minimum of about 10,646 young should have hatched during late May and early June and about 8,516 should have been alive 6 to 8 weeks later. This was not the case. The peak of hatching was about one week later than at the control colony and only 60 percent of the eggs hatched. Juvenile mortality was unusually high, and by 4 July only 645 young Ring-bills were alive at South Manitou which represented a reproductive success rate of only 7.6 percent. In contrast, about 11,305 Ring-bill chicks were alive at the Calcite Colony on this same date, which represented a somewhat higher than normal success rate.

On 20 May 1976 there were only 3,935 Ring-billed Gull nests at South Manitou that contained eggs. This was 1,240 fewer nests (24%) than were present in 1975. The Calcite Colony, however, had a 14.1 percent (748 nests) increase in the number of nests with eggs or young by the census date (total 6,065). In light of this, the decrease in the number of breeding pairs at South Manitou was interpreted as resulting from internal problems rather than circumstances uniformly distributed over northern lakes Michigan and Huron. Average Ring-billed Gull clutch size was reduced in Manitou in 1976 to 1.58 while at the Calcite Colony it increased to 2.97. There was a corresponding decrease in nest density at South Manitou and 2.9 square meters were available per pair.

Apparently as a result of unusually warm summer-like weather in March, hatching at many of the Lake Michigan and Huron gull colonies was about two weeks ahead of schedule. At the Calcite Colony the peak of hatching occurred earlier than at any time during Dr. Southern's 18 years of observations. At South Manitou, however, hatching was retarded rather than advanced seasonally. As a result of unusually poor hatchability and the loss of young, only 9 young Ring-billed Gulls were alive by 1 July. As in 1975, the Calcite Colony had a very good year and about 77 percent of the young hatched were alive on 1 July.

*Herring Gulls.* -- The pattern for Herring Gulls was similar to that of Ring-billed Gulls during the two years at South Manitou. In 1975, there were 474 nests with a mean clutch size of 2.45. Clutch size at the control site was slightly higher with a mean of 2.81 for 823 nests. This species normally has larger territories than Ring-bills and in 1975, there was one nest per 100.4 square meters of colony area at South Manitou. Differences in nesting density had no influence on reproductive success and the fate of Herring Gulls at this colony was similar to that of Ring-bills. On 3 July, only 3 chicks were alive, whereas the predicted number of young was about 696.

In 1976, only 309 nests were present at South Manitou (a 34.8% reduction) and the mean clutch size decreased to 1.4. Reduction in the number of breeding pairs resulted in decreased nest density with a mean area of 154 square meters being available per pair. Juvenile mortality was high again and by 2 July only 2 young were alive. Again, similar circumstances were not duplicated at the Calcite Colony. About 50 additional pairs of Herring Gulls were present in 1976 and the mean clutch size increased to 3.03. Juvenile survival at the Calcite Colony during both years was comparable to that given for Ring-billed Gulls.

These findings substantiate that the Manitou Colonies are in serious trouble and could be faced with extinction. A sufficient number of young are not being added to the local population to replace adults lost through annual attrition (about 12%). Also, lack of nesting success and/or the repeated nocturnal disturbances within the colony appear to be causing adults to abandon the site, either during a particular nesting season or by the subsequent one. The loss of experienced adults from the population that previously produced progeny at South Manitou may threaten colony stability and reduce the probability that any gulls will return to the site.

It is likely that experienced individuals that return to the same breeding colony year after year, i.e., express colony-site tenacity, serve to attract other gulls by their presence. Such a nuclei of established breeders probably signal through their efficient reproductive activities that optimum nesting conditions exist. These stimuli may be particularly attractive to birds seeking a place to nest for the first time (e.g. usually when three years old). Without these older birds, traditional attachment to a site is lost, and subsequent arrivals may not initiate nesting, particularly if disturbances prevail.

If gulls abandon the South Manitou site, it is possible that it will not be used again by mating gulls. During their absence, plant succession is likely to make the terrain unattractive to future immigrants. Normally the concentration of gull wastes within a nesting area usually limits the variety of plant species and the growth patterns of those that do occur. Thus the continuous use of a site by large numbers of gulls increases the length of time that optimum vegetative conditions will exist by retarding succession. If the birds leave, the concentration of organic wastes eventually decreases and plant invasion occurs, which ultimately results in woody species making the area unattractive to gulls.

### *Role of Foxes in Reducing Reproductive Success*

Several factors, to varying degrees, probably contributed to the strikingly high loss of eggs and chicks at the South Manitou Ring-billed and Herring Gull colonies. Any probable effects of weather, human disturbances and habitat characteristics were overshadowed completely by unrelenting Red Fox (*Vulpes vulpes*) predation. Foxes were responsible either directly or

indirectly, for most of the egg losses, embryo deaths, and juvenile and adult mortality. In turn, fox-caused diminution in nesting success detrimentally affected colony size the subsequent year.

Possibly as many as 7 foxes (4 were observed at one time) made frequent nocturnal, and occasionally crepuscular, visits to the colonies during most of the two breeding seasons. Foxes raiding the colonies did not exhibit what most people consider as typical predatory behavior. Instead of just killing the quantity of prey necessary for sustaining themselves and their progeny, foxes characteristically slew dozens or hundreds of individuals. Kruuk (1972, J. Zool. London 166: 233-244), called such exaggerated levels of prey capture "surplus killing". The phenomenon apparently operates in a variety of predatory species when they encounter circumstances that restrict a prey's tendency for escape. In such cases, a carnivore may kill many more individuals than it can possibly eat.

Surplus killing usually is not possible during most feeding attempts by predators. Normally mammalian predators require considerable time to seek out and capture their prey. This procedure usually involves one prey organism at a time, but if the predator encounters more than one, it sorts out a particular one for the capture attempt. If prey are sought from hiding or pursuit, the actual attack on one individual usually scatters the others, thereby making them unavailable without considerable additional effort. Under these circumstances of normal prey density, the amount of energy expended in pursuing and capturing prey is great enough that a predator cannot afford the luxury of leaving captured prey uneaten.

A gull colony, however, represents a unique situation for nocturnal mammalian predators. This novel environment offers a superabundance of potential prey to which foxes respond by spending prolonged periods seeking out and killing prey. At South Manitou, foxes reacted in this fashion although they were exploiting food resources other than gulls during May through early July. We found numerous fox scats near the colonies that contained insects, fruit and hair in addition to gull remains. Thus gulls did not constitute the sole diet of foxes although 15 to 20 gulls were totally or partially eaten almost nightly. Kruuk (1972) also found this to be the case in his study areas. It appears, therefore, that foxes are taking advantage of this situation to kill gulls, possibly in conjunction with training their young or because of benefits accrued to the individual predator as a result of such action.

We firmly believe that the primary selective advantage provided gulls and terns by nesting on small islands is that they generally avoid contact with mammalian predators. Ring-billed and Herring Gulls lack adequate defense tactics against nocturnal predators. Their reaction to an intruder is usually a panic flight wherein masses of birds take off, wheel about the colony and intermittently utter an apparently synchronous low-pitched, guttural call that is transcribed as *aurrrr*. This call is followed by a period of silence unusual to such colonies. After several minutes of this behavior, the birds land and participate in territorial displays necessary for achieving the preceding status quo. If predator attacks reoccur, the adults may spend many minutes or possibly hours as a group on the water.

Because gulls have a strong tendency to incubate or brood young during low nighttime temperatures, they appear hesitant at leaving the nest or remaining away for long. This makes them particularly vulnerable to predators that may await their return. Even if adult gulls leave territories and seek safety in the air or on water, their nest contents remain available to predators. Prior to when young are able to fly (6-8 weeks old), they can escape foxes only by finding security in vegetation or other obstacles too dense for foxes to penetrate. Small young lack the ability to travel great distances in search of such cover. Older chicks that may do so and succeed in avoiding foxes, later experience serious problems when attempting to reunite with their parents. Travel home requires traversing numerous defended territories and pairs of gulls attack them vigorously. As a result, added losses of young may occur through the mixing of broods associated with prolonged periods of disturbance with colonies.

Space considerations will not permit discussion of all aspects of the fox-gull situation at South Manitou. Hopefully data provided in the following sections will document that a problem truly exists and that control measures are essential if the colonies are to persist.

### *Adult Gull Losses to Foxes*

Foxes attacked the colonies at all stages of the breeding cycle. Usually they entered the colonies between 22:00 and 00:20 hours and left between 04:10 and 06:00. Adult gulls, eggs and young were taken during frequent, almost nightly, visits. In 1975, we made daily trips through the colonies and collected the bodies of gulls that died during the preceding night. This gruesome task was essential in determining the number of gulls lost daily and the cause of death. In 1976, only half of each colony was censused by this method and the dead birds were left in place in the other half marked. We used this procedure to determine if removal of dead gulls influenced kill rates in the respective areas. Since no significant difference was found between predation rates for the two areas, we concluded that removal of carcasses the preceding year had not biased our results pertaining to kill rates. This observation provided support for our speculation that foxes returned on subsequent nights to kill more gulls, not to eat those previously killed.

*Adult mortality.* -- During 1975 and 1976, 196 and 177 adult gulls died within the Manitou colonies. This was about 10 times higher than that recorded at the Calcite Colony. In many instances the cause of death was impossible to determine from superficial examination of carcasses; therefore, we autopsied all of the dead adults and about three-fourths of the young in 1975. Skinning often revealed bite marks on the flesh of the back, breast or neck that were invisible from outside a whole carcass. This procedure documented that about 80 percent of the dead adults were direct fox kills. Foxes killed more adult Ring-billed Gulls than Herring Gulls during 1975 and 1976, but when examined on the basis of relative abundance the data show that a slightly larger proportion of the Herring Gull population actually succumbed to foxes (1.5% for Ring-bills; 2.2% for Herring Gulls).

In 1975, we collected 172 dead adult Ring-billed Gulls and 24 Herring Gulls from within the colonies; 128 (74.4%) of the Ring-bills and 13 (54.2%) of the Herring Gulls were positive fox kills. Adult mortality was similar in 1976 when

144 Ring-bills and 33 Herring Gulls died during the study period. The proportion of known fox kills was higher than in 1975, and at least 136 (94.4%) of the Ring-bills and 21 (63.6%) of the Herring Gulls were positive fox kills. Most gull carcasses were left uneaten, but some were consumed partially and others were cached in or near the colony. Caching assumed several forms, but usually prey items were completely or partially buried in sand. Cached adult gulls were usually on their backs and had the head and neck buried. A few were covered almost entirely and possibly we failed to find some that were buried completely. Young and eggs also were cached, but the extent of coverage with sand was proportionately greater. Thus the frequency of completely cached eggs was high as compared with that for adult gulls. Dead gulls and eggs with bite marks were found as far as 1.5 miles from the colonies indicating that foxes probably transported some food material away to their dens.

Some carcasses had been dragged about as if part of playful activity by young foxes that accompanied their parents. Tracks of fox pups were observed several times in the colonies or nearby.

*Egg and embryonic losses.* -- The actual number of eggs lost to foxes was difficult to assess, but there was sufficient evidence to show that foxes removed eggs from nests, ate eggs and cached eggs within or around the colonies.

On census dates in 1975 and 1976, 145 and 279 Ring-billed Gull eggs were found outside nests or broken. In addition, there were 304 and 127 empty nests on census dates for the respective seasons. The high number of eggs out of nests at Manitou was directly related to fox activity. When incubating gulls were startled into flight during fox attacks, they sometimes knocked eggs out of nests because their feet typically are positioned beneath eggs during incubation. Thus prolonged or frequent nocturnal fox attacks contributed to egg loss in ways other than direct consumption.

Reduced hatchability resulted from repeated prolonged nocturnal activity of foxes in colonies that caused adult gulls to leave nests unattended. In 1975 hatchability was reduced to about 60 percent, but in 1976 the effects were even more apparent. The onset of hatching was about two weeks later than at the control colony and the proportion of eggs hatching was reduced to about 15 percent of those laid. Without question fox-caused disturbance was the primary factor responsible for gulls being off nests at night. For efficient incubation gulls must maintain egg temperatures of about 37 to 38°C which requires the eggs being covered by an adult about 99 percent of the time. If left exposed, embryological development probably ceases when egg temperatures reach 25 to 27°C. Between these two extremes, developmental anomalies may occur, such as disproportionate heart growth.

On some nights foxes made separate visits shortly after dark and then again before dawn. The duration of stay within the colonies varied, but sometimes lasted as long as 5 hours. On other occasions, foxes remained in the colony for an extended period of several hours that resulted in some gulls, or most of them, abandoning the area under attack for up to 4.5 hours. These panic responses, particularly among Ring-bills, exposed eggs to cool nighttime temperatures in May and early June of about 4 to 5°C that resulted in embryo deaths because of exposure.

*Juvenile mortality.* -- Chick losses during nights of fox activity were phenomenally high. From 30 May (near the onset of hatching) through 19 June 1975, 7,027 chicks died in the colonies ($\bar{x}$ = 335/night). These figures do not include any chicks removed from the colony by foxes and consumed or cached elsewhere. Of the 5,136 chicks we autopsied, 2,357 (45.9%) showed fox bites. Over 95 percent of the remainder probably died from exposure as they were recently hatched individuals incapable of regulating their own body temperature during exposure to low ambient temperatures (3 to 10°C). Prior to about four days of age, gull chicks are particularly susceptible to chilling especially when wetted by heavy dew or rain. On 5 nights, 4 June and 7 through 10 June, when temperatures averaged 5°C, at least 2,700 chicks died. About 75 percent of these probably died from exposure resulting from fox activity. Most of the chicks that survived long enough to be able to regulate their own body temperature were eventually killed directly by foxes.

Dead young were found throughout the colonies but usually a few areas showed signs of particularly heavy fox activity. In such instances, groups of 5 to 20 dead chicks were located within a few square meters. Usually these areas were sites of high nest density that foxes had missed on previous nights. Autopsies showed that most chicks were bitten on the back as if grabbed from behind while running or while hiding with their head beneath some object. Some had large wounds on the abdomen, others were headless, some were badly mangled, and a few had parts missing or chewed (e.g., the bill or feet).

This description briefly exemplifies the types of information we possess that document that fox predation is having a serious detrimental effect on these particular gull colonies. It is unlikely that gulls will continue to endure the combined effects of heavy predation and low reproductive success. It is difficult to predict precisely what their reaction will be, but experience at other colonies suggests that eventual desertion of the site is likely. Ring-bills probably will express this option sooner than Herring Gulls as they appear less tolerant of disturbances. If gulls are going to continue breeding on South Manitou, concerted effort must be devoted to reducing the impact of foxes on the populations before the next breeding season.

### *Attempts to Date to Modify Fox Predation*

After realizing the nature of the problem in 1975, we notified National Park Service personnel at the National Lakeshore Office and the Regional Office. We indicated the importance of control measures being initiated if the colony was to survive. A decision on managing foxes could not be reached at that time, but we were given permission to use scare tactics to keep predators out of the colonies. This seems like an easy task at the onset; however, any method employed must frighten foxes but not gulls, which significantly limits the horizons. Several possible methods were made unfeasible by lack of funds or because of esthetic reasons. We decided to install a series of broadcast-band radios around the perimeter of the Ring-billed Gull colony. Funding also limited the scope of this endeavor, but 5 radios were installed and loud music played nightly between 19 June and 4 July 1975. This procedure was instigated too late to reduce significantly the seasonal effect of foxes but it did cause a noticeable decline in fox kills. Foxes continued to enter the colony by skirting

the area of noise produced by the radios, but chicks nearest the radios received some protection. This procedure undoubtedly contributed significantly to the survival of 645 young in 1975.

Procedures of this type represent unrealistic solutions to the problem, because they require nightly human surveillance and they must be repeated annually. Additionally, the assumption is made that foxes will not habituate to radio noise as they apparently have done in the case of gull noise. Such an assumption probably will not withstand the test of time.

In 1976, 8 chick shelters (1.25 x 1.25 m by 15 cm high) were constructed by Park Service personnel to our specifications and placed by our group in the Ring-billed Gull colony. Each shelter had a hardware cloth top, side barriers to prevent foxes from digging underneath and stakes to secure it in place. They were positioned in areas of high nest density so that chicks could hide beneath them and obtain protection during fox raids. The structures had no noticeable effect because very few chicks hatched in those portions of the colony or survived long enough to use the shelters. If fox disturbances had been less intense during the incubation-stage, it is possible that these structures would have provided protection for some chicks. This method, like the preceding one, does not represent a long-term, one-shot solution to the problem. Because structures such as these will be covered by blowing sand, or will have to be moved to coincide with nest distribution, annual maintenance is essential. If gulls are to be preserved on the Island, there must be a commitment to continued management of the colonies.

During the fall of 1975, the Park Service reached a decision to control foxes before onset of the 1976 breeding season. Implementation was delayed by Sleeping Bear Dunes National Lakeshore personnel until May 1976 after the gulls were present and significant predation had occurred. Trapping was attempted but it was essentially impossible to attract foxes to bait when so much prey was readily available. After about a week, the Park Service trapper left and essentially no additional effort was devoted to this objective. We continued to monitor the traps for an additional couple of weeks and eventually caught an adult female fox. Foxes continued to raid the colony during this period and the removal of one individual had no noticeable effect.

Trapping and/or hunting foxes remain the most effective means of reducing the fox population and decreasing their influence on gull productivity. Any such effort must be consistent, timed properly and carefully monitored so that the number of animals removed is known. This should be combined with a monitoring program of the Island's hare and rodent populations to determine what effect, if any, fox removal is having on them.

Such action on South Manitou is justifiable because it is one of the few Lake Michigan gull colonies that is under Federal protection. By being preserved it can serve as an epicenter to repopulate other potential sites as they emerge from the lake following periods of high water. Some islands now used by gulls are subject to development or other human uses not compatible with gull colonies. It is important, therefore, that those not so threatened be preserved so that we are able to predict to some degree the fate of these species as human demands on the environment continue to proliferate. Proper management and planning could permit these colonies to be used as valuable interpretive centers by the National Park Service whereby members of the voting public can become acquainted with the fascinating behavioral repertoires possessed by colonial birds.

## SUMMARY

A two-year study was conducted to determine the reasons for reportedly low reproductive success of gulls nesting at South Manitou Island in the Sleeping Bear Dunes National Lakeshore. Information accrued during the 1975 and 1976 breeding seasons was to serve as a baseline for preparation of a management plan for the Ring-billed and Herring Gull colonies.

Soon after initiation of the study it was apparent that most of our data would deal with the impact of Red Foxes on gull colonies. Predator influence was so intense that it overshadowed other variables that normally would be expected to have some effect on breeding success.

Frequent and prolonged nocturnal attacks by foxes reduced egg hatchability to 60 and 15 percent, respectively, during 1975 and 1976. Reproductive success of Ring-billed Gulls was less than 8 percent in 1975 and almost zero in 1976. Herring Gulls produced essentially no young either year. Adult mortality was about 10 times higher than at a control colony near Rogers City, Michigan. There was a corresponding decline in the number of pairs of gulls using the colony-sites in 1976, a 24 percent (1,240 nests) reduction for Ring-billed Gulls and 34.8 percent (165 nests) reduction in the case of Herring Gulls.

Predominant factors contributing to these losses were intra-colony disturbances and surplus killing by Red Foxes. Perhaps as many as 7 foxes made frequent nocturnal raids on the colonies during all stages of the nesting cycle. Both gull species apparently lack effective defense mechanisms against nocturnal predators as they usually achieve protection by nesting on isolated small islands. It is likely that uncontrolled fox predation will cause extinction of both colonies. Probably foxes have contributed to mortality in these colonies for several years, but the problem has become more severe recently because fox control by local human residents has been curtailed. As the Park Service acquired land, long-time residents moved away and alleged fox hunts and trapping activities ceased.

Various methods were tested as means of reducing fox-caused mortality. None of these appeared successful enough to warrant continued use. The only practical method appears to be control of foxes by hunting or trapping. This approach, like the other procedures, will have to be a reoccurring operation, not a one-time proposition. If gulls are to survive as nesting species on South Manitou, a firm commitment to this goal must be made by the National Park Service. Such a program will involve habitat management, predator control and ecological monitoring to determine what effect, if any, reduction in fox numbers will have on local rodent and hare populations.

Preservation of the Manitou Gull colonies is particularly desirable as they are among the few that occur on publicly owned land. Most colonies are on privately owned islands that are subject to activities not compatible with colonial birds. In addition, the gull colonies on South Manitou could become an important part

of any interpretive program planned for the Sleeping Bear Dunes National Lakeshore. If the voting public is to gain an appreciation of our wildlife resources, they must be given an opportunity for exposure to the real thing.

If ecological management is not pursued on South Manitou, several of the Island's unique features, including the gull colonies, will be lost.

# ASSOCIATION OF PHYTOPLANKTON PHOTOSYNTHETIC RATES WITH VERTICAL TEMPERATURE AND LIGHT TRANSMISSION GRADIENTS IN CRATER LAKE, OREGON

Douglas W. Larson[1]

## INTRODUCTION

Crater Lake, Oregon, the deepest lake in the United States, features unusual transparency and thermal gradients; it may show the greatest transmittance of light of all natural waters (Smith and Tyler 1967). Hasler (1938) reported Secchi disk transparencies of 36, 39, and 40 m in August 1937. Temperatures during summer seldom exceed 5C at depths below 40 m and 4C below 100 m (Kemmerer et al. 1924; Utterback et al. 1942). Kibby et al. (1968) recorded temperatures of 5 and 4C at 30 and 70 m during maximum heat content in 1966 (on 25 August).

The phytoplankton in Crater Lake has received little attention apart from cell counts and identifications. Sovereign (1958) identified diatoms from samples collected in the littoral zone and in pools on Wizard Island. The only previous information available concerning production rates by phytoplankton is one profile from 26 July 1967 (Hoffman and Donaldson 1968). This study examined relationships between rates of phytoplankton primary production and the lake's unusual temperature and light transmittance characteristics.

## CRATER LAKE ENVIRONMENT

Crater Lake is located in the southwestern quarter of Oregon, about 105 km north of the Oregon-California border, and 195 km inland from the Pacific Ocean. The lake occupies the collapse caldera of volcanic Mt. Mazama. Radiocarbon dating studies by Fryxell (1965) place its approximate age at 6,600 years. Probably water began to collect in the basin soon after the collapse, but the major accumulation has been within the last 700-1,000 years (Nelson 1967). The recurrence of volcanic activity produced an emergent secondary cone (Wizard Island) and at least two submerged domes on the basin floor.

Annual mean air temperature is 3.9C, the average for October to May about 0C (Phillips and Van Denburgh 1968). Annual precipitation averages 171.2 cm, most occurring as snow (Phillips and Van Denburgh 1968). Heavy snowfalls are common in June.

The summer heat income is comparatively high for a temperate lake (30,010 g cal/cm$^2$ in 1966: Kibby et al. 1968) considering that Lake Michigan (volume 360 times that of Crater Lake) and Lake Baikal (volume nearly 1,500 times that of Crater Lake) have summer heat incomes of 40,800 g cal/cm$^2$ and 42,300 g cal/cm$^2$ (Reid 1961). Because of this and because wind action is exceptionally strong during winter, the lake seldom freezes over. Ice cover was reported for 1898 and 1924 (Waesche 1934), and in 1949, an ice layer varying in thickness from 5-30 cm covered the lake for 3 months (Walker 1949).

Byrne (1965) computed morphometric data for Crater Lake (Table 1).

## METHODS

Limnological sampling was conducted on 14 June, 23 July and 27 August 1968, and on 16 July and 5 and 31 August 1969. Sampling proceeded from a single index station at maximum depth (see Byrne 1962, 1965) usually under clear skies.

Temperature was determined with an electrical resistance thermistor (Whitney portable model TC-5A, meter scale calibrated in 0.1 units) for every meter to a depth of 20 m and every 10 m below that.

Transparency was measured with a submarine photometer (Kahl model 268-WA310, selenium barrier-layer photocell, spectral range in sunlight of 400-640 mμ) and two Secchi disks 20 and 100 cm in diameter.

Water samples were collected with a 2.5-liter plastic water bottle (Van Dorn) at the surface and from several evenly spaced sampling depths extending occasionally to 500 m and routine chemical analyses made in a mobile laboratory within 12 hr after collection. The pH was determined with a Corning pH meter (model 7). Total alkalinity was determined colorimetrically, using Bromcresol Green-Methyl Red indicator solution.

Water samples were taken also at depths of 0, 20, 40, 70, 110 and 200 m for chlorophyll a analysis on 5 August 1969. Samples were treated immediately with saturated $MgCO_3$. Within 6-8 hr, about 1 liter of each sample was filtered (AA Millipore filters, 0.8-μ pore diameter). Filters were stored in a desiccator and placed in a freezer compartment held at -20C. Extraction and determination of chlorophyll a were done according to Strickland and Parsons (1965).

Phytoplankton primary productivity was measured in situ with $^{14}C$. Water samples were collected with the Van Dorn bottle at the surface and from various depths. A 125-ml portion of water from each sampling depth was inoculated with 1 ml of a stock solution of $^{14}C$-$Na_2CO_3$ (5.0 μCi/ml) and returned to the depth from which it was drawn. Dark bottles accompanied light bottles at every other depth. Following a 4-hr incubation period (1000-1400 hours), the samples were retrieved and Millipore filtered (AA-type filters). The filters were stored in a desiccator for 1 or 2 days. Each filter was then immersed in 20 ml of a toluene +PPO+POPOP scintillator solution and counted by liquid scintillation (Packard model 2002 tri-carb spectrometer). Dark-bottle counts were merely subtracted from the light-bottle results. Total available stable inorganic carbon was calculated by multiplying total alkalinity (in mg/liter $CaCO_3$) by a conversion factor derived from in situ temperature and pH data (Saunders et al. 1962). Incident radiation was measured continuously with a Belfort recording pyrheliometer during the incubation periods.

## RESULTS AND DISCUSSION

Thermal profiles (Figure 1) were found to resemble those reported by earlier investigators. Temperatures below 200 m (not shown) were lower than 3.9C because of adiabatic compression.

[1]Hydrology, Army Corps of Engineers, Portland, Oregon 97208.

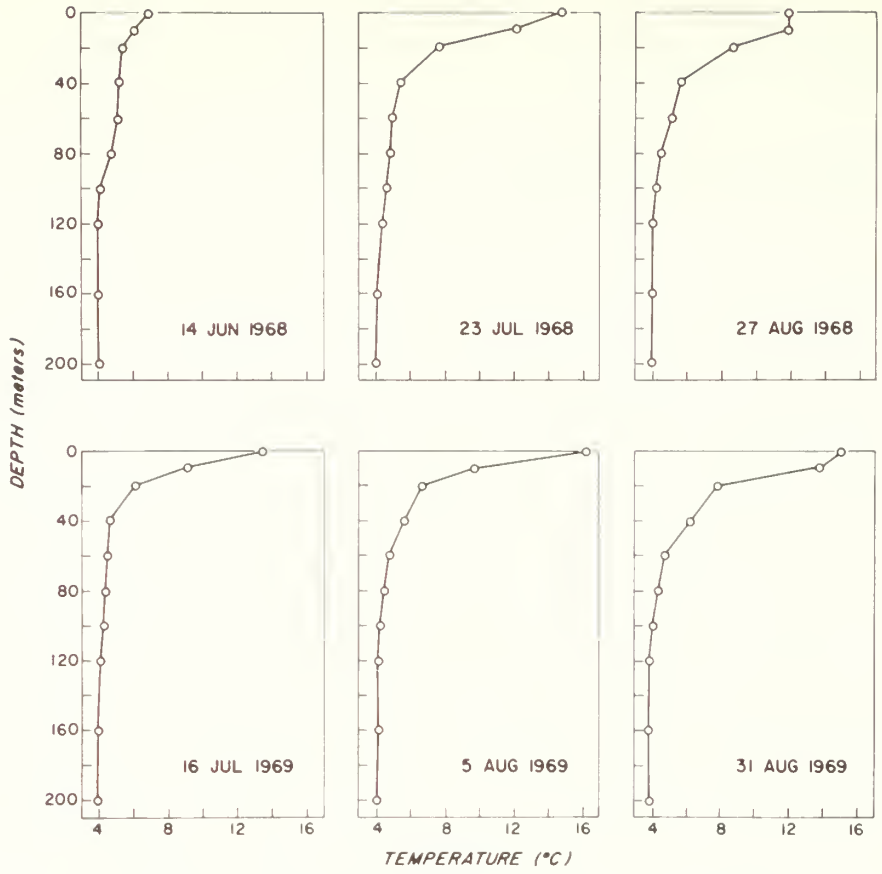



FIGURE 1. Thermal profiles for Crater Lake, Oregon.

TABLE 1. Morphometry of Crater Lake, Oregon (from Byrne 1965).

| | |
|---|---|
| Elevation, surface (m) | 1,882 |
| Area ($km^2$) | 48.0 |
| Volume ($km^2$) | 16.0 |
| Depth, max (m) | 589 |
| Depth, mean (m) | 325 |
| Shoreline length (km) | 31.0 |
| Shoreline development | 1.27 |

Secchi depths (Table 2) and light transmission data (Table 3) are indicative of exceptionally high transparency. The depth of penetration of 1% surface radiation (measured with the photocell) was 95-100 m. This depth corresponds roughly with the compensation depth or the lower limit of the photic zone (Strickland 1957) and can be estimated also by multiplying the average Secchi depth (32.5 m) by 3.

Phytoplankton net productivity in Crater Lake was relatively low (Figures 2 and 3, Table 4). Productivity estimates for 23 July 1968 and 16 July 1969 were comparable to the 1967 results (Figure 3). The $^{14}C$ method used in 1967 was identical to that described here except that HA Millipore filters (0.45-μ pore diameter) were used.

In profile, the depth of maximum productivity (Pmax)-coinciding theoretically with the depth of saturation light intensity (Isat)-was generally between 70 and 100 m (Figures 2 and 3). The highest concentration of chlorophyll *a* appeared at 110 m (Table 5), with an average concentration of 0.175 $mg/m^3$ for the 200-m water column. Kemmerer et al. (1924) and Utterback et al. (1942) found that over 90% of the phytoplankton in Crater Lake was contained between depths of 70 and 150 m, with the greatest density of cells occurring at about 75 m. This is probably common in highly transparent alpine lakes where blue and,

TABLE 2. Incident radiation, IR (in g cal $cm^{-2}hr^{-1}$), during bottle incubations (1000-1400 hours) and Secchi disk transparency depths (in meters) for Crater Lake.

| | Total IR | Secchi disk[a] (20-cm diam) |
|---|---|---|
| 1968 | | |
| 14 June | 69.8 | 31 |
| 23 July | 67.4 | 36 |
| 27 August | 53.6 | 18 |
| 1969 | | |
| 16 July | 68.2 | 39 |
| 5 August | 66.6 | 39 |
| 31 August | 65.4 | 32 |

[a]A 100-cm disk gave a reading of 44 m on 16 July 1969.

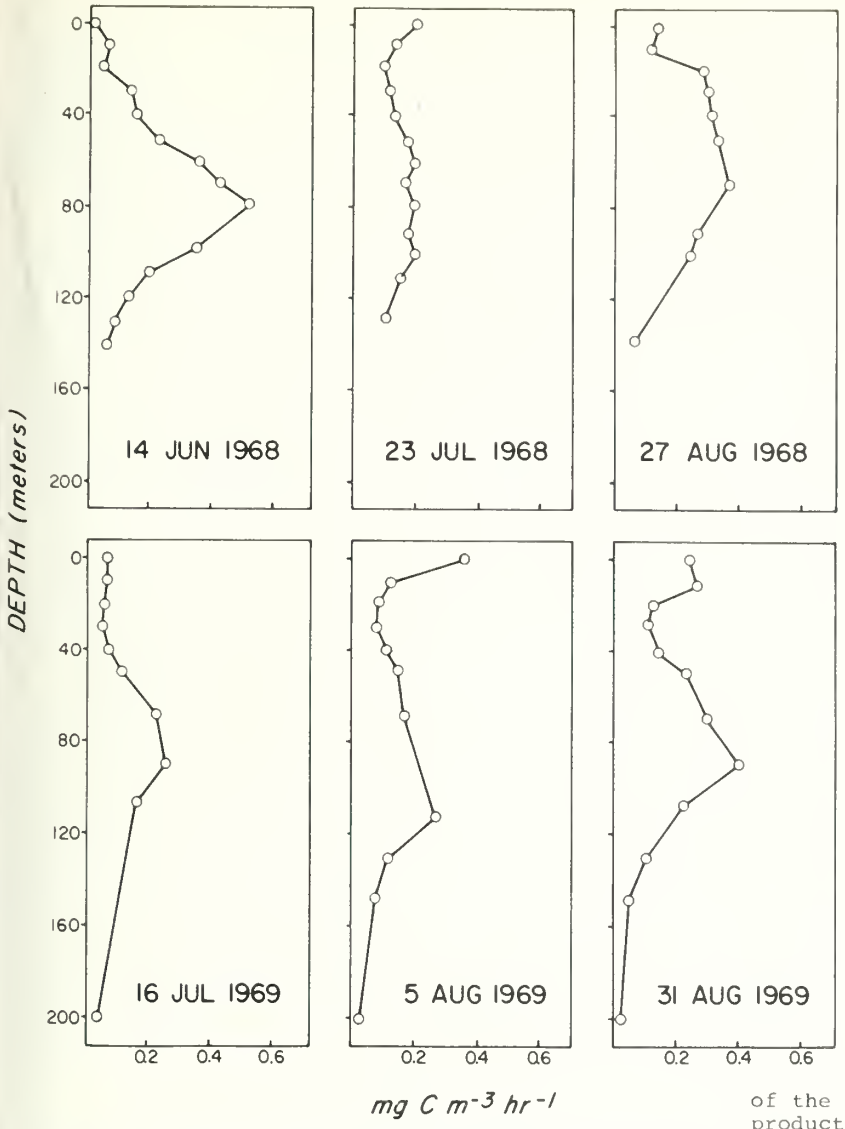



FIGURE 2. Vertical profiles of phytoplankton production rates for Crater Lake, Oregon, 1968-69.

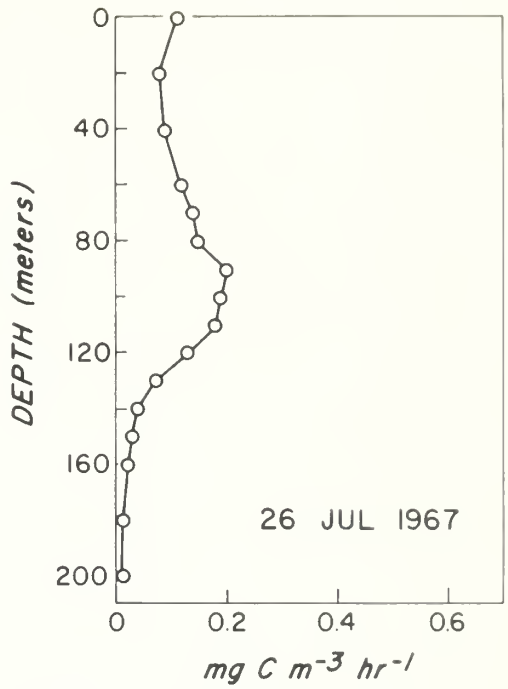



FIGURE 3. Phytoplankton productivity profile raken of 26 July 1967 at Crater Lake, Oregon (Hoffman and Donaldson 1968).

particularly, ultraviolet wavelengths penetrate to great depths, causing inversion of the usual phytoplankton productivity and biomass profiles (Rodhe et al. 1966).

The atypical profile for 23 July 1968 probably is due to sampling error involving bottles suspended at 70, 80, and 90 m. Normally, during mid-July, a prominent maximum could be expected around 90 m.

Storms featuring rain, low overcast, and strong winds occurred before and during sampling on 27 August 1968, possibly altering the general shape of the productivity profile; the zone of high production widened to include 20-50-m stratum. This may have been the result of mixing which disturbed the normal vertical distribution of phytoplankton by bringing cells adapted to low light to the upper strata where they responded favorably to the reduced illumination. Incident light and Secchi transparency then were unusually low (Table 2).

An epilimnetic "maximum"--a phenomenon reportedly typical for oligotrophic lakes in the Alps (Ruttner 1953)--occurred in the 0-10-m stratum (Figures 2 and 3). There, especially in highly transparent Crater Lake, one would expect photosynthesis to be depressed considerably by photoinhibitory or photooxidative effects. Utterback et al. (1942) reported the 0-20-m stratum in Crater Lake as nearly devoid of viable cells. The amount of chlorophyll a present was small in comparison to that at greater depths (Table 5). Nevertheless, the few cells that occupied the surface layers were apparently well acclimated to high light intensity and possibly benefited from increasing temperatures which compensated for limitations placed by strong illumination. Accordingly, as surface temperatures reached the summer maximum in late July and early August (Figure 1), productivity in the 0-10-m stratum became more pronounced, to diminish as surface water cooled in late August. Furthermore, midsummer upwelling in certain areas of the lake (Kibby et al. 1968) may have transported nutrients from greater depths to the

TABLE 3. Extinction coefficients (k) and percent transmittance (% T) values for nonfiltered light,[a] Crater Lake, Oregon.

| Depth (m) | 14 June 68 | | 16 July 69 | | 5 August 69 | |
|---|---|---|---|---|---|---|
| | k | %T | k | %T | k | %T |
| 1 | 0.112 | 89 | 0.103 | 90 | 0.133 | 88 |
| 5 | 0.075 | 69 | 0.079 | 67 | 0.091 | 63 |
| 10 | 0.058 | 56 | 0.065 | 52 | 0.072 | 49 |
| 14 | 0.052 | 46 | 0.059 | 44 | 0.063 | 41 |
| 20 | 0.048 | 38 | 0.049 | 37 | 0.052 | 36 |
| 30 | 0.045 | 26 | 0.044 | 27 | 0.044 | 27 |
| 40 | 0.044 | 17 | 0.042 | 18 | 0.042 | 19 |
| 50 | 0.049 | 9 | 0.041 | 13 | 0.041 | 13 |
| 60 | 0.048 | 6 | 0.047 | 6 | 0.040 | 9 |
| 70 | 0.047 | 4 | 0.046 | 4 | 0.045 | 4 |
| 80 | 0.047 | 2 | 0.046 | 3 | 0.044 | 3 |
| 90 | 0.049 | 1 | 0.049 | 1 | 0.044 | 2 |
| 100 | 0.049 | 0.8 | 0.049 | 0.7 | 0.046 | 1 |

[a]The only light reaching the photocell at great depths in Crater Lake is that transmitted by the water--regardless of filter type used on the photocell. The approximate wavelengths for this light is 450 mμ, having an average k value of about 0.05/m.

surface and thereby enhanced productivity in the upper strata. Most of the minerals introduced into Crater Lake are derived underwater from the dissolution of soluble materials along the caldera walls and from fumaroles and thermal springs (Phillips and Van Denburgh 1968). Upwelling may also have brought phytoplankters to near surface where some found conditions favorable in spite of high temperatures and strong light intensity.

## CONCLUSIONS

During summer, phytoplankton productivity and standing stock in Crater Lake are maximal somewhere between 70 and 120 m despite temperatures near 4C and measurable light less than 4% of that at surface. Certain diatoms (e.g., *Asterionella* sp.) are distributed between even greater depths, from 100-200 m (Kemmerer et al. 1924). This suggests that most of the phytoplankton in the lake, by exhibiting very low $I_{sat}$ values and high tolerance to low temperatures, consist of either winter species (i.e. coldwater, shade plants: Hutchinson 1967), well adapted for low light and temperature extremes or eurytopic forms (Ruttner 1953) able to tolerate a wide range of light and temperature conditions. Both types would have a definite advantage, considering the harshness and uniqueness of the Crater Lake environment.

Throughout the year, variations in temperature below 70 m in Crater Lake are presumably rather small. Except for inverse stratification near the surface--noting, however, the rarity of ice cover--the lake is probably homothermal at 4C during October-April. In view of this, there may be little change in productivity throughout the year. A seasonal reduction of incident radiation would enable oligothermal-oligophotic species to inhabit the 0-70-m stratum resulting in an upward displacement of $P_{max}(I_{sat})$.

One can also speculate about the source of deep-water phytoplankton in Crater Lake. Kiefer et al. (1972) suggested that the accumulation of phytoplankton at great depths in Lake Tahoe, California (i.e., 100-400 m) was due to the passive sinking of cells through the euphotic zone. Similarly, in Crater Lake, this process may account, in part, for the concentration of phytoplankton near the compensation depth, and at

TABLE 4. Phytoplankton net productivity per un area per hour for Crater Lake.

| | mg C $m^{-2}hr^{-1}$ (1000-1400 hours |
|---|---|
| 26 July 1967 | 18.2[a] |
| 14 June 1968 | 27.3 |
| 23 July 1968 | 19.7 |
| 27 August 1968 | 28.1 |
| 16 July 1969 | 21.4 |
| 5 August 1969 | 20.7 |
| 31 August 1969 | 32.7 |

[a]Hoffman and Donaldson (1968).

TABLE 5. Concentrations of chlorophyll *a* in vertical profile for Crater Lake. Samples collected between 1100-1300 hours on 5 August 1969.

| Depth (m) | Chlorophyll *a* (mg $m^{-3}$) |
|---|---|
| 0 | 0.086 |
| 20 | 0.159 |
| 40 | 0.232 |
| 70 | 0.334 |
| 110 | 0.436 |
| 200 | None detected |

greater depths. Possibly, cell production is substantial in the 0-70 m stratum during winter due to more favorable light conditions. Eventually, these cells settle into deeper water to create the summer productivity maxima near 100 m. Continued sinking of cells carries them below the summer depths of optimal light intensity (i.e., approximately 90-110 m) where they continue to photosynthesize albeit at a progressively lower rate in response to gradually decreasing illumination with increasing depth.

## LITERATURE CITED


BYRNE, J. V. 1962. Bathymetry of Crater Lake, Oregon. Ore Bin 24:161-164.

_____. 1965. Morphometry of Crater Lake, Oregon. Limnol. Oceanogr. 10:462-465.

FRYXELL, R. 1965. Mazama and Glacier Peak volcanic ash layers, relative ages. Science 147:1288-1290.

HASLER, A. D. 1938. Fish biology and limnology of Crater Lake, Oregon. J. Wildl. Manage. 2: 94-103.

HOFFMAN, F. O., and J. R. DONALDSON. 1968. Zooplankton population dynamics, Crater Lake. Crater Lake Rep. 2. U.S. Nat. Park Serv. 12 p.

HUTCHINSON, G. E. 1967. A treatise on limnology v. 2. Wiley, 1115 p.

KEMMERER, G., J. F. BOVARD, and W. R. BOORMAN. 1924. Northwestern lakes of the United States: Biological and chemical studies with reference to possibilities in production of fish. U. S Bur. Fish. Bull. 39:51-140.

KIBBY, H. V., J. R. DONALDSON, and C. E. BOND. 1968. Temperature and current observations in Crater Lake, Oregon. Limnol. Oceanogr. 13: 363-366.

KIEFER, D. A., O. HOLM-HANSEN, C. R. GOLDMAN, R. RICHARDS and T. BERMAN. 1972. Phytoplankton in Lake Tahoe: Deep-living populations. Limnol. Oceanogr. 17(3):418-422.

NELSON, C. H. 1967. Sediments of Crater Lake, Oregon. Bull. Geol. Soc. Amer. 78:833-848.

PHILLIPS, K. N., and A. S. VAN DENBURGH. 1968. Hydrology of Crater, East and Davis lakes, Oregon. U. S. Geol. Surv. Water-Supply Pap. 1859-E. 60 p.
REID, G. K. 1961. Ecology of inland waters and estuaries. Reinhold. 375 p.
RODHE, W., J. E. HOBBIE, and R. T. WRIGHT. 1966. Phototrophy and heterotrophy in high mountain lakes. Int. Ver. Theor. Angew. Limnol. Verh. 16:302-313.
RUTTNER, F. 1953. Fundamentals of limnology. Univ. Toronto. 295 p.
SAUNDERS, G. W., F. B. TRAMA, and R. W. BACHMANN. 1962. Evaluation of modified $C^{14}$ technique for shipboard estimation of photosynthesis in large lakes. Mich. Univ. Great Lakes Res. Div. Publ. 8. 61 p.
SMITH, R. C., and J. E. TYLER. 1967. Optical properties of clear natural water. J. Opt. Soc. Amer. 57:589-595.
SOVEREIGN, H. E. 1958. The diatoms of Crater Lake, Oregon. Trans. Amer. Microsc. Soc. 77: 96-124.
STRICKLAND, J. D. H. 1957. Solar radiation penetrating the ocean. Fish. Res. Bd. Can., Pac. Oceanogr. Group, Nanaimo, B.C. Rep. 55 p.
_____, and T. R. PARSONS. 1965. A manual of seawater analysis. Bull. Fish. Res. Bd. Can. 125. 203 p.
UTTERBACK, C. L., L. D. PHIFER, and R. J. ROBINSON. 1942. Some planktonic and optical characteristics of Crater Lake. Ecology 23: 97-103.
WAESCHE, H. H. 1934. The lake (physical characteristics). U. S. Nat. Park Serv. Files, Crater Lake, Oregon. 7 p.
WALKER, B. F. 1949. The frozen lake. Crater Lake Nature Notes 15:8.

# SPATIAL AND TEMPORAL DISTRIBUTION OF ALGAE AND SELECTED WATER QUALITY PARAMETERS IN THE BUFFALO RIVER, ARKANSAS[1]

Richard L. Meyer and Laura L. Rippey[2]

The Buffalo National River rises in the Boston Mountains and courses eastward 148 miles through narrow valleys of the Ozark Plateau until it enters the White River. The Buffalo River watershed is primarily an upland oak-hickory deciduous forest interspersed with pastoral lands. The terrain of the region is rugged and the valleys are typically narrow with tall vertical bluffs.

Along the 110 miles of river within the area of study the river changes gradient significantly. In the upper third of the river, a slope of 16 feet per mile occurs in the headwaters area of Boxley to Ponca and 13 feet per mile from Ponca to Pruitt. In the central third, Pruitt to Tyler Bend, the gradient averages 5 feet per mile, and a shallow slope of 3 feet per mile occurs in the lower reaches. In the headwaters region the stream is narrow and meanders through a flood plain forest. This section is characterized by broad riffle areas with pools which undergo a transition to isolated pools before it dries from late June until September. The riffle and pool margins are invaded by beds of vascular phaenerogams, predominantly *Justicia americana* (Water Willow) (Rippey 1976). The central portion has typically a low flow rate, especially in the summer when languid pools are formed. The large pools are principally silt covered with a few large boulders exposed. The interconnecting areas are extensive gravel bars. Densely wooded steep bluffs surround the stream with *Salix* spp. growing on the gravel bars. The lowermost section has an aspect very different from the steeper portions. Here the river bed is silty with little exposed gravel. The valley has widened and forms a sluggish pool with the banks shaded by large *Populus deltoides* (Cottonwood) trees.

Research on lotic ecosystems in the United States was initiated in the 1900s with a study of the Illinois River by Kofoid in 1908. These early studies were confined to summer months and larger organisms (Blum 1956a). Annual studies of algae along an entire river's course are limited and none are known for the Ozark Highlands. Algae of the rivers are of two primary types, planktonic and attached. The planktonic organisms are either rheoplankton or tychoplankton. Rheoplankton are usually found only in slowly moving rivers. Their abundance is inversely proportional to the stream gradient (Blum 1956b). Streams may lack an annual plankton but develop seasonal rheoplankton in pools during low flow periods. Prior studies on the Buffalo River described the development of these populations during the summer when euplanktonic species were present and chlorophyll values higher. In other seasons temporary or tychoplankters were derived from the several periphyton subcommunities, but continued to reproduce in a planktonic state (Meyer 1975).

Meyer (1975) has previously shown that the principal algal component of the Buffalo National River is the periphyton. These organisms were shown to develop assemblages in the epilithic, epiphytic, epizoic, epipelic and metaphyton subcommunities. The development of these subcommunities is associated with variations in flow rate around the substrate units; providing diverse niches. Although the causal factors are not completely known there is an inherent "current demand" (Whitford and Schumacher 1961). Ruttner (1964) suggested that streams are physiologically rich since zones of depletion do not form in the microhabitat surrounding the periphyton. Douglas (1958) demonstrated that low flow was adverse to growth of diatom assemblages. The effect of current has been clearly demonstrated by comparing algal populations in adjacent pools and riffles with similar oxygen, temperature and nutrient levels. The differential distribution of algae between these zones can be interpreted in terms of a current demand. However, maximum as well as minimum flow rates must be considered since scouring may remove algae from the substrate.

Collections of phytoplankton and periphyton at regular time intervals demonstrate a definite algal periodicity. Temporal distribution is generally accepted for plankton but distribution of periphyton may follow two patterns. In certain systems the species composition is relatively constant but abundance varies seasonally. Butcher (1940) observed this pattern in the River Hull. In other streams or regions of streams there may be a constant reappearance of algal associations in a particular season; e.g., the summer *Spirogyra* bloom in the lower Buffalo National River (Rippey and Meyer 1975). It should be noted that the occurrence of an algal species is more dependent on the chemical and physical characteristics of the water and the structure of the river basin than on previous sequences of algal species (Patrick 1971).

The reported research, conducted from September 1974 through September 1975, was designed to provide a description of the Buffalo National River's spatial and temporal distribution of the algal flora and selected water quality parameters. Emphasis was placed on gaining insight into major biogeographical zones, seasonal succession and determining which physico-chemical parameters may affect algal distribution.

## MATERIALS AND METHODS

Algal and physico-chemical samples were collected at monthly intervals at nine stations (Figure 1). Periphyton grab samples from each subcommunity and phytoplankton tows were preserved in $M_3$ fixative (Meyer 1971). Diatoms were cleaned and[3]Hyrax mounted prior to examination.

Temperature was measured *in situ* and oxygen concentration was determined by azide modification of the Winkler titration (APHA 1971). Turbidity was determined on unfiltered water samples using a Hach Turbidimeter Model 2100A. Analyses were performed on filtered water samples for determination of orthophosphate, nitrate and silica. Determination of orthophosphate was by

[1]This study was supported with funds provided in part by the Buffalo National River, National Park Service through the Water Resources Research Center at the University of Arkansas. A portion of this work was in partial fulfillment of a Master's of Science degree for L.L. Rippey.

[2]Department of Botany & Bacteriology, University of Arkansas, Fayetteville.

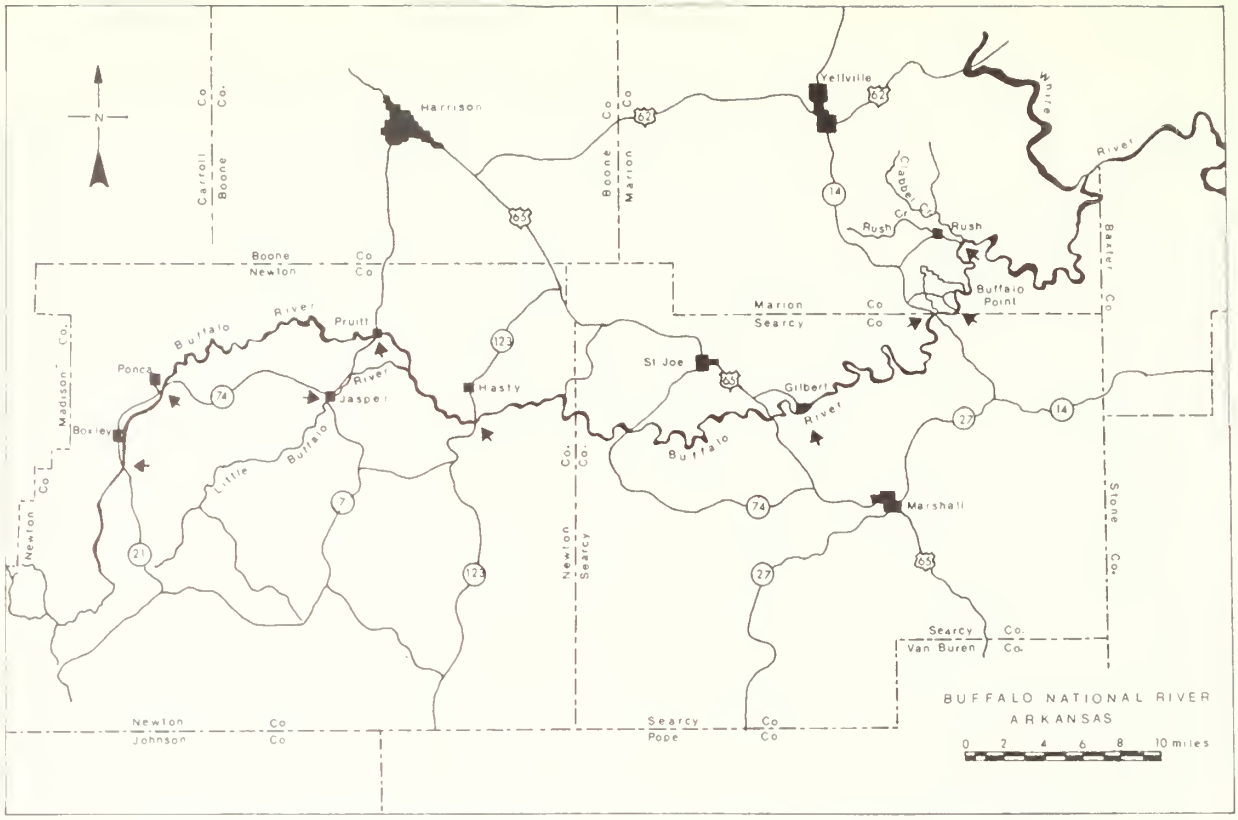



FIGURE 1. Buffalo National River. Arrows indicate sampling stations.

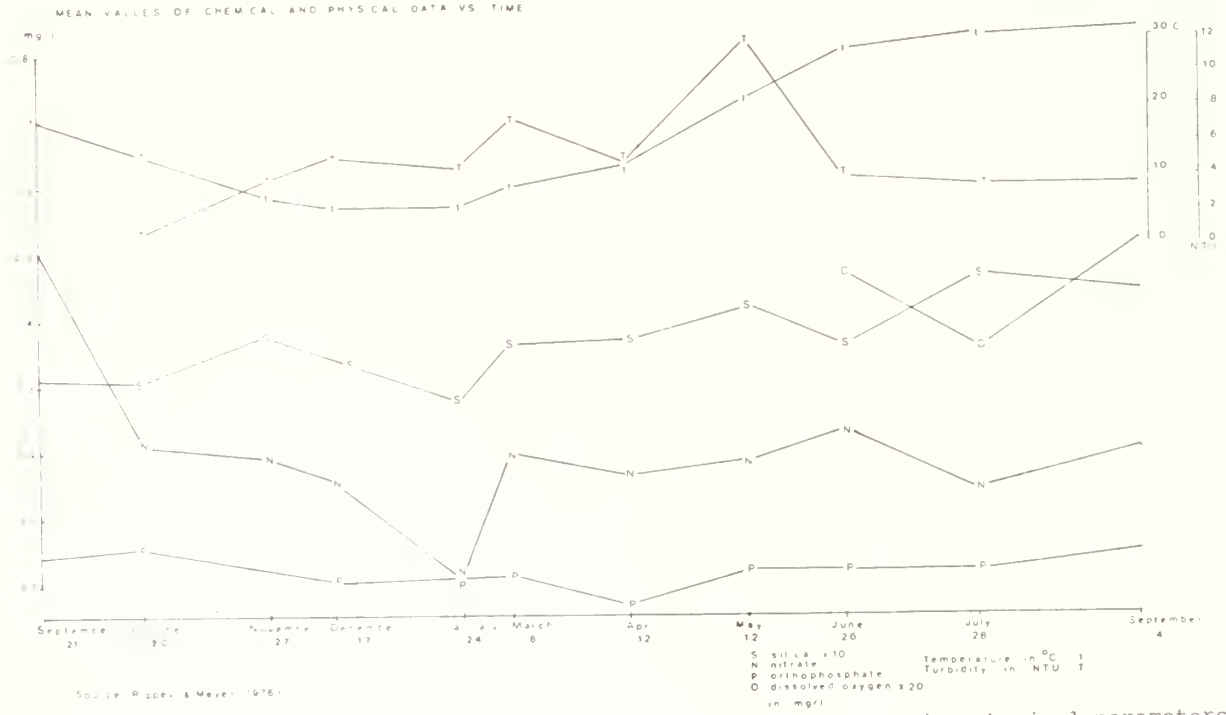



FIGURE 2. Temporal distribution of mean values for selected physico-chemical parameters.

the stannous chloride procedure, nitrate by the ultraviolet technique and silica by the heteropolyblue method (APHA 1971).

## RESULTS AND DISCUSSION

The results presented are a summation of more detailed analysis presented by Rippey and Meyer (1975, 1976) and Rippey (1976). A generalized spatial distribution of the algal flora is described and temporal distribution patterns described. Similar generalizations are given for temporal and spatial fluctuations of select physico-chemical parameters.

The mean seasonal temperature profile is a smooth sinusoidal curve with a maximum of 32° i early September 1975. The lowest water tempera ture recorded was 5° in December 1974. The stream was spatially cooler in the headwater with a maximum of a 2° rise along the 110-mile study area (Figure 2). The minimal change in

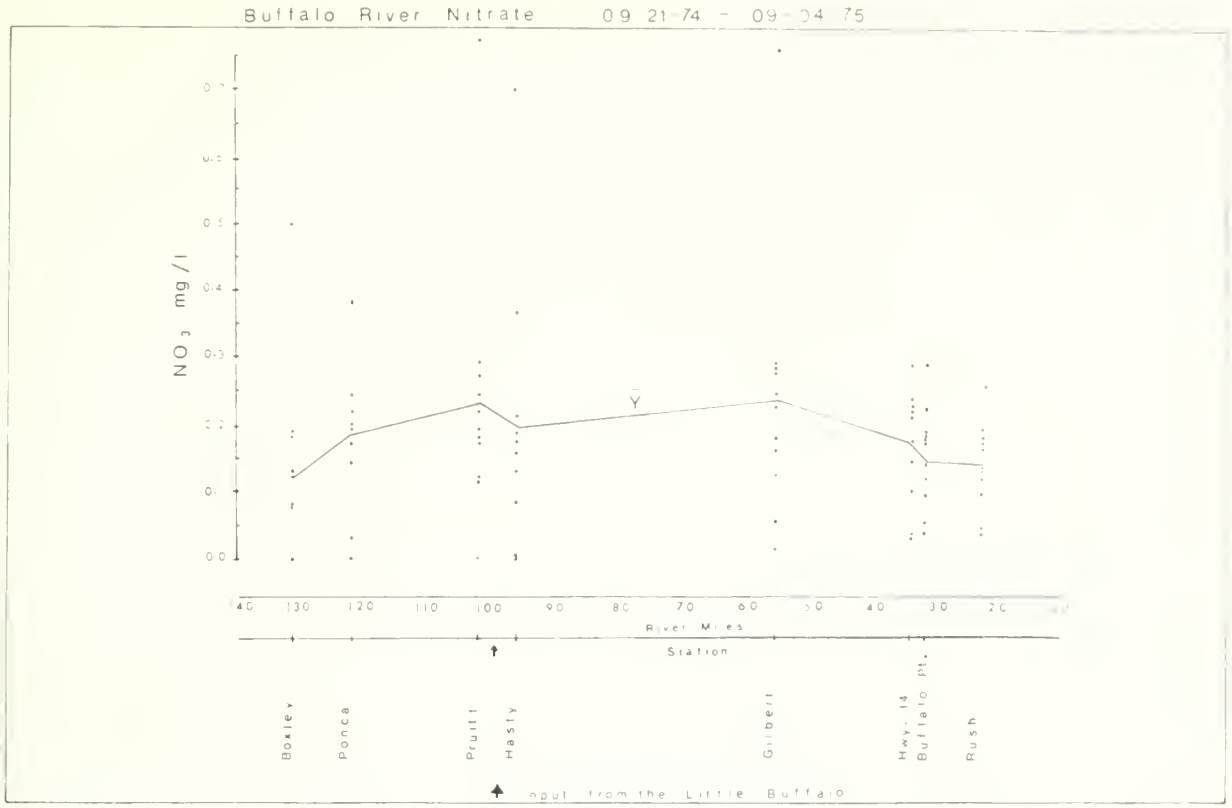



FIGURE 3. Buffalo River nitrate data. Concentrations vs. river mile (line represents the mean value).

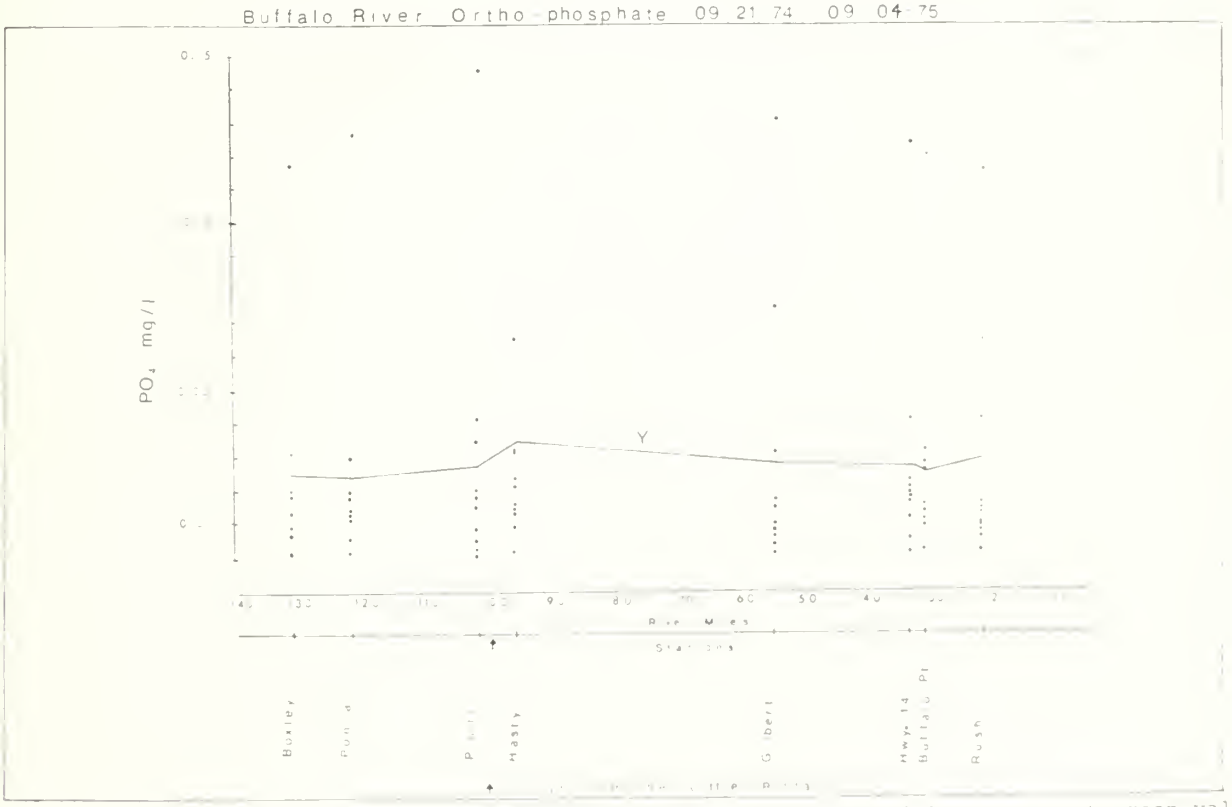



FIGURE 4. Buffalo River phosphate data. Concentration vs. river mile (line represents mean value).

temperature is probably the result of the inflow of numerous springs and the large volume of water passing through the gravel substrate.

Dissolved oxygen is subject to diurnal, and spatial fluctuations. The magnitude of the diurnal change varies seasonally according to algal productivity. Rippey and Meyer (1976) reported that marked changes in oxygen production vs. respiration were dependent upon the composition and density of the standing crop as well as insolation. The mean values for mid-day dissolved oxygen ranged from 4.1 to 12.6 mg/l from June to September (Figure 2). Later research indicates that oxygen concentrations were near saturation. Similar results have been reported by Nix (1973). These data suggest there is probably no organic overloading.

Rippey and Meyer (1975, 1976) have shown that oxygen concentrations are affected by temperature, flow rate and productivity. The minimum concentration of 4.1 mg/l in July may be accounted for by reduce flow, which results in a reduction of reaeration, elevated water temperatures, and high respiration associated with a large standing crop.

Turbidity values which represent the total amount of organic and inorganic suspended materials ranged from 0.29 to 19.0 NTU. Summer and autumnal turbidities were low with the maximum values recorded in the spring during high runoff (Figure 2). However, all of the variation could not be accounted for by flow. Disturbance in the watershed was also an important factor. During high flow the turbidities produced by flooding or man-made perturbation usually return to normal levels within 24 hours. Flooding generally affects the entire stream system and typically results in a twofold increase. Man-made disturbances result in higher values but affect a shorter stream segment.

Previous studies have suggested nitrate loading in May and June (Parker 1975) because of a slight increase concentration downstream. It is generally assumed that there is a downstream accumulation of nutrients from runoff and ion exchange with the substrate. An inverse relationship was observed by Cushing (1964) in the Montreal River, Saskatchewan. He attributed this reduction to nutrient assimilation by large autotrophic assemblages.

A review of the temporal and spatial data during the study period reveals distinct seasonal periodicity, but minimal change along the river (Figure 3). The most important source of nitrate is agricultural runoff and discharge of wastes. The correlation coefficient between nitrate and turbidity showed a significant positive correlation. Nix (1973) found a maximum near river mile 80 with submaxima at river miles 70 and 50. The reduced nitrate concentrations and high turbidity values in January are the result of a flooding event. The dilution of a certain parameter while others increase during high runoff has been observed on other Arkansas streams, i.e. the Caddo River (Nix 1973).

The nitrate concentrations along the Buffalo River are typical for the Ozark Plateau with a range from <0.03 to 0.77 mg/l, with the highest concentration reported at Pruitt in September 1974 (Figure 3). The nitrate concentration in the autumn tends to be higher as a result of a general increase in flow. The flow increase appeared to be associated with abscission layer formation in the trees which resulted in reduced transpiration and increased ground water flow.

Orthophosphate concentrations tend to be stable throughout the temporal cycle with mean value ranging between <0.002 to 0.07 mg/l (Figure 2). Spatial distribution of this ion indicates that orthophosphate is nearly constant along the riv except for slightly higher concentrations at Ha (Figure 4). The sorbtion on silt particles dur periods of high runoff and on the substrate red the availability of this ion. The rapid uptake the algal standing crop is an important factor the reduction of orthophosphate concentration. The rapid turnover rate of phosphorus permits a large standing crop although low concentrations available phosphorus are reported.

The concentrations of silica tend to increas during the annual cycle and attain a maximum in later summer (Figure 2). There was a slight te dency for silica concentrations to increase dow stream.

Silica has been suggested by Lund (1965) to the limiting factor for when concentrations are below 0.3 mg/l. If that is indeed the limiting concentration, silica levels on the Buffalo Riv never are limiting. Silica concentrations of 1.55 to 6.47 mg/l are comparable to data record for other streams of the Ozark Highlands (Rice 1974; Meyer 1975). The presence of high silica concentrations suggest that the seasonal periodicity of diatoms in the Buffalo River must be attributed to other factors.

The 270 members of the algal flora of the Bu falo National River show a marked spatial and te poral distribution of species. Spatially the stream can be subdivided into three major segments: an ephemeral segment from the headwaters to beyond Ponca, a central portion with a conti uously inundated gravel substrate, and a segmen having alternately gravel and silt substrate in the riffles and pools, respectively. This latte segment is also continuously inundated. The al in the upper segment can only be present during periods of inundation, e.g., October through Ma The forms present are those which can withstand desiccation and/or produce a resistant structure The organisms are present during the period of high runoff and rapid flow. These conditions tend to select for organisms which are epilithic, i.e., sessile Rhodophyceae, filamentous greens, coccoid and filamentous bluegreens, and pennate diatoms. The central segment contains diverse flora which includes the species presen in the upper segment plus epiphytic, metaphytic and euplanktonic species. Stands of *Justicia americana* develop in the pool margins and serve as a substrate for *Oedogonium, Bulbochaete, Cyl drocapsa, Oscillatoria, Lyngbya* and the algal epiphytes *Chamaesiphon, Gomphonema* and *Cocconei*. A metaphyton subcommunity containing coccoid greens, desmids and miscellaneous flagellates i associated with the vascular phaenerogams. Epizooic blue-green algae and *Gongrosira debaryana* are present on snails. The pools may contain euplanktonic as well as tychoplanktonic species derived from the metaphyton population. The tru planktonic forms, i.e., *Mallomonas, Dinobryon, Eudorina, Kirchneriella, Scenedesmus*, produce minor, temporary populations. A more permanent pool resident is *Spirogyra*.

The lower river segment includes up-stream o ganisms with the addition of epipelic and embedded species. The epipelic algae, *Oscillatoria, Phormidium, Spirulina, Vaucheria* and naviculoi diatoms produce a pellicle at the silt-water interface of the quiet pool. These languid pool often contain stands of *Chara* embedded in the bottom. The deeper pockets are filled with floa ing masses of *Spirogyra*. The euplanktonic compo ent is similar to the control segments flora bu contains the euglenoids, *Euglena* and *Phacus*.

Substrate composition and period of inundatio tends to control spatial distribution of algae. The riffle areas and gravel margins of pools

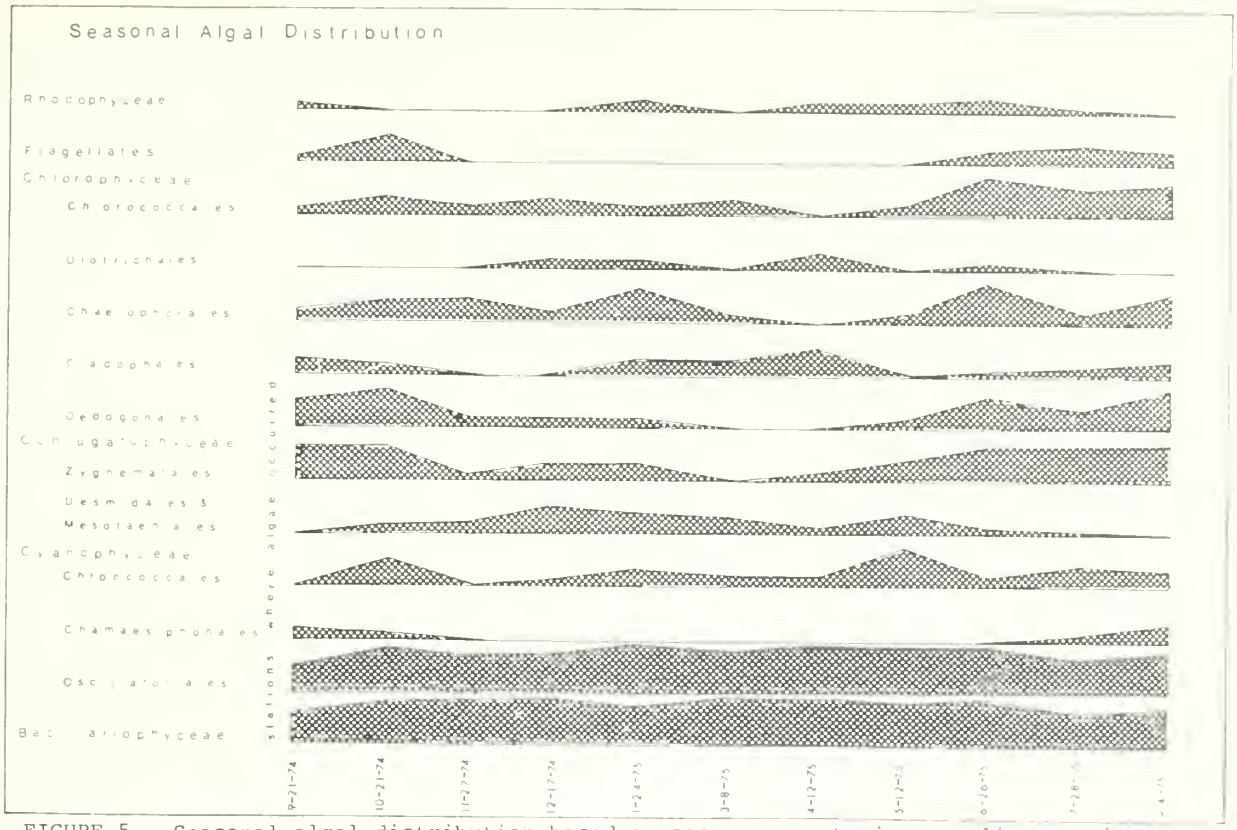



FIGURE 5. Seasonal algal distribution based on occurrence at nine sampling stations.

contain the same assemblages of algae throughout the stream's length. The algae at the soil-water interface and true plankton are substrate associated. Differences seem to be due largely to substrate availability rather than nutrient differences.

Temporal variations in species composition can be described for the Buffalo River. In contrast, the sessile algae of the Hull River did not demonstrate seasonal periodicity (Butcher 1940). The distribution of the Buffalo River algal flora with time tends to be by major taxonomic level. A summation of the seasonal variation in occurrence of species within major taxa at each of the nine sampling stations is presented in Figure 5.

The Rhodophyceae (red algae) were restricted to the epilithic subcommunity. *Batrachospermum* and most other genera of red algae occur in habitats with clean, cool, rapidly running water in eastern piedmont streams (Minckley and Tindall 1963). *Batrachosperum, Audouinella* and *Lemanea* showed no well defined temporal periodicity in the Buffalo River. They were found at every station, with the exception of Jasper and Buffalo Point, although they were never very common.

Flagelletes are a composite grouping composed of the Volvocales, Euglenophyceae, Pyrrhophyceae and Chrysophyceae. Their occurrence probably was directly related to flow rate and the presence of sluggish pools since they occurred only during the summer and fall. As soon as flow rate exceeds swimming rate and reproductive rate, the taxa are washed from the system. These usually were found as euplankton although they also may oc ur as metaphyton.

Within the Chlorophyceae (green algae) there are several distributional patterns. Chlorococcales, represented by *Scenedesmus, Kirchneriella, Pediastrum*, etc., occurred in varying numbers throughout the study period. These nonmotile unattached forms were often found in plankton tows taken during the summer, but they were found more frequently as metaphyton in close association with periphytic communities.

The filamentous Ulotrichales were present from December until June. They are totally absent from the summer population. *Ulothrix* and *Cylindrocapsa* grow best in cool, well-oxygenated waters with maxima in late winter and in the spring. In more northern streams the seasonal occurrence is delayed approximately two months (Blum 1960).

Representatives of the Chaetophorales were found in both epiphytic habitats, e.g., *Coleochaete* and epilithic habitats, e.g., *Gomantia* and *Stigeoclonium*. *Stigeoclonium* was more prevalent during the winter (November through April), when it developed in the exposed sunny rapids; although it was found in quiet pools. In contrast, Blum (1960) reported that Stigeoclonium of northern streams displayed peak growth during the summer in swiftly flowing waters.

Cladophorales, of which *Cladophora* was the most prominent member, was found more frequently in the winter. This distribution probably was influenced by both temperature and flow rate. Cladophora has been shown to have a lack of tolerance to summer increases (Dillard 1969). Whitton (1970) concurred by noting a decrease in *Cladophora* has been shown to have a lack of tolerance to summer increases (Dillard 1969). Whitton (1970) concurred by noting a decrease in *Cladophora* when water temperatures were above 24°C.

Dillard (1969) reported that in a North Carolina piedmont stream the summer community was composed of several species of *Spirogyra* associated with *Oedogonium*. This situation parallels the warm weather aspect of the Buffalo River where *Oedogonium* and *Bulbochaete* were predominant in the rapids and high velocity zones during the summer. *Spirogyra* occurred within the same time period as *Oedogonium* and *Bulbochaete*, but they were spatially separated.

Of the Conjugatophyceae, the Zygnematales were more common during the summer and fall. *Spirogyra* was represented by several species which were found floating in large masses during the summer as tychoplankton in the quiet pools. *Mougeotia*, also a member of the Zygmematales, occurred predominantly during the winter and spring. Desmids *Cosmarium, Closterium, Penium* and *Staurodesmus* were important as metaphyton and occurred mainly from November through May.

The seasonal distribution of the Cyanophyceae is less well defined. Blue-greens in the Buffalo River were the second most predominant encrusted epilithic algae. These diverse encrusting forms have certain features in common. They have a compact habit with a broad surface of contact with the substrate leaving very little surface exposed to the current. Chroococcalian blue-green algae, such as *Aphanocapsa, Chroococcus, Gloeocapsa* and *Merismopedia,* were an important component in the encrusting epilithic subcommunity, as well as in the epipelic layer. The appearance of the epiphyte *Chamaesiphon* corresponded with the period when its most frequent host *Oedogonium* was most abundant. The occurrence of Oscillatoriales was common throughout the study period. Common representatives, including *Lyngbya, Oscillatoria* and *Phormidium,* were usually epilithic.

By far the most abundant and diverse algal taxon represented on the river was the Bacillariophyceae. Epilithic diatoms of the littoral zone of lakes show a well-defined seasonal succession, with only a few genera such as *Gomphomena, Cymbella* and *Achnanthes* present the year round (Stockner and Armstrong 1971). The seasonal distribution of diatoms in the Buffalo River was not so well defined with many genera observed having sporadic distributions and others occurring throughout the study period. *Achnanthes, Cocconeis, Cymbella, Navicula, Nitzschia, Surirella,* and *Synedra* occurred frequently along the river on each sampling date. Some of these diatom genera, including *Achanthes, Cocconeis, Cymbella* and *Gomphonema*, are especially suited to fast flowing streams because of their ability to affix themselves firmly to the substrate (Fox et al. 1969). The occurrence of some genera of Bacillariophyceae in the Buffalo River apparently is restricted by rapid flow: these are *Amphipleura, Cymatopleura, Frustulia, Gyrosigma, Pinnularia, Rhophalodia, Stauroneis* and *Cyclotella.* This effect may be due to substrate availability, as well as disturbance due to stream disturbance and/or rapid flow. For example, *Cymatopleura* and other diatoms live on silt banks which are unstable in rapid currents (Blum 1956b). A few genera in the Buffalo showed a temporal distribution that may be related to seasonal changes. *Diatoma, Fragilaria, Meridion* and *Pleurosigma* occurred more frequently during the winter.

The data provide a baseline from which specific, concise patterns emerge and are a standard from which clearly defined questions can be addressed. These studies have shown that the Buffalo National River is a unique system. That is, it contains three major habitat types with intergradations with an associate flora. The flora is not only spatially diverse but also exhibits seasonal variation. These spatial and temporal patterns are evident in each of the subcommunities.

If conserved, the Buffalo National River ecosystem can provide an excellent series of study sites for reaching an understanding of the impact of natural and man-generated perturbations. For example, the upper stream segment, the ephemeral segment is a naturally disturbed region which is recolonized and becomes productive soon after inundation. An analysis of this response would provide insight into the potential recovery of "use" disturbed areas and lead to the development of a management plan. The diversity within this one stream system provides the National Park Service an opportunity and an obligation to preserve an important ecosystem.

## LITERATURE CITED


AMERICAN PUBLIC HEALTH ASSOCIATION. 1971. Standard methods for the examination of water and waste water. 13th ed. N.Y. 769 p.

BLUM, J.L. 1956a. The application of the climax concept to algal communities of streams. Ecology. 37:603-604.

BLUM, J.L. 1956b. The ecology of river algae. Bot. Rev. 22:291-341.

BLUM, J.L. 1960. Algal populations in flowing waters. p. 11-21. *In:* The ecology of algae. Pymatuning Laboratory of Field Biology. Spec. Publ. No. 2. University of Pittsburgh. 96 p.

BUTCHER, R.W. 1940. Studies in the ecology of rivers IV. Observations on the growth and distribution of the sessile algae in the River Hull, Yorkshire. J. Ecol. 28:210-223.

CUSHING, C.E. 1964. Plankton and water chemistry in Montreal River lake-stream system, Saskatchewan. Ecology. 45:306-313.

DILLARD, G.E. 1969. The benthic algal communities of a North Carolina Piedmont stream. Nova Hedwigia. 18:9-29.

DOUGLAS, B. 1958. The ecology of the attached diatoms and other algae in a small stony stream. J. Ecol. 46:295-322.

FOX, J.L., T.O. ODLAUG, and T.A. OLSON. 1969. The ecology of periphyton in western Lake Superior. Part I. Taxonomy and distribution. Water Resources Research Center. Minneapolis, Minnesota. 127 p.

LUND, J.W.G. 1965. The ecology of freshwater phytoplankton. Biol. Rev. 40:271-239.

MEYER, R.L. 1971. A study of phytoplankton dynamics in Lake Fayetteville as a means of assessing water quality. Water Resources Research Center Publ. No. 10. University of Arkansas, Fayetteville. 59 p.

MEYER, R.L. 1975. Biochrome analysis as a method for assessing phytoplankton dynamics Phase II. Water Resources Research Center Publ. No. 32. University of Arkansas, Fayetteville. 58 p.

MINCKLEY, W.L. and D.R. TINDALL. 1963. Ecology of *Batrachospermum* sp. (Rhodophyceae) in Doe Run, Meade County, Kentucky. Bull. Torrey Bot. Club. 90(6):391-400.

NIX, J. 1973. Intensive "one shot" survey. *In:* Preliminary reconnaissance water quality survey of the Buffalo National River. Babcock, R.E., and H.C. MacDonald (eds.). Water Resources Research Center Publ. No. 19. University of Arkansas, Fayetteville. 147 p.

PARKER, D.G. 1975. Seasonal water quality analysis. *In:* Buffalo National River ecosystems Part I. Babcock, R.E., and H.C. MacDonald (eds.). Water Resources Research Center Publ. No. 34. University of Arkansas, Fayetteville. 228 p.

PATRICK, R. 1971. The effects of increasing light and temperature on the structure of diatom communities. Limnol. Oceanogr. 16(2): 405-421.

RICE, R.G. 1974. Water chemistry and algal studies. pp. 16-34. *In:* A preliminary study of the water quality of the Illinois River, Arkansas. Final report to the Illinois River Property Owners of Arkansas, Inc. 158 p.

RIPPEY, L.L. 1976. Spatial and Temporal Distribution of Algae and Selected Water Quality Parameters in the Buffalo River, Arkansas. Arkansas Water Resources Research Center. Thesis and Dissertation Series Report No. 1. University of Arkansas, Fayetteville. 91 p.

RIPPEY, L.L., and R.L. MEYER. 1975. Spatial and temporal distribution of algae and

associated parameters. p. 103-115. *In:* Buffalo National River Ecosystems Part I. Babcock, R.E., and H.C. MacDonald (eds.). Water Resources Research Center Publ. No. 34. University of Arkansas, Fayetteville. 228 p.

IPPEY, L.L., and R.L. MEYER. 1976. Spatial and temporal distribution of algae and associated parameters. *In:* Buffalo National River Ecosystems Part II. Babcock, R.E., and H.C. MacDonald (eds.). Water Resources Research Center Publ. No. 38. University of Arkansas, Fayetteville.

RUTTNER, F. 1964. Fundamentals of Limnology. University of Toronto Press, 295 p.

STOCKNER, J.G., and F.A.J. ARMSTRONG. 1971. Periphyton of the experimental lakes area, northwestern Ontario. J. Fish Res. Board Canada. 28:215-229.

WHITFORD, L.A., and G.J. SCHUMACHER. 1961. Effect of current on mineral uptake and respiration by a fresh-water alga. Limnol. Oceanogr. 6:423-425.

WHITTON, B.A. 1970. Biology of *Cladophora* in fresh waters, a review paper. Water Research. 4:457-476. Pergamon Press, N.Y.

# PRELIMINARY STUDIES INTO THE AQUATIC RESOURCES OF GULPHA GORGE CREEK, HOT SPRINGS NATIONAL PARK, ARKANSAS

M. S. Ogra, A. C. Sims and G. S. Rai[1]

## INTRODUCTION

The uppermost reaches of Gulpha Gorge Creek watershed, lying within and adjacent to Hot Springs National Park, is the few remaining undeveloped portion of its watershed.

Changing land use has trended increased urbanization which, if allowed to continue uncontrolled, will alter the hydrological balance of the area by increasing the frequency and magnitude of local flooding. Changes in water quality are expected to affect all life systems supported by it, some of which may endanger the health and well being of park visitors.

Pollution in any form will cause some kind of disturbance in a naturally occurring ecosystem. May it be chemical, physical, physiological or biological, it will have strong influence on the relationship between components and species population using it. Unlike chemical or physical pollutants, biological pollutants may develop purely as a result of disturbance to a steady state in an ecosystem.

This study was directed towards planning for the conservation and proper development of water with related land resources of the watershed, and to serve as a focal point to initiate the involvement of Federal, state, and local agencies, including the general public, for the protection and restoration of the environment and people who inhabit the area.

## MATERIALS AND METHODS

Water samples for analysis were collected from seven sampling stations established along the course of Gulpha Gorge Creek. Station #1 was established South of camp ground in order to determine the influence of the camping facility on downstream water quality. Station #2 was located North of camp ground. Sation #3 was located upstream of Highway 70 bridge in Sleepy Valley; short distance prior to the creek enters into the Large Lake. Station #4 was established at downstream side of low-water-bridge above Upper Lake in Sleepy Valley. Possible affects of a nearby quarry would be determined. Station #5 was located Southwest of bridge #147 on Highway 70, comparatively a fast current section; short distance from the confluence of the central and left branches of the watershed. Station #6 was located on Stone-Bridge Road, Southside and below the dam at the foot of the Large Lake. Station #7 was located on old road off Highway 70 short distance from Spring House. Spring House has been a center for commercial bottled water supply.

Representative samples were collected in wide-mouth polyethylene sample bottles, underwater after several rinsing and flushings and avoiding air bubbles. Two to four samples were obtained at each sampling station. Collections were made between 7:a.m. to 9:00 a.m. on each trip. The bottles were stored in ice chests and transported to the laboratory without any loss of time. Weather conditions during and up to forty-eight hours prior to sampling are summarized on Table 1.

## PHYSICAL PARAMETERS

COLOR: Units of apparent color were determined colorimetrically by employing Platinum-Cobalt Standards for water, on the basis that one unit of color is produced by 1 mg/l of platinum in the form of chloroplatinate ion.

CONDUCTIVITY: Readings were taken directly by using HACH - DR-EL/2 spectrophotometer and expressed as ohm/cm. Analysis was made while holding the samples at 25°C.

DISSOLVED OXYGEN: Dissolved oxygen levels were determined by Wimbler-Azide Filtration Method for Water and Wastewater (APHA Standard Methods 1971). In later readings the probe method employing Yellow Spring Oxygen Meter (YSI) Model #54 was used for determining dissolved oxygen on the spot.

pH: A colorimetric method as recommended in "APHA" Simplified Procedures for Water Examination (1964) was used to determine pH of water.

TEMPERATURE: Temperature measurements were made by using conventional type laboratory thermometers and/or Yellow Spring Oxygen Meter probe by placing them for four to five minutes half way between the top and bottom of the water body. Degrees in centigrade represent the averages of at least three readings taken at each sampling station

TURBIDITY: Test for turbidity expressed as formazin turbidity units (FTU) was made by employing "Absorptometric Method for Water" recommended in FWPCA Methods for Chemical Analysis (1969).

## CHEMICAL PARAMETERS

Determinations for acidity, alkalinity, chloride, chromium, copper, fluoride and hardness in the creek water were made according to APHA Standard Methods (1971).

IRON: Determininations for total iron were made by 1, 10-Phenanthroline Method employing HACH analysis procedure and direct reading spectrophotometer.

LEAD: Water samples were analyzed for lead using Koslow Scientific Company's lead detection Kit #1182, which uses improved diphenylthiocarbazone method (APHA Standard Methods 1971).

MANGANESE: Periodate Oxidation Method (High Range for Water - APHA Standard Methods 1971) was employed to determine the amount of manganese in water samples. HACH Analysis Procedure (1973) and DR-EL/2 spectrophotometer were used for reading mg/l manganese.

MERCURY: Detection of mercury was carried out by employing Koslow Scientific Company's Mercury Trace Kit #1280.

NITROGEN-AMMONIA AND NITROGEN-NITRATE: These were determined by employing Nessler's Method and Cadmium Reduction Method (APHA Standard

[1]Department of Biology, Southern University, New Orleans, Louisiana 70126.

TABLE 1. Gulpha George Creek aquatic resources Hot Springs National Park: weather report for periods during which sampling was done.

| Date | Maximum temperature | Minimum Temperature | Rainfall inches |
|---|---|---|---|
| 8/14/76 | 90 | 63 | 0.03 |
| 8/15/74 | 91 | 64 | 0.28 |
| *8/16/74 | -- | -- | -0- |
| 9/19/74 | 79 | 58 | -0- |
| 9/20/74 | 86 | 58 | -0- |
| *9/21/74 | -- | -- | -0- |
| 10/29/74 | 68 | 57 | 2.82 |
| 10/30/74 | 80 | 64 | traces |
| *10/31/74 | -- | -- | -0- |
| 7/15/75 | 91 | 62 | -0- |
| 7/16/75 | 91 | 64 | -0- |
| 7/17/75 | -- | -- | -0- |

*Samples were collected between 7 a.m. and 9 a.m. on these days. There was no rainfall.

Methods 1971) Analysis procedures were adopted from Water Handbook by HACH (1973) using HACH direct reading spectrophotometer.

PHOSPHATE: Tests for ortho and total phosphates were performed according to APHA Standard Methods (1971) employing HACH DR-EL/2 spectrophotometer.

SILICA: Amounts of silica were determined by silicomolybdate method (APHA Standard Methods 1971) and results were expressed as mg/l silica (as $SiO_2$).

SULFATE AND SULFIDE: Amounts of sulfate and sulfide in creek water were determined by employing turbidimetric and methylene blue methods respectively (APHA Standard Methods, 1971).

SUSPENDED SOLIDS: Determinations for suspended solids were made by "Photometric Method for Water and Waste Water" outlined in Sewage and Industrial Wastes, 31 (1959).

COLIFORM BACTERIA: Enumeration was made by APHA Standard Method (1971) employing lactose broth incubation technique. For separating fecal strains of *E. coli* from other coliformes, Eijkman's lactose broth medium was used and for the isolation of fecal streptococci, KF streptococcus broth was used as a selective medium.

Determinations for dissolved oxygen, pH and temperature were made on the spot at each of the seven sampling stations on each collection. Analysis for copper, iron, lead and zinc was also carried out employing germanium lithium detector using multi-channel analyzer for characteristic gamma rays.

## RESULTS AND DISCUSSION

Water Quality data collected during August, September and October 1975, and July, 1975 are presented in Tables 2-5.

COLOR: Figures for color units ranged from 20 to 55. Since levels of suspended solids were not high therefore color may be mainly due to metallic salts and other dissolved organiz matter. Variations seem to correlate with changes in temperature.

CONDUCTIBILITY: Conductivity of the creek wate seemed to increase downstream indicating increa in concentration of ionized substances from the sediment. These values were slightly lower during October which may be due partly to lower temperature in October.

DISSOLVED OXYGEN: Levels of dissolved oxygen w quite high ranging from 9 ppm to 12.5 ppm. Val for August were slightly higher, rains may be the contributing factor. High levels of DO indi cate that there were no organic loading problem in the creek water or that the process of self-purification was in progress at high rates.

pH: pH values ranged between 7.0 to 7.4 at vari ous stations. These values seem to be inversel proportionate to temperature values. Month to month differences during August to October were small. Slightly alkaline pH seems to be due to $CO_3$ and $HCO_3$ which is not uncommon in natural waters.

TEMPERATURE: Temperature ranged from 17.2°C to 19.8°C during August, 1974 observations at various sampling stations. As most of the creek ar is shaded, therefore, the temperature differenc are mostly due to size of the water body and depths along the course. Relatively higher temperatures as observed at station #6 seem to be due to the Large Lake at the foot of which this station is located, however explanation for higher readings at station #3 may be due to comparatively exposed upstream section of the cree Same trend was noticed at other sampling trips which followed in September and October 1974, a July, 1975. Temperature differences in betwee months at various stations were as anticipated with the change in seasons.

TURBIDITY: Turbidity (F.T.U.) was low and seem to correlate with temperature.

ACIDITY AND ALKALINITY: None of the samples ha detectable acidity which indicates absence of mineral acids or weak organic acids in creek water.

Total alkalinity values differed markedly fr station to station at each of the four trips. Since phenolphthalein alkalinity was equal to each case therefore the alkalinity may be bica bonate alkalinity. Highest level 120 mg/l was detected at station #7 in August. Since level of alkalinity are directly dependent on source water, it is therefore reasonable to believe th area surrounding station #7 is rich in bicarbo ates and that previous day's rains contributed t the increase in bicarbonate levels. On the oth hand area around station #6 seems to be poor i bicarbonate contents. Low figures for station may be due to dilution factors introduced by Large Lake through which the creek flows. Alk linity increases downstream from the lake, sed ment and the surrounding areas may be contribu ting factors. Relatively lower figures in Sep tember and October may be due to relatively dr weather prior to collecting the samples.

CHLORIDE: Chloride levels varied from 8 mg/l 12.2 mg/l estimated as NaCl. Small variations were noticed at various stations during August determination, however marked variations were observed during September and October when the levels were slightly higher as compared to tho observed in August. These concentrations were much less than the one which can give salty

TABLE 2. Alalysis of Gulpha Gorge Creek water. Values derived from water samples collected during August 1974.

| | STATIONS | | | | | | |
|---|---|---|---|---|---|---|---|
| PHYSICAL PARAMETERS | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 1. Color Units | 15 | 20 | 35 | 20 | 20 | 40 | 30 |
| 2. Specific Conductivity ohm/cm | 150 | 140 | 70 | 65 | 140 | 70 | 120 |
| 3. Dissolved Oxygen ppm | 10 | 11 | 11 | 12 | 12 | 14 | 12 |
| 4. pH. | 7.3 | 7.2 | 7.1 | 7.3 | 7.4 | 7.2 | 7.2 |
| 5. Temperature $^{o}C$ | 17.2 | 17.2 | 19.8 | 18 | 17.8 | 19.2 | 18.8 |
| 6. Turbidity (F.T.U.) | 10 | 10 | 22 | 10 | 10 | 18 | 9 |
| CHEMICAL ANALYSIS | | | | | | | |
| 7. Acidity, mg/l m.o. (as$CaCO_3$) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8. Alkalinity mg/l $CaCO_3$ | 70 | 80 | 30 | 30 | 100 | 30 | 120 |
| 9. Chloride: Na Cl mg/l$^3$ | 8.3 | 8.2 | 8.4 | 8.0 | 8.3 | 8.3 | 8.1 |
| 10. Chloride: $CaCO_3$ | 7.1 | 7.0 | 7.1 | 7.3 | 7.1 | 7.1 | 7.1 |
| 11. Chromate, (as $^3NaC_3O_4$) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12. Copper, ppm | .3 | .2 | .2 | .2 | .2 | .1 | .1 |
| 13. Fluoride, ppm | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.2 | 0.1 |
| 14. Hardness mg/l (as $CaCO_3$) | 80 | 82 | 38 | 40 | 90 | 32 | 128 |
| 15. Iron, ppm | T | R | A | C | E | S | |
| 16. Lead | Below the Detection Limit (0.02-0.05 micrograms/l) | | | | | | |
| 17. Manganese ppm | T | R | A | C | E | S | |
| 18. Mercury | Below the Detection Limit (0.1 mg/l) | | | | | | |
| 19. Nitrogen as Nitrate-N-mg/l | 0.1 | 0.2 | 0.1 | 0.2 | 0.1 | 0.1 | 0.1 |
| 20. Phosphate mg.l | 0.42 | 0.40 | 0.60 | 0.25 | 1.20 | 0.35 | 0.35 |
| 21. Silica mg/l (as $SiO_2$) | 6.5 | 8.0 | 6.5 | 0.5 | 9.0 | 7.0 | 10.0 |
| 22. Sulfate mg/l | 8 | 9 | 5 | 9 | 9 | 6 | 11.0 |
| 23. Suspended solids mg/l | 8 | 6 | 5 | 7 | 6 | 6 | 3 |
| 24. Zinc | T | R | A | C | E | S | |
| MICROBIAL ANALYSIS | | | | | | | |
| 25. Coliform/100 ml Total | 120 | 110 | 180 | 220 | 280 | 110 | 70 |
| 26. Coliform Fecal | 19 | 10 | 44 | 29 | — | - - | - - |

taste as to be considered objectionable. It may be mentioned that maximum allowable chloride concentration is 250 mg/l.

CHROMATE: Chromate level estimated as sodium chromate was not detected in most samples during all four trips, however in a few samples minute traces were detected. These findings were not confirmed in subsequent tests in samples collected at the same time, about the same place.

FLUORIDE: Fluoride concentration ranged between .1 ppm to .2 ppm at various sampling stations during August, 1975. There was a marked increase in these levels in September and furthermore in October when levels ranged between .14 to .15 ppm at six stations and it was .3 ppm at station #1. There is no possible explanation for this concentration trend. Further studies may be made in order to determine the source. And it is also worth noting that free water from natural sources may have such fluoride levels.

HARDNESS: Determinations for hardness revealed levels ranging from 32 to 128 mg/l of $CaCO_3$ in August. These figures declined markedly in September and significantly further down to 15 to 30 mg/l ($CaCO_3$) in October. Although complete analysis was not conducted so far as the divalent metallic cation are concerned with hardness, yet it was sufficiently clear that most of the hardness was due to Ca++. Most drinking water contain hardness up to 250 mg/l ($CaCO_3$) whereas the highest figures obtained from the above study were 128 mg/l. It is therefore safe to say that the creek water was safe for use in domestic and industry after proper treatments.

NITROGEN: Values on Tables 2-5 reveal the level of nitrogen as nitrate N-mg/l. It may be observed that nitrate levels were very low ranging from .1 to .2 mg/l during August. These levels rose to .5 mg/l in September and comparatively higher levels up to 1 mg/l were observed in October. No definite pattern was observed so far as monthly reading are concerned. Very low levels of nitrate rule out any runoffs and domestic pollution etc. Comparatively low levels in August indicate dilution due to rains.

PHOSPHATE: Phosphate ($PO_4$) levels during the period under study were within 0.14 to 0.6 mg/l range. Slightly higher figures were obtained in August, 1974. No explanation can be offered at this time for relatively higher level of 1.2 mg/l of $PO_4$ observed at station #5 in August, 1974. Although there has been .28 inches of rainfall 24 hours before sampling yet there was no indication of possible contamination by water treatment, biological wastes and residues or agricultural fertilizer runoffs.

SILICA: Amounts of Silica ($SiO_2$) were within or below the range normally found in fresh waters. These levels were between 6.5 to 10 mg/l. Differences between stations were not marked. Similarly differences from month to month were minute. Slight variations reflect only the flow and geographic locations of various stations.

SULFATE: Levels of sulfate varied from 5 mg/l to 12 mg/l. These levels are insignificant as compared to 250 mg/l which is the maximum level allowed in drinking water by Public Health Service. Differences in values between stations and between months were minute. October values which were slightly lower than those of previous months may represent true sulfate levels in the creek because there had been no rains prior to collecting samples, for sometime.

SUSPENDED SOLIDS: Values for suspended solids

TABLE 3. Analysis of Gulpha Gorge Creek water. Values derived from water samples collected during September 1974.

| | STATIONS | | | | | | |
|---|---|---|---|---|---|---|---|
| PHYSICAL PARAMETERS | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 1. Color, Units | 15 | 15 | 25 | 20 | 20 | 30 | 20 |
| 2. Specific Conductivity ohm/cm | 140 | 125 | 80 | 75 | 140 | 80 | 80 |
| 3. Dissolved Oxygen ppm | 9 | 10 | 9 | 9 | 9 | 10 | 9 |
| 4. pH | 7.4 | 7.3 | 7.1 | 7.2 | 7.4 | 7.2 | 7.2 |
| 5. Temperature $^{o}C$ | 16.2 | 17.2 | 21.0 | 16.8 | 17.6 | 19.0 | 18.1 |
| 6. Turbidity (F.T.U.) | 12 | 15 | 25 | 15 | 20 | 15 | 10 |
| CHEMICAL ANALYSIS | | | | | | | |
| 7. Acidity, mg/l m.o. (as $CaCO_3$) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8. Alkalinity mg/l ($CaCO_3$ | 40 | 50 | 50 | 40 | 60 | 40 | 80 |
| 9. Choloride: NaCl mg/l$^3$ | 15 | 15 | 25 | 20 | 20 | 30 | 30 |
| 10. Choloride: $CaCO_3$ mg/l | 7.8 | 8.2 | 8.4 | 7.5 | 9.0 | 8.2 | 7.3 |
| 11. Chromate, (as $Na^3CO_3O_4$) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12. Copper, ppm | .1 | .2 | .1 | .1 | .1 | .2 | .1 |
| 13. Fluoride, ppm | .1 | .2 | .2 | .3 | .3 | .2 | .1 |
| 14. Hardness gm/l (as $CaCO_3$) | 55 | 60 | 35 | 30 | 65 | 35 | 80 |
| 15. Iron, ppm | T | R | A | C | E | S | |
| 16. Lead | Below the Detection Limit (0.02-0.05 micrograms/l) | | | | | | |
| 17. Manganese ppm | T | R | A | C | E | S | |
| 18. Mercury | Below the Detection Limit (.1 mg/l) | | | | | | |
| 19. Nitrogen as Nitrate N-mg/l | .3 | .5 | .3 | .4 | .3 | .2 | .2 |
| 20. Phosphate mg/l | .30 | .20 | .14 | .20 | .20 | .20 | .20 |
| 21. Silica mg/l (as $SiO_2$) | 6 | 8 | 7 | 9 | 8 | 7 | 8 |
| 22. Sulfate mg/l | 9.0 | 8.5 | 7 | 10 | 10 | 7 | 9 |
| 23. Suspended solids mg/l | 8 | 5 | 5 | 6 | 5 | 5 | 2 |
| 24. Zinc | T | R | A | C | E | S | |
| MICROBIAL ANALYSIS | | | | | | | |
| 25. Coliform/100 ml Total | -- | -- | -- | -- | -- | -- | -- |
| 26. Coliform Fecal | -- | -- | -- | -- | -- | -- | -- |

TABLE 4. Analysis of Gulpha Gorge Creek water. Values derived from water samples collected during October 1974.

| | STATIONS | | | | | | |
|---|---|---|---|---|---|---|---|
| PHYSICAL PARAMETERS | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 1. Color, Units | 20 | 25 | 55 | 20 | 20 | 25 | 20 |
| 2. Conductivity ohm/cm | 95 | 70 | 55 | 40 | 80 | 55 | 80 |
| 3. Dissolved Oxygen, ppm | 10 | 10 | 9 | 12.5 | 9.5 | 9 | 9 |
| 4. pH | 7.4 | 7.3 | 7.0 | 7.0 | 7.3 | 7.1 | 7.4 |
| 5. Temperature $^{o}C$ | 17 | 17 | 18 | 17.8 | 17.8 | 17.8 | 17.6 |
| 6. Turbidity, F.T.U. | 10 | 15 | 30 | 10 | 10 | 20 | 10 |
| CHEMICAL ANALYSIS | | | | | | | |
| 7. Acidity, mg/m.o. (as $CaCO_3$) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8. Alkalinity, mg/l (as $CaCO^3$) | 30 | 25 | 20 | 15 | 40 | 35 | 45 |
| 9. Chlorides, NaCl, mg/l | 8.3 | 12.3 | 8.4 | 8.3 | 12.3 | 9.9 | 8.2 |
| 10. Chlorides, $CaCO_3$ mg/l | 7.1 | 10.6 | 7.1 | 7.1 | 10.6 | 8.5 | 7.0 |
| 11. Chromate (as $NaCrO_4$) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12. Copper, ppm | 0.1 | 0.2 | 0.1 | 0.1 | 0.2 | 0.1 | 0.1 |
| 13. Fluoride, ppm | 0.3 | 0.5 | 0.4 | 0.4 | 0.5 | 0.4 | 0.5 |
| 14. Hardness, mg/l (as $CaCO_3$) | 30 | 30 | 25 | 15 | 35 | 20 | 40 |
| 15. Iron, ppm | T | R | A | C | E | S | |
| 16. Lead | Below the Detection Limit (0.002-0.05 micrograms/l) | | | | | | |
| 17. Manganese | T | R | A | C | E | S | |
| 18. Mercury | Below the Detection Limit (.1 ppm) | | | | | | |
| 19. Nitrogen, Nitrate-N, mg/l | 0.8 | 0.9 | 0.7 | 0.9 | 0.6 | 0.1 | 0.1 |
| 20. Phosphate, mg/l (as $PO_4$) | 0.20 | 0.18 | 0.20 | 0.15 | 0.15 | 0.20 | 0.15 |
| 21. Silica, mg/l (as $SiO_2$)$^4$ | 5 | 7 | 6 | 8 | 8 | 6 | 5 |
| 22. Sulfate, mg/l (as $SO_4^7$) | 5 | 5 | 8 | 8 | 8 | 6 | 5 |
| 23. Suspended Solid, mg/l | 7 | 5 | 3 | 6 | 5 | 7 | 5 |
| 24. Zinc | T | R | A | C | E | S | |
| MICROBIAL ANALYSIS | | | | | | | |
| 25. Coliform/100 ml Total | 75 | 70 | 55 | 40 | 80 | 140 | 90 |
| 26. Coliform Fecal | 34 | 18 | 48 | 0 | 25 | 44 | 29 |

TABLE 5. Analysis of Gulpha Gorge Creek water. Values derived from water samples collected in July 1975.

| | STATIONS | | | | | | |
|---|---|---|---|---|---|---|---|
| PHYSICAL PARAMETERS | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 1. Color, Units | 30 | 20 | 25 | 35 | 25 | 60 | 30 |
| 2. Conductivity ohm/cm | 140 | 120 | 75 | 65 | 130 | 80 | 90 |
| 3. Dissolved Oxygen, ppm | 10 | 9 | 12 | 11 | 13 | 11 | 12 |
| 4. pH | 7.3 | 7.2 | 7.0 | 7.2 | 7.3 | 7.2 | 7.2 |
| 5. Temperature, $^{o}C$ | 18.0 | 18.2 | 20.1 | 18.6 | 18.2 | 19.6 | 18.4 |
| 6. Turbidity, F.T.U. | 11 | 14 | 20 | 15 | 15 | 12 | 10 |
| CHEMICAL ANALYSIS | | | | | | | |
| 7. Acidity, mg/ m.o. (as $CaCO_3$) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8. Alkalinity, mg/l (as $CaCO_3$) | 50 | 60 | 40 | 45 | 55 | 35 | 80 |
| 9. Chlorides, NaCl, mg/l | 8.2 | 8.2 | 8.6 | 8.2 | 8.4 | 8.2 | 8.2 |
| 10. Chlorides, $CaCO_3$, mg/l | 7.3 | 7.3 | 7.8 | 7.1 | 7.8 | 7.6 | 7.4 |
| 11. Chromate (as $NaCrO_4$) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12. Copper, ppm | T | R | A | C | E | S | |
| 13. Fluoride, ppm | 0.2 | 0.2 | 0.1 | 0.2 | 0.1 | 0.2 | 0.1 |
| 14. Hardness, mg/l (as $CaCO_3$) | 75 | 80 | 45 | 45 | 85 | 50 | 100 |
| 15. Iron, ppm | 0.1 | 0 | 0 | 0.1 | 0 | 0 | 0 |
| 16. Lead | T | R | A | C | E | S | (.02 Microgram/l) |
| 17. Manganese | T | R | A | C | E | S | |
| 18. Mercury | T | R | A | C | E | S | |
| 19. Nitrogen, Nitrate-N, mg/l | 0.2 | 0.15 | 0.1 | 0.2 | 0.1 | 0.2 | 0.1 |
| 20. Phosphate, mg/l (as $Po_4$ | 0.40 | 0.30 | 0.3 | 0.45 | 0.50 | 0.30 | 0.25 |
| 21. Silica, mg/l (as $SiO_2$) | 6.0 | 7.8 | 6.6 | 8.7 | 8.8 | 7.8 | 10.0 |
| 22. Sulfate, mg/l (as $SO^2$ | 7.0 | 8.2 | 7.0 | 7.9 | 10.0 | 7.8 | 10.0 |
| 23. Suspended Solid, mg/l | 7 | 5 | 6 | 6 | 6 | 4 | 4 |
| 24. Zinc | T | R | A | C | E | S | (.01 mg/l) |
| MICROBIAL ANALYSIS | | | | | | | |
| 25. Coliform/100 ml Total | 350 | 540 | 170 | 540 | 48 | 240 | 25 |
| 26. Coliform Fecal | 44 | 29 | 25 | 19 | 34 | 18 | 6 |

ranged from 3 to 8 mg/l at various sampling stations. It may be observed that lowest values were obtained at station #7 which is located at the uppermost reach of the creek. The higher values were obtained at sampling station #1 which is located just below the camp ground and at station #4 and 6 which are located at downstream of low-water-bridge and at the foot of Large Lake respectively. Keeping in view the geographic location of these sampling stations, slightly higher values are expected. On the whole these values were low.

## COLIFORM BACTERIA

A. Total Coliforms: Most probable number of coliform ranged between 70 to 220 in August 1974. These numbers were 40 to 140, in October 1974. Values for July 1975 were relatively higher between 25 to 540. No definite correlation was observed between total coliform and temperature or pH. One explanation may be the fact that the extent of variations in temperature and pH were too small to significantly influence the total count. On the other hand, average total count of coliform was quite low. Such low coliform count does not necessarily indicate any specific pollution possibility.

B. Fecal Coliform: Incidence of fecal coliforms was very low. Their MPN varied from 10 to 44 per 100 ml. Whereas the presence of fecal coliform indicates fecal contamination, the coliforms are reported to be almost always found in surface water in small numbers.

These values suggest that camping, hiking or other activities had minimal affect in the creek water. It may be observed that whereas human element did not disturb the ecosystem of the creek, the creek water did not seem to be a threat to human exposure.

## REFERENCES


ASTM STANDARDS, Part 23, Water: Atmospheric Analysis, 1973.

EDWARDS, P. R. and W. H. EWING. Identification of the Enterobacteriaceae, 3ed. Edition. Burgess Publishing Company, Minneapolis, Minn. 1972.

EWING, W. H. Enterobacteriaceae: Taxonomy and Nomenclature. Center for Disease Control, Atlanta, Georgia, 1966.

HACH CHEMICAL COMPANY, Iowa: Handbook on Water Analysis, 1973.

HANDBOOK for Analytical Quality Control in Water and Waste Water Laboratories, U. S. Environmental Protection Agency-Technology Transfer, June, 1972.

HANDBOOK for Monitoring Industrial Wastewater; U.S. Environmental Protection Agency-Technology Transfer, August, 1973.

KOPP, J. F. and R. C. KRONER. Trace Metals in Waters of the United States. USDI, FWPCA, DPS, Cincinnati, Ohio.

KOSLOW SCIENTIFIC COMPANY, New Jersey. Mercury Trace Kit # 1280; 1972.

MACKETHUN, K. M. and W. M. INGRAM. Biological Associated Problems in Fresh Water Environments; Their Identification, Investigation and Control. FWPCA, U. S. Department of Interior, Washington, D.C.

METHODS for Chemical Analysis of Water and Wastes, FWPCA, 275:1969.

METHODS for Chemical analysis of Water and Wastes, E.P.A., 16020-07/71, 1971.

PHOTOMETRIC METHOD for Water and Waste Water: Sewerage and Industrial Wastes, 31; 1959.

SIMPLIFIED PROCEDURES for Water Examination, Manual M12, APHA, 1964.

STANDARD METHODS for the Examination of Water and Waste Water, 13th Edition APHA, 1971.

STOKER, H. S. Environmental Chemistry: Air and Water Pollution. Scot, Foresman and Company, London. 1972.

U.S. DEPARTMENT OF INTERIOR . Water Quality Criteria: Reprot of the National Technical Advisory Committee to the Secretary of the Interior. FWPCA, Washington, D.C. 1968.

WAGNER, R. H. Environment and Man. W. W. Norton and Company Inc. 1971.

WEINBERG, E. D. Systematic Salmonellosis: a Sequela of Sideremia. Texas Rep. Biol. Medicine., 30:4. 1972.

WEINBERG, E. D. Infectious Diseases Influenced by Trace Element Environment. Ann. N.Y. Acad. Sci. 199:27, 1972.

# BACTERIOLOGICAL INDICATORS AND EVALUATION OF BATHER CONTAMINATION IN FRESHWATER PONDS IN THE CAPE COD NATIONAL SEASHORE[1]

Jesse S. Ortiz, Stephen A. Souza and William L. Levine[2]

## INTRODUCTION

The role water plays in the transmission of disease has been well established. Most of the major water-borne disease epidemics have been due to contamination of drinking water with human or animal feces or urine. Amongst them, cholera (14,16), typhoid fever (Salmonellosis) (21,33,34), Shigellosis (26), Leptospirosis (10), enteropathogenic *E. coli* (25,26), hepatitis (2,18), amoebic encephalitis (4), and possible Polio and various other viral diseases (6,24).

Attention has also been given to the role swimming plays in the transmission of diseases in recreational waters. Although many instances of swimmer infections have been cited, few have been clearly proven through microbiological and epidemiological studies. Some confirmed cases of the role waters used for swimming play in the transmission of disease are: [1] "Swimmer's itch", due to Schistosomes of non-human origin (7); [2] Swimming pool conjunctivitis (3); [3] Swimming pool granuloma (32); [4] "Swimmer's ear", an otitis externa whose major etiological agent is *Pseudomonas aeruginosa* (17); and [5] Skin rash due to *Pseudomonas aeruginosa* (20,22,23); [6] Typhoid fever (34).

One major limitation of recreational water studies is the fact that most infections transmitted through swimming are not usually reported, and can also be transmitted by other means. This problem is evident in all studies done to date, but one well-controlled investigation found a high incidence of eye, ear, nose, and throat infections to account for 50% of all swimming-related ailments, with gastrointestinal complaints accounting for 20%, and skin irritations and other ailments accounting for 30% (31). The swimmers, however, showed no significant difference in illness when comparing high level to low level water pollution. This is in contrast to other epidemiological studies clearly showing that individual cases of disease or the rate of illnesses associated with the use of recreational water is correlated to a given level of pollution as measured by any of several indicators of water quality (5).

Although the coliform group has been used as an indicator of the sanitary quality of water, it has been demonstrated that coliforms can grow and multiply in the environment, in the magnitude of 10 to 40 fold increases within 30 hours of discharge (11,12).

Recent studies have shown that pathogens may be present in waters where there is an absence of coliforms (11,19,29). An outbreak of salmonellosis in Riverside, Calif., was confirmed when *Salmonella* was isolated from the drinking water containing ratios of *Salmonella* to coliforms of 5:0, 1:4, 5:4, and 5:2 (27). Therefore, the logical indicator of water quality would be to demonstrate the presence of actual pathogenic organisms.

The use of fecal coliform and fecal *streptococci* as indicators of water quality have been questioned because of their ubiquitous presence in the environment (1,11,15). Subsequently researchers have been constantly trying to identify a better recreational water quality indicator, because the danger of disease transmission in swimming water is greater when the pathogens are derived from the skin or the upper-respiratory tract. The use of *Pseudomonas* and *Staphylococcus* have been suggested as indicators of bathing water quality (5,13).

*Pseudomonas aeruginosa* has been confirmed as the primary etiological agent of "swimmer's ear" (17), and recently has been incriminated as a causal agent of skin rash in swimmers (20,22,23). *Staphylococcus aureus*, another known pathogen, has also been proposed as an indicator of recreational water quality. *S. aureus* counts in swimming pools show a definite correlation to the bather load on the pool, as they are derived from the nose, throat, and skin of swimmers (13). Although *S. aureus* has been isolated from swimming pools, no definite relationship has yet been established between their presence and the health of the bather.

The sanitary quality of the various freshwater ponds within the Cape Cod National Seashore, Wellfleet, MA., was questioned because of an abnormally high incidence of ear and throat infections within the community during the summer of 1974. This situation led the local physicians (9), to suspect the ponds as the source of infection, because the infections appeared to be related with swimming in the ponds. The purpose of this study was to determine the sanitary quality of these ponds and to determine whether the ponds could be implicated as the source of these infections. The water quality criteria for analyzing the ponds was based on the standard coliform and fecal *streptococci* levels as well as the proposed indicators of water quality previously suggested.

## METHODS AND MATERIALS

### Survey Area

This survey was limited to those fresh water ponds heavily used for swimming within the boundaries of the Cape Cod National Seashore, near and around the towns of Wellfleet and Truro, Mass. (Figure 1). This area is bounded on the South by the town of Eastham, on the North by the town of Truro, on the East by the Atlantic Ocean, and on the West by Cape Cod Bay and Wellfleet Harbor. There are 21 fresh water ponds within the area. However, only the 4 ponds extensively used for swimming were included in this study.

### *Sample Collection and Processing*

The frequency of sampling the ponds was set up to correspond with swimmer use, and condition of the ponds. Water samples were collected three times a week from the following ponds: Dyer Pond, Long Pond, Great Pond (Wellfleet), and Gull Pond.

[1]This work was supported by NPS contract CX-1600-5-0005 and in part by grants from the Towns of Truro and Wellfleet, Massachusetts.

[2]School of Health Sciences, Division of Public Health, and the NPS Cooperative Research Unit, University of Massachusetts, Amherst 01003.

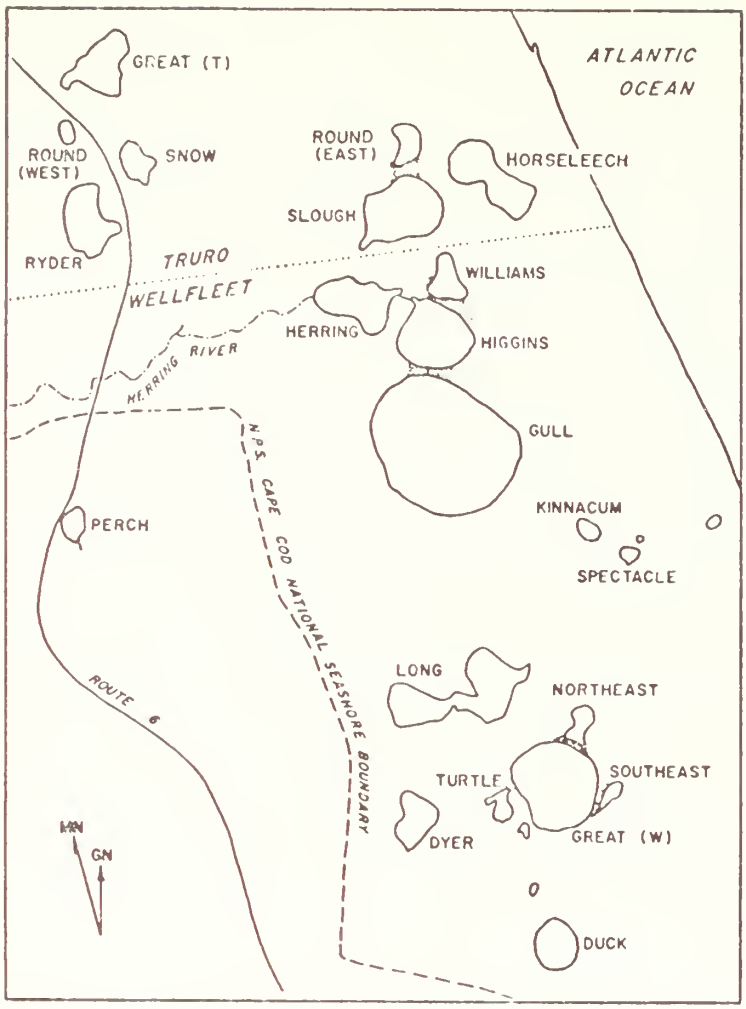



FIGURE 1. The ponds under investigation in Cape Cod National Seashore. Stippled areas indicate freshwater beach deposits, which have secondarily partitioned the original lakes. (Courtesy of M. Soukup.)

Grab samples were taken ten feet from shore in the maximum bathing areas at a depth of 6 to 12 inches between the hours of 10:00 AM and 1:00 PM, the time of peak use. Water temperature and bathing load were noted, as well as the time of the sample collection. Processing of samples was done by the membrane filtration technique according to Standard Methods, 13th Edition (30).

The samples were filtered through the membranes, gridded side up, using two sample volumes of 10 ml and 100 ml. The membrane filters were rinsed twice with 50 ml portions of peptone buffer, and then placed gridded side up on the surface of the appropriate bacteriological medium.

*Bacteriological Methods and Processing of Organisms*

The various bacteriological media employed were prepared according to manufacturer's instructions. Prepared media were stored at 4 degrees C for periods no longer than recommended in the 13th Edition of Standard Methods. Total coliforms were tested on M-Endo L.E.S. agar; fecal coliforms on M-F.C. broth with 1.5% agar added; fecal *Streptococci* on KF agar; *Pseudomonas aeruginosa* in Pseudosel agar and *Staphylococcus aureus* on Vogel-Johnson agar. All samples were incubated according to standard methods.

*Bacteriological Classification of Isolates*

In order to make a complete assessment of bacteria found in the ponds, all plates containing typical colonies of total coliforms, fecal coliforms, fecal *Streptococcus, Pseudomonas* and *Staphylococci* were saved for further classification.

a. Identification of isolates from M-Endo an M-F.C. agar plates were based on the reaction obtained from the following biochemical tests Indole, Methyl red, Voges-Proskauer, Citrate, $H_2S$(triple sugar iron), Urease, Motility, Lysine decarboxylase, Arginine dehydrolase, Ornithine decarboxylase and lactose.

The results from these tests were compared to tables of biochemical reactions for *Enterobactericeae, Aeromonas,* and *Vibrio* (8). These results gave a profile of the various species of bacteri isolated from water samples incubated on M-F.C. and M-Endo agar plates.

b. Identification of isolates from KF agar plates, were based on the reactions obtained from the following biochemical tests: Catalase test; growth in BHI: at $45^0$C; at $10^0$C; in 6.5

NaCl; and in pH 9.6; reduction of Potassium Tellurite ($K_2TeO_2$); Triphenyl Tetrazolium Chloride (TTC); 0.1% Methyl blue milk; Hydrolysis of gelatin and starch; fermentation of: D.Sorbitol; Glycerol; L-Arabinose; Lactose, and hemolysis of 10% horse blood.

c. *Staphylococcus aureus* were confirmed by their ability to coagulate citrated rabbit plasma.

d. *Pseudomonas aeruginosa* were confirmed by the oxidase test, growth on asparagine broth by the woods lamp to determine fluorescence.

## RESULTS

Bacteriological data obtained from the three fresh water ponds (Great, Gull, and Long ponds), utilized by the Town of Wellfleet, MA., as designated public bathing areas, are presented in Tables 1-3. A fourth pond (Dyer Pond) was used as a control of non-public bathing area to show variations due to bather load. The data for Dyer Pond are presented in Table 4.

Examination of data collected shows that the total coliform counts were not excessively high. Gull Pond had a mean total coliform count of 271.0 per 100 ml sample with a standard error of 109.6. The counts were high on a few occasions, but were relatively low on the following days. Great Pond had a mean total coliform count of 32.8 per 100 ml sample with a standard error of 27.1. On only one occasion did Great Pond have an excessively high total coliform count. Long Pond had high background counts on almost all samples with a mean coliform count of 48.4 per 100 ml sample with a standard error of 20.6. Long Pond had only one extremely high count, however, the other counts may have been affected by the background bacterial levels. Dyer Pond had the lowest mean total coliform count of 29.1 per 100 ml sample with a standard error of 19.7.

Using fecal coliforms as an indicator of pollution (Tables 1-4), only Gull Pond would be of questionable sanitary quality. Gull Pond had a mean fecal coliform count of 156.5 per 100 ml sample with a standard error of 86.7. In a few instances, Gull Pond was excessively high, but the counts were reduced significantly by the next day and were not cause for concern. Great Pond was very clean with a mean fecal coliform count of 19.1 per 100 ml sample with a standard error of 15.6. On only one day Great Pond had significantly high fecal coliform counts. Long Pond had the second highest level of fecal coliforms with a mean of 94.9 per 100 ml sample with a standard error of 74.0. Long Pond had only two extremely high counts, but otherwise it was OK. Dyer Pond was significantly lower than the other ponds with a mean fecal coliform count of 2.4 per 100 ml sample with a standard error of 0.96. The lack of background growth along with variations shown between Dyer Pond and the other ponds, makes the fecal coliform test seem to be far superior to the total coliform test. As for the presence of fecal *Streptococci*, Gull Pond, had the highest mean fecal *Streptococcus* level of 71.4 per 100 ml sample with a standard error of 22.4. On several occasions, Gull Pond had extremely high counts that would tend to show that Gull Pond is of poor sanitary quality as a bathing area. Great Pond was consistently low with a mean fecal *Streptococcus* count of 4.3 with a standard error of 1.3. Long Pond also was very good with a mean fecal *Streptococcus* of 11.1 and a standard error of 5.1.

TABLE 1. Bacteriological assessment of individual ponds. Gull Pond.

| Date 1975 | Total Coliform | Fecal Coliform | Fecal Streptococci | Staphylococcus Aureus | Pseudomonas |
|---|---|---|---|---|---|
| 7/2 | 8 | 0 | 1 | | |
| 7/7 | 109 | >2000 | 9 | | |
| 7/8 | 40 | 6 | 3 | | |
| 7/9 | 38 | 38 | 35 | | |
| 7/14 | 80 | 9 | 45 | 55 | - |
| 7/15 | 180 | 140 | 170 | 200 | ++++ |
| 7/16 | 90 | >2000 | 190 | 83 | ++ |
| 7/17 | 170 | 31 | 61 | 70 | ++++ |
| 7/21 | 19 | 3 | 4 | 11 | ++ |
| 7/22 | >2000 | 120 | 36 | 240 | + |
| 7/24 | 7 | 100 | 230 | 153 | + |
| 7/27 | 71 | 25 | 56 | 5 | +++ |
| 7/28 | 1150 | 90* | 350 | 112 | ++ |
| 7/30 | 76 | 26 | 38 | 123 | ++++ |
| 8/4 | >2000 | 16 | 580 | 121 | ++++ |
| 8/6 | >2000 | 31 | 40 | 83 | ++++ |
| 8/11 | 24 | 23 | 11 | 13 | E |
| 8/12 | 21 | 5 | 20 | 11 | +++ |
| 8/13 | 40 | 3 | 58 | 28 | +++ |
| 8/15 | 30 | 16 | 48 | 26 | ++ |
| 8/16 | 90 | 95 | 28 | 14 | ++ |
| 8/19 | 24 | 21 | 77 | 34 | - |
| 8/20 | 13 | 4 | 0 | 0 | - |
| 8/21 | 34 | 26 | 3 | 3 | + |
| 8/22 | 33 | 9 | 10 | 2 | - |
| 8/25 | 10 | 5 | 1 | 4 | - |
| 9/3 | 3 | 0 | 0 | 3 | - |
| 9/4 | 3 | 3 | 2 | 1 | - |
| 9/5 | 0 | 0 | 1 | 175 | - |
| 9/10 | 2 | 0 | 2 | 2 | ++ |
| Mean | 271.0 | 156.5 | 71.4 | 56.3 | |
| Std Error | 109.6 | 86.7 | 22.4 | 12.7 | |

On only one instance did Long Pond have a very high count. Dyer Pond had a rather higher than expected mean fecal *Streptococci* level of 36.2 with a standard error of 24.9. This high mean may be explained when it is shown that on two days there were extremely high counts. The percent of variability in the mean was 68.8% so that the actual pond mean may easily be lower than the sample taken. As for *Staphylococci,* Gull Pond showed the highest mean *Staphylococcus aureus* of 56.3 per 100 ml sample with a standard error of 12.7. On some days Gull Pond was found to be extremely high and above what was considered a dangerous level (100/100ml). Great Pond and Long Pond in contrast were within acceptable limits with *S. aureus* mean counts of 7.8 per 100 ml sample with a standard error of 3.7, and 8.7 with a standard error of 3.9 respectively. Dyer Pond, on the other hand, was excessively low with a mean *S. aureus* count of 0.39 with a standard error of 0.18.

The second non-enteric indicator studied was *Pseudomonas aeruginosa.* The study was done on a qualitative basis due to the diffusion of pigment that interferes with individual colonies, as well as a lack of supportive evidence that each *Pseudomonas* organism will form an individual colony on a membrane filter. Gull Pond follows its usual trend by having the highest percentage of positive samples for *Pseudomonas* with 68%. Great (W), Long, and Dyer ponds had positive percentages of 11.5%, 33.3%, 6.7% respectively. The presence of *Pseudomonas aeruginosa* in the ponds with any regularity, must be cause for concern. Statistically, the frequency of occurrence of *Pseudomonas* at Gull Pond versus the other ponds proved to be significantly higher at Gull with P = .005 level of significance.

## CONFIRMATION OF ISOLATES

Confirmation of the typical green sheen colonies from M-Endo LES agar (BBL) are presented on Table 5. Almost 80% of the typical green colonies confirmed out to be of the coliform group, however, the atypical (background) colonies on the same agar gave almost a 40% false negative.

Confirmation of typical blue pigmented colonies from M-FC (BBL) agar plates gave extremely satisfactory results as shown on Table 7. Approximately 93% of the typical blue colonies confirmed out to be fecal coliforms, using the E.C. test, but 19% of the atypical (background) colonies also were confirmed as fecal coliforms. These results, when compared with the classification of the isolates from M-Endo agar (Table 6) and M-FC agar (Table 8) show that background organisms on these agars may be of significant sanitary value.

TABLE 2. Bacteriological assessment of individual ponds. Great Pond (Wellfleet).

| Date 1975 | Total Coliform | Fecal Coliform | Fecal Streptococci | Staphylococcus Aureus | Pseudomonas |
|---|---|---|---|---|---|
| 7/2 | 0 | 0 | 0 | | |
| 7/7 | 15 | 0 | 0 | | |
| 7/8 | 1 | 0 | 3 | | |
| 7/9 | 3 | 0 | 1 | | |
| 7/14 | 11 | 0 | 2 | 1 | - |
| 7/15 | 0 | 0 | 20 | 1 | - |
| 7/16 | 0 | 0 | 1 | 1 | - |
| 7/21 | 11 | 4 | 1 | 1 | + |
| 7/22 | 25 | 70 | 23 | 20 | - |
| 7/24 | 16 | 3 | 1 | 0 | - |
| 7/27 | 14 | 6 | 12 | 0 | - |
| 7/28 | 790 | 450 | 26 | 52 | - |
| 7/30 | 3 | 4 | 5 | 75 | - |
| 8/4 | 6 | 1 | 1 | 0 | - |
| 8/6 | 0 | 0 | 1 | 2 | - |
| 8/11 | 39 | 14 | 1 | 0 | E |
| 8/12 | 3 | 1 | 2 | 0 | ++++ |
| 8/13 | 0 | 2 | 0 | 1 | + |
| 8/19 | 2 | 0 | 10 | 1 | - |
| 8/20 | 5 | 0 | 2 | 29 | - |
| 8/21 | 1 | 0 | 4 | 4 | - |
| 8/22 | 1 | 0 | 2 | 0 | - |
| 8/25 | 2 | 0 | 0 | 0 | - |
| 9/3 | 1 | 0 | 1 | 0 | - |
| 9/4 | 0 | 0 | 0 | 0 | - |
| 9/5 | 0 | 0 | 1 | 4 | - |
| 9/10 | 2 | 0 | 0 | 3 | - |
| 9/11 | 0 | 0 | 3 | 0 | - |
| Mean | 32.8 | 19.1 | 4.3 | 7.8 | |
| Std Error | 27.1 | 15.6 | 1.3 | 3.7 | |

TABLE 3. Bacteriological assessment of individual ponds. Long Pond.

| Date 1975 | Total Coliform | Fecal Coliform | Fecal Streptococci | Staphylococcus Aureus | Pseudomonas |
|---|---|---|---|---|---|
| 7/2 | 10* | 6 | 3 | | |
| 7/7 | 16* | 1 | 1 | | |
| 7/8 | 22* | 15 | 1 | | |
| 7/9 | 25* | 18 | 14 | | |
| 7/14 | 9* | 9 | 9 | 6 | - |
| 7/15 | 500* | 280 | 10 | 67 | - |
| 7/16 | 190* | >2000 | 15 | 42 | - |
| 7/17 | 40* | 13 | 2 | 2 | + |
| 7/21 | 2* | 0 | 3 | 0 | + |
| 7/22 | 25* | 25 | 17 | 6 | + |
| 7/24 | 240* | 85 | 2 | 0 | - |
| 7/27 | 10* | 3 | 11 | 0 | ++ |
| 7/28 | 19* | 20 | 42 | 8 | + |
| 7/30 | 11 | 3 | 9 | 56 | + |
| 8/4 | 13* | 1 | 8 | 0 | - |
| 8/6 | 110* | 67 | 136 | 5 | - |
| 8/11 | 11* | 3 | 0 | 0 | E |
| 8/12 | 5* | 0 | 0 | 1 | - |
| 8/13 | 3* | 0 | 1 | 3 | - |
| 8/19 | 15 | 2 | 3 | 0 | - |
| 8/25 | 3 | 3 | 1 | 0 | - |
| 9/3 | 1 | 0 | 1 | 0 | - |
| 9/4 | 1 | 0 | 1 | 0 | - |
| 9/5 | 0 | 0 | 1 | 3 | - |
| 9/10 | 0 | 0 | 0 | 0 | - |
| 9/11 | 19 | 9 | 9 | 0 | + |
| Mean | 48.4 | 94.9 | 11.1 | 8.7 | |
| Std Error | 20.6 | 74.0 | 5.1 | 3.9 | |

*Klebsiella, Serratia, Aeromonas,* and *Shigella* were isolated and classified by biochemical tests; with *Klebsiella* being the only one isolated in significant quantity. *Klebsiella* accounted for approximately 22% of the fecal coliforms and 15-22% of the total coliforms isolated off their respective agars.

The relative significance of fecal *Streptococcus* as an indicator of water pollution is questionable when the classification of isolates from KF (BBL) agar are categorized. Almost 50% of the isolates classified as fecal *Streptococcus* were of the subspecies *S. faecalis* var. *liquifaciens* (Table 9). The sanitary significance of fecal *Streptococcus* may be limited due to the presence of this subspecies in such high quantities, since this subsepcies is regularly found in the environment in the absence of fecal contamination.

The confirmation of *Staphylococci* colonies, both typical and atypical is presented on Table 10. Eighty-nine percent of typical colonies were confirmed as coagulase positive *S. aureus*. Eleven percent of typical colonies were coagulase negative and therefore belong to the micrococci group. All atypical colonies were coagulase negative. Vogel-Johnson medium therefore, is quite suitable for the isolation of *S. aureus* from natural swimming waters, because of its high specificity.

Confirmation of *Pseudomonas* was quite difficult because the organism produces a diffusible pigment which tends to color other colonies. Only about 60% of isolated colonies proved to be *Pseudomonas aeruginosa*. For this reason it is better to test *Pseudomonas* by the most probable number (MPN) test using asparagine broth.

## DISCUSSION

A study of the sanitary quality of four freshwater ponds on the Cape Cod National Seashore during the Summer of 1975 has raised many questions regarding the validity of the water pollution indicators presently being used. Standards set up for total coliform, fecal coliform and fecal *Streptococci* are based on the assumption that the swimmer will be drinking large quantities of the water in which he is swimming. This is not usually the case, and even if the swimmer does drink some of the water, any infection which he may acquire would manifest itself in gastrointestinal disorders.

Our studies using the above three parameters indicate that the pond(s) bacterial levels are well below the national standard and therefore, quite safe for total body immersion. However, the high degree in false negative results obtained would immediately question the preceding statement. For instance, in the total coliform test almost 40% of the results gave initial false negative conclusions. The fecal coliform test gave 20% false negative and almost 50% of the fecal *Streptococci* belonged to *S. feacalis* var. *liquifaciens*, which is a species frequently found in the environment in the absence of human or animal fecal pollution. We must therefore conclude that the present indicators used in the testing of natural waters for fecal pollution are completely inadequate.

The use of coliforms as indicators of fecal contamination may be valid, but the limits set are not usually supported by local epidemiological data that would specify the significance of

TABLE 4. Bacteriological assessment of individual ponds. Dyer Pond.

| Date 1975 | Total Coliform | Fecal Coliform | Fecal Streptococci | Staphylococcus Aureus | Pseudomonas |
|---|---|---|---|---|---|
| 7/2 | 10 | 0 | 4 | | |
| 7/7 | 0 | 0 | 1 | | |
| 7/9 | 420 | 0 | 520 | | |
| 7/14 | 10 | 2 | 19 | 0 | - |
| 7/15 | 20 | 15 | 130 | 1 | - |
| 7/16 | 20 | 4 | 10 | 1 | - |
| 7/21 | 38 | 15 | 15 | 0 | ++ |
| 7/22 | 7 | 2 | 11 | 0 | - |
| 7/24 | 3 | 0 | 5 | 0 | - |
| 7/27 | 4 | 1 | 11 | 0 | - |
| 7/28 | 21 | 6 | 7 | 0 | - |
| 7/30 | 11 | 3 | 8 | 0 | ND |
| 8/4 | 1 | 0 | 1 | 0 | - |
| 8/11 | 10 | 1 | 4 | 0 | E |
| 8/12 | 1 | 1 | 2 | 0 | - |
| 8/13 | 6 | 0 | 3 | 1 | - |
| 8/25 | 1 | 0 | 4 | 0 | - |
| 9/4 | 3 | 1 | 0 | 0 | - |
| 9/5 | 3 | 1 | 3 | 3 | - |
| 9/10 | 0 | 0 | 0 | 1 | - |
| 9/11 | 24 | 0 | 3 | 0 | - |
| Mean | 29.1 | 2.4 | 36.2 | 0.39 | |
| Std Error | 19.7 | 0.96 | 24.9 | 0.18 | |

TABLE 5. Confirmation of isolates from M-Endo LES ager plates.

| Type of Colony | | Positive | Negative | Total |
|---|---|---|---|---|
| Typical | # | 110 | 30 | 140 |
| (Green Sheen) | % | 79% | 21% | 100% |
| Atypical | # | 28 | 44 | 72 |
| (Background) | % | 39% | 61% | 100% |

TABLE 6. Classification of confirmed coliform isolates from M-Endo LES agar plates.

| Classification | # of Colonies | % of Total |
|---|---|---|
| Typical Colonies | | |
| Enterobacter | 70 | 50.0 |
| Klebsiella | 31 | 22.2 |
| Escherichia | 39 | 27.8 |
| Total | 140 | 100.0% |
| Background Colonies | | |
| Enterobacter | 18 | 25.0 |
| Klebsiella | 11 | 15.4 |
| Escherichia | 14 | 19.4 |
| Serretia | 2 | 2.8 |
| Citrobacter | 4 | 5.6 |
| Unclassified Enterics | 9 | 12.5 |
| Non-Enterobacteriaceae | 14 | 19.4 |
| Total | 72 | 100.0% |

TABLE 7. Confirmation of isolated colonies from M-FC agar plates.

Confirmation of Isolated Colonies
From M-FC Agar Plates

| Type of Colony | | E.C. Positive | E.C. Negative | Total |
|---|---|---|---|---|
| Typical | # | 162 | 12 | 174 |
| Colonies | % | 93.1% | 6.9% | 100% |
| Atypical | # | 5 | 21 | 26 |
| Colonies | % | 19.2% | 80.8% | 100% |

TABLE 8. Classification of isolated colonies* obtained from M-FC agar plates.

| Classification | # of Isolates | % of Total |
|---|---|---|
| Eschrichia | 122 | 61.0 |
| Klebsiella | 43 | 21.5 |
| Enterobacter | 5 | 2.5 |
| Aeromonas | 2 | 1.0 |
| Shigella | 4 | 2.0 |
| Unclassified | 24 | 12.0 |
| Total Isolates | 200 | 100.0% |

* Includes typical and atypical (background) colonies.

TABLE 9. Classification of isolates obtained from K F agar plates.

| Classification | # of Isolates | % of Total |
|---|---|---|
| Streptococcus faecalis | 13 | 15.1 |
| var. liquifaciens | 26 | 30.2 |
| var. zymogenes | 6 | 7.0 |
| Streptococcus durane | 6 | 7.0 |
| Streptococcus faecium | 13 | 15.1 |
| Unclassified* | 22 | 25.6 |
| Total Isolates | 86 | 100.0% |

* Includes 12 catalase positive isolates that are termed micrococci (coagulase negative).

the coliform indicator. Previously it has been brought out that the coliform to pathogen ratio may vary considerably (27), so that standards may be set at a number that is generally accepted as safe in the absence of any supportive epidemiological data.

Due to the natural occurrence of coliforms and fecal *Streptococci* in the environment, it has been suggested that *Pseudomonas* and *Staphylococcus* be used as indicators of bather contamination. *Staphylococcus aureus* was found to have a positive correlation with the number of swimmers using the ponds. Additionally, this test gave a low percentage of false negative and these false negatives were in typical colonies. Thus the error is in the safe side. On the other hand, *Pseudomonas* proved difficult to confirm. In view of our results we feel that *S. aureus* is a much better test as an indicator of bather pollution.

Some of the organisms isolated from the ponds have been shown to be opportunistic pathogens (i.e., *Klebsiella pneumonia, Pseudomonas aeruginosa* and *Serratia)*, while *Shigella* and *S. aureus* are downright pathogens.

The presence of these organisms in the pond is cause for concern. They may not however, present an immediate health hazard because they were isolated in low numbers.

Limnological studies conducted by Drs. M. Soukup and S. Ludlam concomitant with our study showed a significant degree of cultural eutrophication and extensive hypolimnetic oxygen

TABLE 10. Confirmation of isolates from Vogel-Johnson agar.

| Type of Colony | | Coagulase Positive (S. Aureus) | Coagulase | Total |
|---|---|---|---|---|
| Typical | | | | |
| (Black) | # | 160 | 20 | 180 |
| | % | 89 | 11 | 100 |
| Atypical | | | | |
| (Grey) | # | 0 | 78 | 78 |
| | % | 0 | 100 | 100 |

depletion on the ponds (28). If this degree of eutrophication is allowed to continue, the conditions would become ideal to allow multiplication of the above mentioned opportunistic and frank pathogens and they would subsequently become a definite health hazard to the bather.

BIBLIOGRAPHY


1. BACTERIOLOGICAL ANALYSIS OF WATER AND WASTEWATER. 1973. Millipore Corp., Bedford, MA.
2. BRYAN, J. A., J. D. LEHMAN, I. F. SETIADY, and M. H. HATCH. 1974. An outbreak of hepatitis associated with recreational lake water. Amer. J. of Epid. 99:145-154.
3. BURROW, W. 1973. Textbook of Microbiology. 20th Ed. p. 864.
4. BUTTS, C. G. 1966. Primary amoebic meningoencephalitis. New Eng. J. Med. 274: 1473-1476.
5. CABELLI, V. J., M. A. LEVIN, A. P. DUFOUR, and L. J. MCCABE. 1974. The development of criteria for recreational waters. International Symposium on Discharge of Sewage from Sea Outfalls, London. Paper #7:1-10.
6. CHANG, S. L. 1968. Waterborne viral infections and their prevention. Bull. WHO 38:401-414.
7. CORT, W. W. 1950. Studies on *Schistosome* dermatitis. Amer. J. of Hygiene. 52: 251-307.
8. DAVIS, B., R. DULBECCO, H. EISEN, H. GINSBERG, W. WOOD, and M. MCCARTHY. 1973. Microbiology, Second Edit. Harper and Row, Publishers, Inc. Hagerstown, MD.
9. DICKSON, W. A., A.I. M. Medical Center, Wellfleet, MA. Personal Interview June 12, 1975.
10. DIESCH, S. L. and W. F. MCCULLOUGH. 1966. Isolation of Pathogenic *Leptospires* from water used for recreation. Pub. Hlth. Rpt. 81:209.
11. DUTKA, B. J. 1973. Coliforms are an inadequate index of water quality. J. Env. Hlth. 36:39-46.
12. ELIASSEN, R. 1968. Aftergrowth of colifors in estuarine water receiving chlorinated overflow. J. Sanit. Engr., Proc. ASCE. 94:371-380.
13. FAVERO, M. S., C. H. DRAKE, and G. B. RANDALL. 1964. Use of *Staphylococci* as indicators of swimming pool pollution. Pub. Hlth. Rpt. 79:61-70.
14. GANGAROSA, E. J. 1971. The epidemiology of cholera: past and present. Bull. N.Y. Acad. of Med. 47:1140-1142.
15. GELDREICH, E. E. and B. A. KENNER. 1969. Concepts of fecal *Streptococci* in stream pollution. J. Water Pol. Cont. Fed. 41:2, A336-352.
16. HORNICK, R. B., S. I. MUSIC, R. WENZEL, R. CASH, J. P. LIBONATI, M. J. SNYDER, and T. E. WOODWARD. 1971. The Broad Street pump revisited: Response of volunteers to ingested cholera Vibrios. Bull. N.Y. Acad. Med. 47:1181.
17. JONES, E. H. 1965. External otitis, diagnosis and treatment. C. C. Thomas, Publishers. Springfield, Ill.
18. KRUGMAN, S. 1965. Studies on the natural history and prevention of infectious hepatitis. Advances in Hepatology. S. Karger, Publishers. Basel, Switzerland.
19. LEHR, E. and C. JOHNSON. 1954. Water quality of swimming places. Pub. Hlth. Rpt. 69:742-748.
20. MCCAUSLAND, W. J. and P. J. COX. 1975. Pseudomonal infection traced to motel whirlpool. J. Env. Hlth. 37:455-459.
21. MOORE, B. 1954. A survey of beach pollution at a seaside resort. J. of Hygiene. 52:71.
22. MORBIDITY AND MORTALITY. 1975. Center for Disease Control. Atlanta, Ga. Weekly Report. 24:165-167.
23. MORBIDITY AND MORTALITY. 1975. Center for Disease Control. Atlanta, Ga. Weekly Report. 24:350-352.
24. PAUL, J. R. 1955. Epidemiology of poliomyelitis. WHO Monograph Series, #26.
25. REDDICK, R. A. and E. K. AYCOCK. 1971. Water, a vehicle of disease dissemination. J. of S.C. Med. Assn. 56-60.
26. RELLER, L. B., E. J. GANGAROSA, and P. S. BRACHMAN. 1970. Shigellosis in the United States: Five year review of nationwide surveillance, 1964-1968. Amer. J. Epid. 91:161.
27. SELIGMANN, R. and R. REITLER. 1965. Enteropathogens in water with low *E. coli* titer. J. of Amer. Water Wks. Assn. 57:1572-1574.
28. SOUKUP, M. and LUDLAM, S. 1976. An Investigation of the Freshwater Ponds of Cape Cod National Seashore. Institute Man and Environment, U. of Mass. N.P.S. C.R.U. Report #19.
29. SNOW, J. 1965. Snow on Cholera, Being a reprint of two papers. Hafner Publishing Company. New York, N.Y. (Originally published, 1936).
30. STANDARD METHODS FOR THE EXAMINATION OF WATER AND WASTEWATER. 1971. 13th Ed. APHA Publishers.
31. STEVENSON, A. H. 1953. Studies of bathing water quality and health. Amer. J. of Publ. Hlth. 43:529-538.
32. SWIFT, S. and H. COHEN. 1962. Granuloma of the skin due to *Mycobacterium baimei* after abrasion from a fish tank. N. Eng. J. Med. 267:1244-1246.
33. WATER QUALITY STANDARDS CRITERIA DIGEST: A COMPILATION OF FEDERAL/STATE CRITERIA ON BACTERIA. 1972. U.S. Environmental Protection Agency.
34. WINSLOW, C. E. A. and D. MORAN. 1928. Bacterial pollution of bathing beach waters in New Haven Harbor. Amer. J. of Hygiene. 8:299.

# WARMING PROCESS IN THE KAWEAH RIVER, SEQUOIA NATIONAL PARK, CALIFORNIA

Dana L. Abell[1]

## INTRODUCTION

Water has been diverted from the Kaweah River in Sequoia National Park for power production for nearly 74 years. Water is taken by means of low barriers on two forks of the river four and one-half miles inside of the park and is carried in open hillside ditches and a lone siphon to the Southern California Edison Company's Kaweah Power-house No. 3 at the park line. Despite the small size of this powerhouse (26,000 kw) the facility is capable of taking all the water from the river for as much as five months out of the year. The capacity of the main ditch is 90 cubic feet per second (cfs.) as opposed to an average flow of 102 cfs. in the river.

For the first 50 years of the diversion the river carried only a trickle through all of the dry months. A new special use permit negotiated in 1963 brought minimum flow releases totaling 14 cfs. to the channel on the four driest months of the year (September through December). Slightly higher levels were agreed upon during the peak rec-reation season, and approximately twice as high a discharge (30 cfs.) was obtained during the spring spawning season for trout. These flows brought restoration of considerable permanent aquatic habi-tat but they are still only equivalent to the lowest flows of historic record for the respective seasons. Thus, there is a growing feeling outside the utili-ty itself that impact of this prolonged minimal flow may be excessive, given the stated purposes of the park and of the Park Service. The park ante-dates the diversion by 23 years. The most recent (1973) authorization by Congress for the permit carries specific instructions to the service to re-port no later than 1983 on the nature and extent of those impacts.

First attention has been given to temperature out of concern for a resident population of rain-bow trout which presumably carries some genetic material from a strain that was native to the river. Temperatures do reach critical levels for rainbow trout (72-76°F) in the lower mile and a half of the river. A belief that temperature will vary here in inverse proportion to discharge (Brown 1969) has guided thinking in this case. Work on streams in Europe, most of which have very low gradients, sug-gests however that streams remain in some kind of equilibrium with their surroundings regardless of discharge (Macan 1958, 1962). This normally means that temperature in a stream increases logarithmi-cally with distance from the source (Schmitz and Volkert 1959; Hynes 1970). The ongoing study of the Kaweah offers an opportunity to examine this apparent conflict.

The bulk of the data underlying this report were obtained by National Park Service personnel, including me, using Ryan Submersible thermometers at nine stations in and just above the diverted sections. I have extended the study under contract to the park and have continued working on it inde-pendently since then. The Park Service is also continuing the work. Thanks are extended to Maurice Zardus, Fish and Wildlife Specialist at Sequoia and Kings Canyon, and to Robert Brown and Norman Alstott of the Southern California Edison Company for their contributions to the study.

## TYPICAL WARMING PATTERNS

Rivers in the southern Sierra normally warm at a rate of about half a degree Fahrenheit per mile during the summer but this warming takes place discontinuously based on material in Blod-gett, 1973. The typical pattern is one of long reaches which are temperature stable (less than 0.2 degrees F. gain per mile alternating with shorter warming reaches (1-2 degrees F. per mile). The limit of warming in naturally flowing rivers in this region appears to be close to 2 degrees F per mile, although warming rates as high as 10 degrees per mile can occur below high dams which release deep, cold water to natural channels. Warming rates fall to a more normal 1-2 degrees within one or two miles, however. Diversion ditches for run-of-the-river power plants are usually temperature-stable, so whenever a large percentage of the flow is diverted, return of the water to a natrual channel will bring rapid warming of that water. Typical rates here are in the 4-5 degree F per mile range. This rate also returns to normal within one or two miles.

Southern Sierran rivers present a rather variable picture when reaches which lie in the same altitudinal range as the Kaweah No. 3 diver-sion are compared (Table 1). Like the Kaweah, most of them warm at rates of 1/3 to 1/2 degree per mile during both the snowmelt period (June values in Table 1) and midsummer (August). There is no consistent increase in warming rates when discharges fall to the summer low. In fact, on the Kaweah the reverse appears to be true when a 12 mile reach, from the Middle Fork diversion on out to Three Rivers, is examined. The down-stream temperature station is below two addi-tional river-run power houses. Their influence in cooling the stream is apparently greater when flow is low. The variable responses to de-creased flow suggest that several additional factors are at work. Warming per thousand feet of elevation (the last two columns in Table 1) follows no consistent pattern.

## CONDITIONS IN THE KAWEAH STUDY AREA

Water is taken for Powerhouse Number 3 from both the Middle and Marble forks of the Kaweah (Figure 1). Discharge in the Marble Fork which is about 10% of the total during the low flow period will be included with that of the larger Middle Fork in this report, since less than a half mile of the smaller fork is affected and its influence upon the combined flow is slight. Vegetation in these lower canyons is largely chaparral, but this gives way, close to the river, to an open oak savannah. Riparian vege-tation is scant, so a large percentage of the rocky channel is directly exposed to sunlight, particularly in early summer when the angle of the sun is high. Cliffs and steep hillsides on the southeast side of the river shade parts of the channel later in the summer and shorten the daily warming period. Thus, peak temperatures are as likely in early July, when the snowmelt is still in progress, as during the low-flow periods in August and September, when air tempera-tures tend to be highest. Water temperatures reach 74 to 75 degrees F. near the powerhouse on

[1]The Kaweah Institute, Three Rivers, Calif.93271

TABLE 1. Warming rates in comparable rivers in the Southern Sierra.

| | station elevations | Dif. in altitude | Miles of river | Degrees F. per mile | | Degrees F. per 1,000' el. | |
|---|---|---|---|---|---|---|---|
| | | | | June | August | June | August |
| Kern River | 1,900-700' | 1,100' | 12 | 0.31 | 0.31 | 3.3 | 3.3 |
| Tule River | 2,900-800' | 2,100' | 10 | 0.36 | 1.80 | 1.7 | 5.2 |
| Kaweah River | 2,100-800' | 1,300' | 12 | 0.47 | 0.32 | 4.3 | 2.8 |
| Kings River | 3,000-1,200' | 1,800' | 4 | 0.45 | 0.45 | 1.0 | 1.0 |
| San Joaquin R. | 2,200-1,200' | 1,000' | 7 | loss | loss | loss | loss |
| Merced River | 3,900-1,200' | 2,700' | 20 | 0.27 | 0.45 | 2.0 | 3.3 |

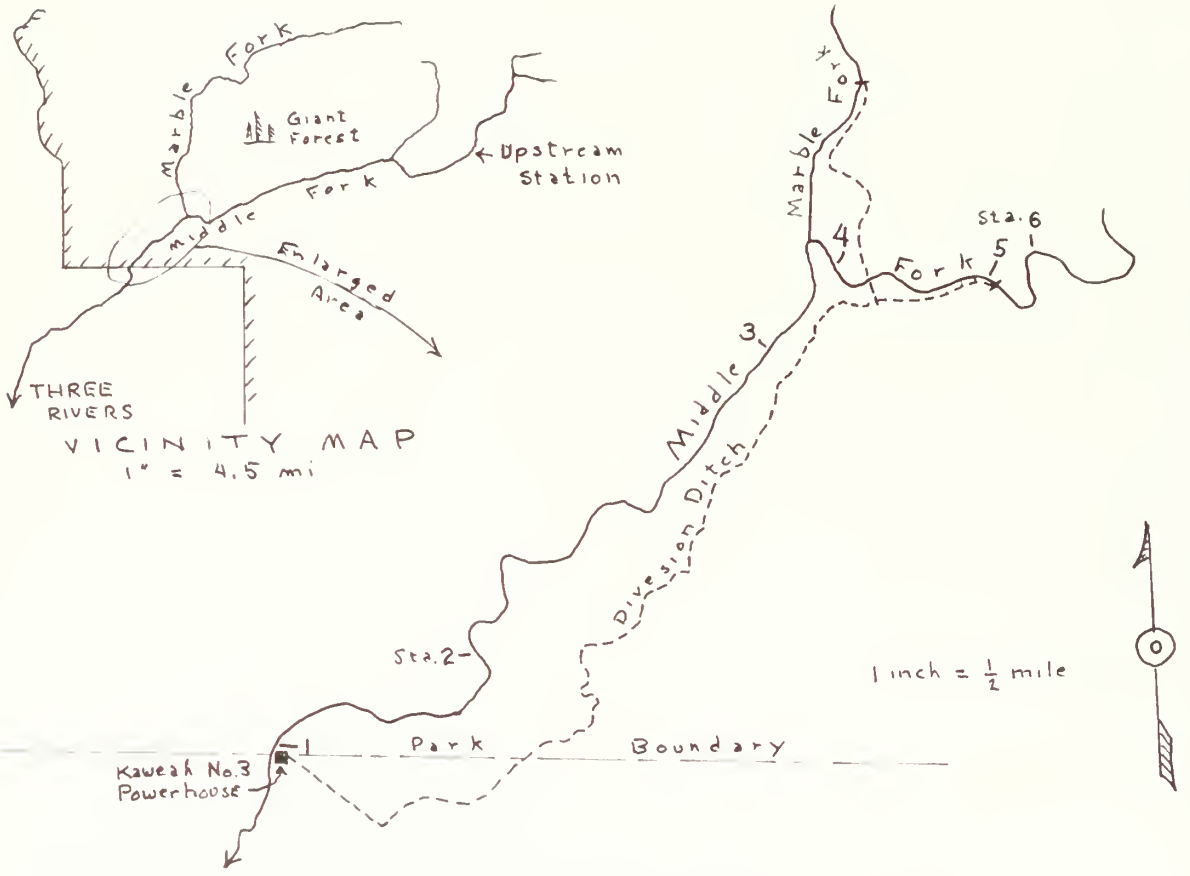



FIGURE 1. Kaweah River hydroelectric project number three study area.

TABLE 2. Stream types in relation to warming.

| | % Pool | % Riffle | Average Width | Character |
|---|---|---|---|---|
| Station 2-3 | 73 | 15 | 30.5 ft. | Stable |
| Station 4-5 | 53 | 34 | 43 | Warming |
| Station 1 to dam | 70 | 19 | 32 | Mixed |

several occasions each summer. Such temperatures are commonly regarded as critical for trout.

The Kaweah is still a relatively steep stream here, with a gradient of 215 feet per mile. Water from snowpack areas at 6,000 to 11,000 feet bring snowmelt peaks in May and June. These are usually well over 1,000 cfs. Annual minimum flows to the diversion points average just under 20 cfs. and typically continue for no more than two to three weeks immediately preceding a natural increase in flow which results from the decline in transpiration in the fall. Minimum flow releases from September 1 to December 31 approximate the lowest flows that have ever been recorded in the Kaweah (14 cfs.). Flow in July and August corresponds to minimum flows of record for these months.

## WARMING RATES IN THE KAWEAH

A value for the warming rate in the Middle Fork above the diversion barrier has been estimated using hand-held thermometer readings taken on five days in the summer of 1976. Each of six readings from River Valley, 12 miles above the dam was simply correlated with temperature at the same time of day on the chart at Station 6, yielding an average temperature gain over the twelve miles of 6 degrees F., or 1/2 degree per mile. This is the same warming rate that was determined for June from USGS data for the 12 miles below the diversion point (Table 1). As noted above, the warming rate drops in this section during August, when other diversions apparently dominate the temperature regime.

Increases in summer water temperature within the 4-1/2 miles of natural channel that is affected by the Kaweah No. 3 diversion are considerably higher than in the longer sections above and below the Middle Fork barrier. Those increases are typically in the five to seven degree range, which is a warming rate of 1.1 to 1.6 degrees F. per mile. This reach shows the same sort of discontinuities that were noted on the larger scale of the USGS data (Figure 2). Most notable is the sharp climb in the curve just below the diversion dam. In this 0.6 mile reach water warms at the abnormally high rate of 4.6 degrees F. per mile. Below this, warming slows down markedly for 2.75 miles (average warming rate 0.7 degrees per mile) and then increases somewhat once again (average, 1.6 degrees per mile) as the river approaches the powerhouse. Other fine-scale discontinuities, including occasional loss of heat in the downstream direction, have been recorded in this section of the Kaweah.

## EFFECTS OF HIGH DISCHARGE ON WARMING RATE

We have three thin leads to an answer for the question of whether an increase in discharge will reduce temperature in the Kaweah. First, Table 1 shows no consistent increase in warming rates as the high discharges of June fall to the low flows of August. Second, a number of specific instances can be given in which marked increases in discharge have brought no reduction in temperature. For example, an increase in flow from 65 to 112 cfs. on July 16 to July 17, 1971 was accompanied not by a decrease in temperature but by a half degree *increase*. The third lead derives from a simple comparison of temperature accrual curves along the affected reach at two very different discharges (Figure 3). The total temperature gain in the natural channel from headworks to powerhouse is the same at 120 cfs. (May 29, 1976) and 14 cfs. (September 9, 1975). The difference is in the shape of the curves, with temperature accrual being a more gradual process at high flow. The stream responds more rapidly at low flow to changes in the conditions which govern warming, but water temperature apparently cannot exceed for very long a level that is governed by ambient conditions. The conditions under which the river between stations four and five serve as a warming reach need to be examined more carefully before it can be claimed that diversion is the controlling factor here.

If diversion does prove to be the factor causing the localized change in warming rates, the differing shapes of the temperature accrual curve can be used to provide a generalized measure of that impact, as shown in Figure 4. The key concept is that there are temperature control points scattered along a stream that are analogous to the controls which govern highway alignment. At these points equilibrium with air temperature will normally be reached. During low flow this will be through a sequential process of rapid warming, then of mixing and storage and occasionally, of temperature loss. At higher flow the warming process is simply spread over the entire distance. Habitat of organisms which have a downstream limit in the range of mean temperatures that are encountered between points A and B will be compressed to the extent that that limit is moved upstream by the change in temperature accrual. A collective measure of this compression effect can be calculated then by averaging the length of horizontal arrows between the two curves or, alternatively by measuring the area between the curves.

## THE NATURE OF WARMING REACHES

Comparison of the major warming reach, Stations 4 through 5, and a temperature stable reach, Stations 2 through 3, provides valuable information on the conditions which favor warming and heat storage (Table 2). In this stream warming apparently takes place in wide shallow riffles more than in pools. The common assumption has been that most warming takes place as water is standing in pools. Pools appear instead to function here as mixing and storage areas. Work that is underway now is strongly supporting this observation. An additional question that needs to be explored is the possibility that net warming in the downstream direction requires a sequence of exposed riffles followed by a reach containing a high percentage of pools. Future studies will explore the relationship between time of flow, heat input, mixing, storage and back-radiation.

## SUMMARY

Diversion of water for power production from the Kaweah River in Sequoia National Park reduces flow in summer to as little as one third of the natural volume and provides an opportunity to test the conflicting assumptions (1) that reduction of flow results in higher water temperatures and (2) that free-flowing streams remain in equilibrium with temperature of the air, whatever their size.

Streams in the southern Sierra normally warm a half a degree Fahrenheit per mile but do so discontinuously. Temperature-stable reaches (warming rates less than 0.2 degrees F. per mile) that are two or three miles in length alternate with much shorter warming reaches. Rates of warming in natural streams appear to exceed 2 degrees per mile only rarely. Higher rates occur where

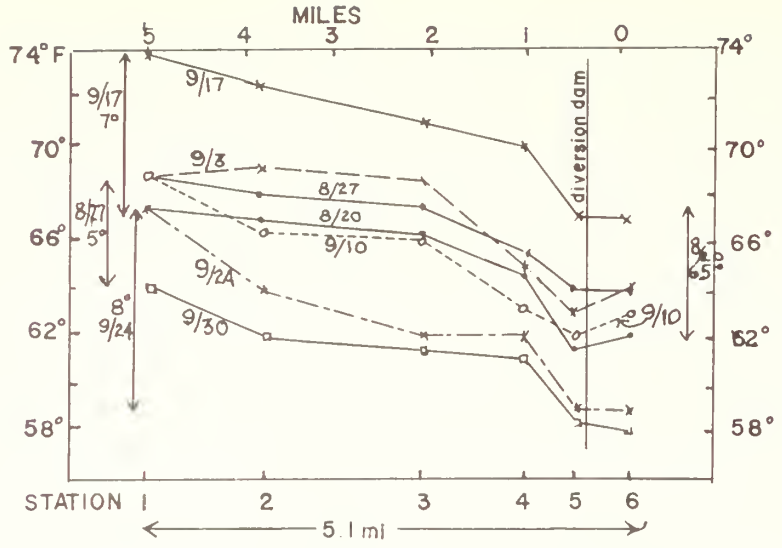



FIGURE 2. Mean water temperatures (high + low/2 on selected dates in 1975.

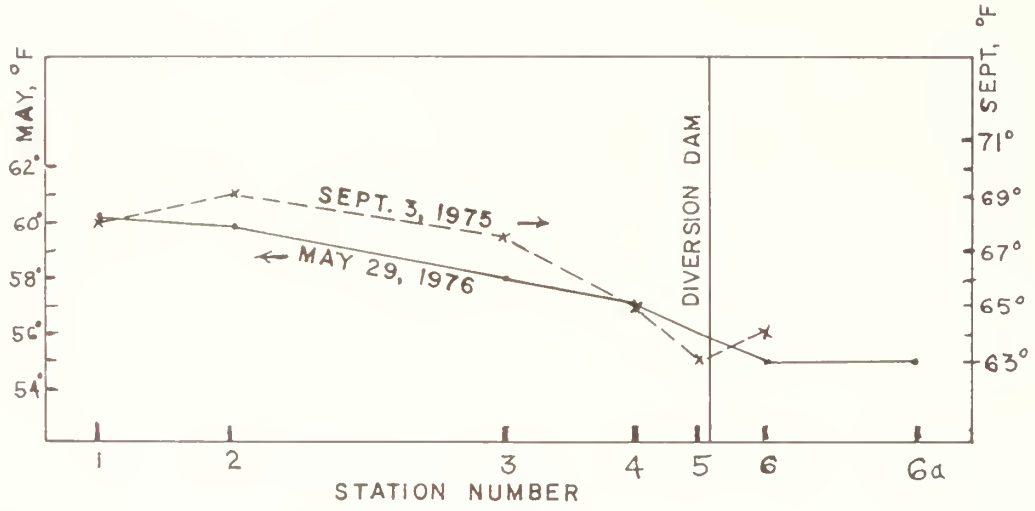



FIGURE 3. Temperature increase under minimum flow (9/3/75 - 20 cfs) and intermediate flow (5/29/76 - 120 cfs) conditions.

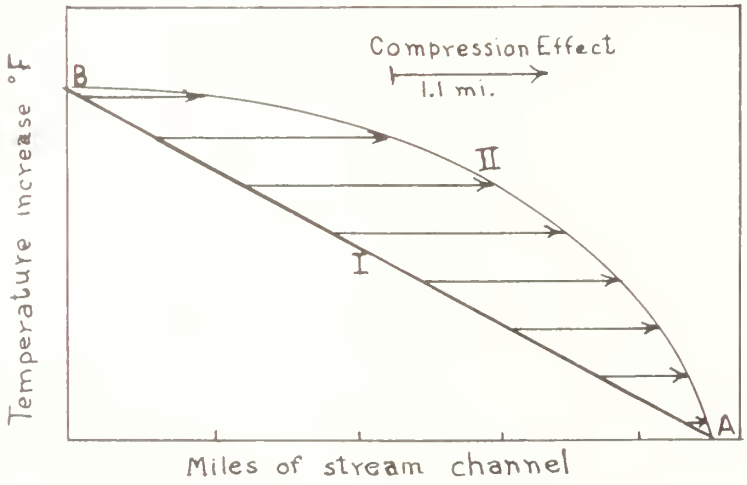



FIGURE 4. Diagrammatic demonstration of the compression effect under minimum flow sonditions (Curve II). Curve I is an idealized curve of temperature accural without the full 90 cfs diversion.

man has altered natural flow, e.g., up to 5 degrees per mile for short distances below river-run powerhouses and up to 10 degrees per mile below high dames. A warming rate of 4.6 degrees per mile (data from 1975 only) in the first half mile below the Kaweah diversion in summer indicates a significant immediate effect, but overall warming in the 4.5 miles to the power house tail race is practically the same at 14 and 120 cfs. Temperature accrual curves for that distance show rapid, then slow warming at low flow but more gradual warming, which never exceeds 2 degrees per mile, at 120 cfs. This is relatively high discharge level. Those same curves show fine-scale discontinuities, including at least one reach of occasional temperature loss.

Correlation of these shorter discontinuities with aerial photographs indicates that heat input is high where broad, shallow riffles predominate and that pools are associated with the temperature-stable reaches. The actual warming process appears to depend upon a favorable relationship between time of flow and the combined factors of heat input, mixing, and low back-radiation.

REFERENCES


BROWN, G. W. 1969. Predicting Temperatures of Small Streams. Water Resources Research, 5(1):69-75.

BLODGETT, J. C. 1973. Water Temperature of California, San Joaquin Subregion. U.S. Geological Survey Open File Report. Menlo Park CA. 92 p.

HYNES, H.B.N. 1970. The ecology of Running Waters. V. Toronto Press, Toronto. 555 p.

MACAN, T. T. 1958. The temperature of a small stony stream. Hydrobiologia 12:89-106.

MACAN, T. T. 1962. Biotic Factors in Running Waters. Schweiz Z. Hydrol. 24:386-407.

SCHMITZ, W. and E. VOKERT. 1959. Die Messung von Mitteltemperaturen auf reaktions-kinetischer Grundlage mit Kreispolarimeter und ihr Anwendung in Klimatologie und Bioekologie, speziel in Forst - und Gewasserkunde. Zeiss Mitt. Fortschrift 1:300-337.

# ACID DRAINAGE TOXICITY AND ASSESSMENT OF SODIUM HYDROXIDE NEUTRALIZATION IN STREAMS OF THE GREAT SMOKY MOUNTAINS

R. C. Mathews[1], J. D. Sinks[2] and E. L. Morgan[2,3]

## INTRODUCTION

Acid drainage has long been recognized as a problem affecting aquatic systems resulting from man's influences, particularly those associated with surface mining and mine refuse. A unique situation exists in the Great Smoky Mountains National Park in that both man induced and natural acid drainage affect streams due to the presence of outcropping mineralized strata.

The Great Smoky Mountain National Park roughly encompasses 800 square miles extending 54 miles east to west and averaging 15 miles north to south. It is characterized by an uninterrupted chain of mountains bisecting the area from the northeastern to the southwestern extremity. Tennessee and North Carolina share a common boundry along this ridge and contain approximately 600 miles of rather cold, swift streams which drain the heavily vegetated slopes within the park. The mineralized formation which is the source of the acid drainage problem is the geologic strata Anakeesta, which extends in a belt from Georgia to Virginia. This mineralized formation is comprised primarily of dark silty and argillaceous rock altered to slate, pyritic phyllite or schist. The argillaceous rock contains small amounts of free iron sulfides which, upon dissolution and oxidation, produce ferrous sulfate and sulfuric acid (King, et al., 1968; Parson, 1958).

Completion of U.S. Highway 441 in 1963 on an overlook near Newfound Gap resulted in intolerable survival conditions for many aquatic organisms downstream of a roadfill containing Anakeesta rock. Decimation of the native brook trout population in Beech Flats Creek was the initial indication that some toxic material was exerting an influence on the stream. Attempts by the U.S. Fish and Wildlife Service to restock brook trout failed on two occasions before the problem was reexamined through electro-shocking studies. These studies revealed that no brook trout or other species of fish were present for at least 8 kilometers downstream from the roadfill. Established fish populations above the roadfill and in the downstream tributaries of Beech Flats Creek showed that components derived from the roadfill material were the agents exerting the observed toxic influences. In 1973, instream survivability tests on fingerling Eastern brook trout (*Salvelinus fontinalis*) resulted in all fish below the roadfill dying within 50 hours, while those above the fill survived (Huckabee et al., 1975). These investigations and routine water analysis, which revealed a depression of the pH from a range of 5.9 to 6.7 to a range of 4.5 to 4.9, indicate that the low pH, although not necessarily the direct cause, is directly related to the absence of fish in Beech Flats Creek downstream of the roadfill.

The purpose of this study was to assess the chemical and toxicological properties of the mineralized components of Anakeesta leachate before and after neutralization. The shovel-nosed Salamander (*Leurognathus marmoratus*), a species native to the upstream portions of Beech Flats Creek. was chosen as the test organism to determine the toxicity of water altered by Anakeesta contact before and after sodium hydroxide neutralization. Information gained from these studies provides a basis for possible Park management strategies in acid stressed streams.

## MATERIALS AND METHODS

Collections of the salamanders for these assays were made above the roadfill in Beech Flats Creek. Anakeesta rock was collected directly from the roadfill and broken up to expose a greater surface area to the test water. In the laboratory, the Anakeesta rock was placed in a 300 gallon tank lined and covered with plastic sheeting. Stream water was subsequently introduced and the leachage was allowed to reach saturation conditions (Figure 1). Temperature control and oxygenation were maintained with a continuous flow coil cooling agitator. Unaltered stream water was also maintained under identical conditions for utilization as acclimation and dilution water.

A series of 96 hour flow-through bioassays utilizing buffered and unbuffered Anakeesta leachate were conducted to determine the effects of neutralization on the chemical and toxicological properties of Anakeesta leachate. Prior to the 96 hour exposures to these solutions, salamanders were acclimated for one week in stream water at 12°C, the temperature of the stream from which they were obtained. In the first series of bioassays, examining the unbuffered solution, three replicate groups of salamanders were each subjected to various concentrations of the Anakeesta leachate via a continuous flow Esvelt serial diluter. After this 96 hour assay, Anakeesta rock was again introduced into a 300 gallon tank of stream water and chemical stabilization allowed to occur. After stabilization, the pH of the Anakeesta leachate was altered to its original value utilizing sodium hydroxide as a neutralizing agent. The neutralized leachate was then delivered to replicate groups of salamanders which had been previously acclimated in unaltered stream water.

During both assessments, salamanders were determined to be dead when all bodily movements ceased and they did not respond to stimulus with a blunt-ended glass rod. Dead salamanders were removed from the test chambers throughout the 96 hour interval. During these bioassays, test solutions were periodically removed from the final distributing chambers for chemical analysis (Tables 1 and 2). Metal analysis using atomic absorption spectrophotometry and chemical determinations was performed according to methods outlined in "Standard Methods".

[1]Tennessee Wildlife Resources Agency, Crossville, Tennessee.

[2]Environmental Biology Research Center, Tennessee Technological Uiniversity, Cookeville, Tennessee.

[3]The authors are indebted to the National Park Service for the shovel-nosed salamanders collected from Beach Flats Creek. Acknowledgment is also due the Fleetguard Corporation without whose assistance water analysis for heavy metals could not have been completed. This study was funded in part by the Aquatic Ecology Funds from the Environmental Biology Research Ceneter, Tennessee Technological University.

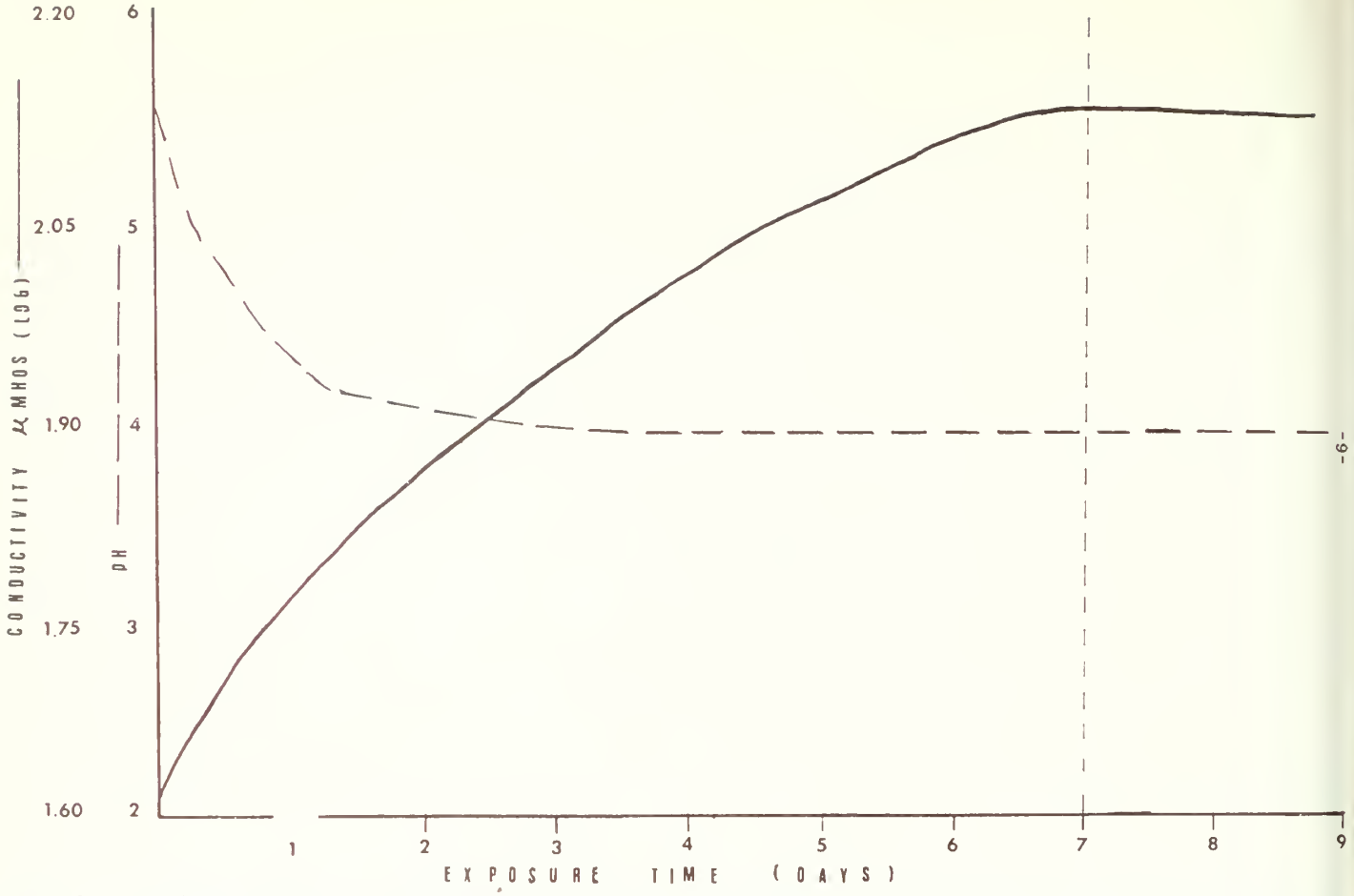



FIGURE 1. Chemical parameters monitored to determine saturation of stream water with Anakeesta leachate.

TABLE 1. Metal analysis of stream water following saturation with Anakeesta during the 96 hour unneutralized leachate bioassay.

| | Mean Concentration (mg/l) | | | | | | |
|---|---|---|---|---|---|---|---|
| | Fe | Cu | Co | Mn | Zn | Al | Pb |
| Unaltered Control Water | 0.10 | 0.12 | 0.01 | 0.05 | 0.01 | 2.30 | 0.04 |
| 100% Anakeesta Leachate | 0.50 | 0.73 | 0.33 | 1.10 | 0.19 | 4.80 | 0.04 |

TABLE 2. Metal analysis of stream water following saturation with Anakeesta during the 96 hour neutralized leachate bioassay.

| | Mean Concentration (mg/1) | | | | | | |
|---|---|---|---|---|---|---|---|
| | Fe | Cu | Co | Mn | Zn | Al | Pb |
| Unaltered Control Water | 0.22 | 0.00 | 0.00 | 0.00 | 0.05 | 0.09 | 0.00 |
| 100% Anakeesta Leachate Before Neutralization | 0.47 | 0.00 | 0.00 | 0.92 | 0.11 | 0.23 | 0.00 |
| 100% Anakeesta Leachate After Neutralization | 0.62 | 0.00 | 0.00 | 0.30 | 0.11 | 0.15 | 0.00 |

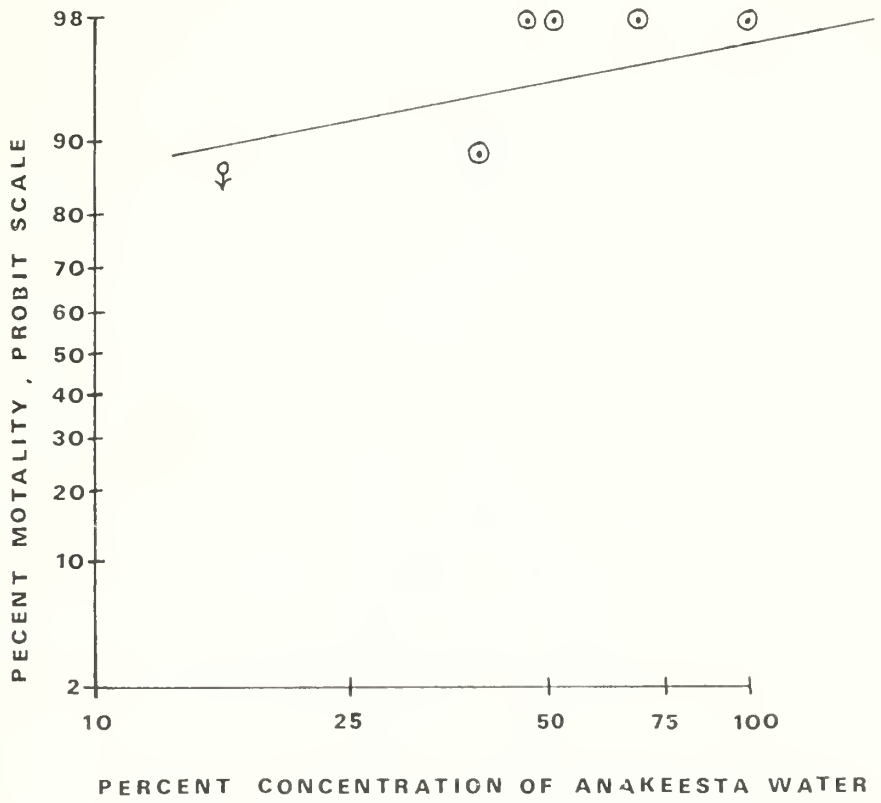



FIGURE 2. Log-probit plot of salamander mortality after 96 hour exposure to Anakeesta leachate.

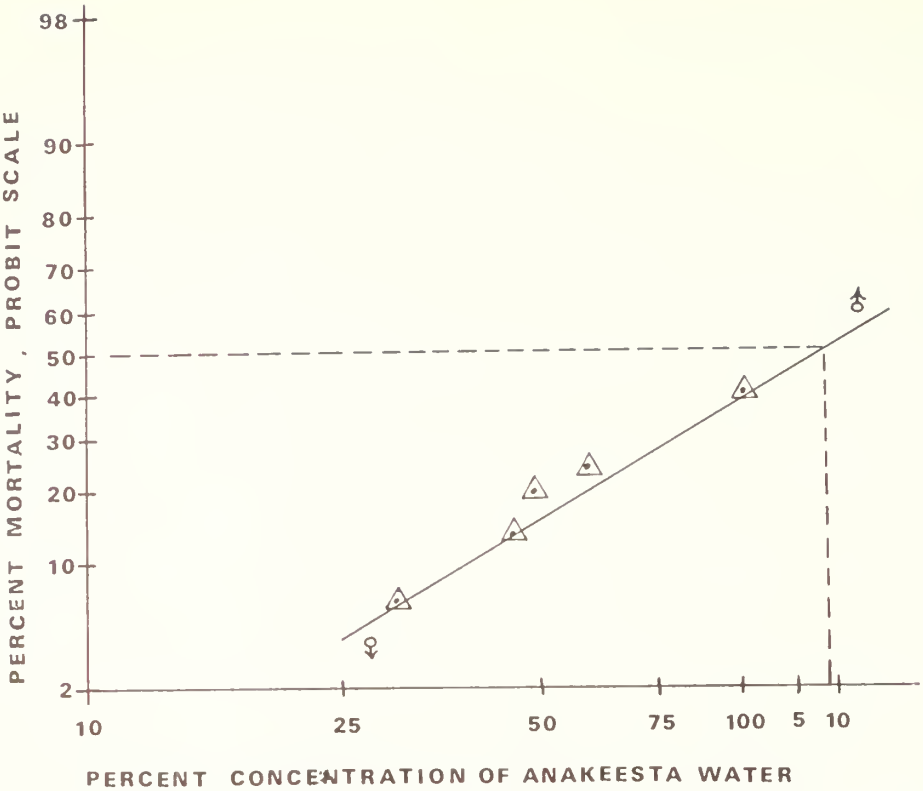



FIGURE 3. Log-probit estimation of 108% LC50 for 96 hour exposure to neutralized Anakeesta leachate.

In order to evaluate the mode of intoxication, the variances of the test organisms tolerance were examined for equality (Bliss, 1935). The equality of variances is shown in the probit analysis by parallelism of the probit regression lines (Finney, 1947). Litchfield and Wilcoxon (1949) provided a rapid test for parallelism by calculating a function known as the slope function ratio. Once parallelism was calculated, a second value, potency ratio, was computed to determine whether significant differences of the LC50 values existed.

## RESULTS

Toxicity generally increased with increasing concentrations of the unbuffered Anakeesta leachate. This was due to the increase in component mineral concentrations, notably zinc, manganese, copper, iron, aluminum and cobalt and a significant decrease in the pH, from 7.4 to 3.9.

Utilizing probit analysis, an LC50 of 53% Anakeesta leachate was estimated for 24 hours of exposure time, 47% for 48 hours of exposure time and 33% for 72 hours of exposure. No LC50 could be estimated for 96 hours of exposure due to the high mortalities observed in even the lowest concentrations (Figure 2). Decreasing LC50's with increasing time of exposure indicates increasing mortality with time due to constituents of the mineralized leachate.

Copper and zinc were both detectable at or above levels reported to be toxic to brook trout (Butler et al., 1973; Bandt, 1946). The reactions of copper and zinc have also been reported as synergistic in their toxicity to several aquatic organisms, among them, trout (Skidmore, 1964). Aluminum's solubility characteristics enable it to enter into the solution around the pH levels created by Anakeesta contact (A. W. A. R. E., 1974). Sinks and Morgan (1975) demonstrated the toxicity of aluminum to a closely related salamander, the Dusky salamander (*Desmognathus fuscus*), but observed fewer mortalities at aluminum levels much higher than those introduced by Anakeesta. The same investigation revealed no mortalities after 24 hours of exposure to pH levels lower than those encountered in the Anakeesta leachate. It seems most likely that mortality due to Anakeesta introduction is the result of the combined effects of low pH and increased concentrations of heavy metals (aluminum, copper and zinc). Gill hyperplasia, a symptom of aluminum, zinc and copper poisoning (Jones, 1964; Aquatic Life Comm., 1975), was readily obvious on all mortalities which occurred during treatment with Anakeesta leachate.

Comparatively lower mortalities occurred during the assessment of the neutralized Anakeesta solution. No LC50 could be estimated for 24 hours of exposure due to the low mortality rates. Reduction of mortality due to neutralization necessitated the projection of LC50's beyond 100% of the buffered leachate. LC50's of 140%, 113% and 108% were calculated for 48, 72 and 96 hours respectively (Figure 3). As with the unbuffered LC50 profile, the decreasing LC50's with increasing exposure time indicate increasing mortality with time due to leachate toxicity. Higher LC50's resulting from neutralization however reflect the greatly reduced mortality rate.

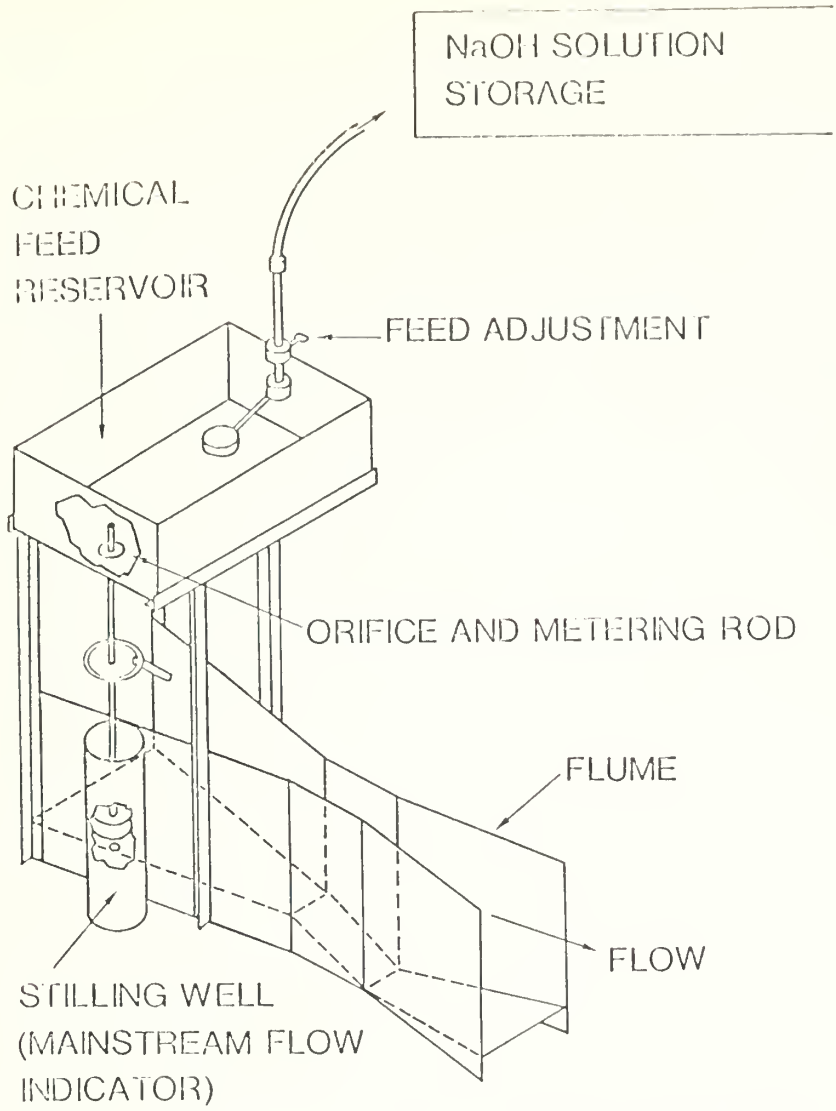



FIGURE 4. Chemical sodium hydroxide feeder for treating acid drainage (from Kennedy, 1973).

Parallelism was established between mortality urves in the neutralized and unneutralized assess- ents ($p > 0.05$), therefore it appears that similar onstituents were responsible for mortality in oth tests. A significant difference ($p > 0.05$) as found between the potency ratios of the two reatments further establishing the reduction in eachate toxicity due to neutralization.

## SUMMARY

Results from this investigation indicate that sodium hydroxide neutralization decreases the toxicity of Anakeesta derived leachate. The toxic properties of this form of acid drainage result presumably from the combination of depressed pH levels and increased heavy metal concentrations. Proper neutralization returns pH levels to a range normally encountered and consequently reduces the heavy metal burden by decreasing solubility and inducing formation of metal complexes. Although original chemical features of the receiving water and complete reduction of its toxic nature were not achieved in laboratory studies, natural recovery processes might be considerably hastened in field applications. The implementation of field neutralization utilizing sodium hydroxide has been accomplished in similar situations and has several advantages over other forms of neutralization. Means of automatically dispensing sodium hydroxide have been devised that are particularly effective for isolated discharges since they require no power and little maintenance, dispense the neutralizing agent at a rate commensurate with stream flow, and are relatively inconspicuous (Figure 4). Further investigations examining the chemical dynamics of the acid leachate previous to and following neutralization and expanded toxicological studies on an array of stream organisms might further identify neutralization as a feasible management alternative in this and similar situations.

## LITERATURE CITED

AQUATIC LIFE ADVISORY COMMITTEE OF THE OHIO RIVER VALLEY WATER SANITATION COMMISSION. 1955. Aquatic life water quality criteria. Sewage Ind. Wastes. 27:321-331.

A.W.A.R.E. 1974. Aquatic aluminum: chemistry, toxicology and environmental prevalence. Associated Water and Air Resources Engineers Inc. Prepared for the Aluminum Assoc. New York. 146 pp.

BANDT, H. J. 1946. Veber verstarkte Schadwirkungen auf Fishe, insbesondere uber erhohte Giftwirkung durch Kimbination von Abswassergiften. Beitr. Wasser Chem. 1:15-23.

BLISS, C. I. 1935. The comparison of dosage - mortality data. Ann. Appl. Biol. 22:307-333.

BUTLER, R. L., E. L. COOPER, J. K. CRAWFORD, C. C. HALES, W. G. KIMMEL, and C. C. WAGNER. 1973. Fish and food organisms in acid mine waters of Pennsylvania. Ecological Research Series, Publication No. EPA-R3-73-032. Office of Research and Monitoring, U.S.E.P.A., Washington, D. C. 158 pp.

FINNEY, D. J. 1947. Probit Analysis. Cambridge Univ. Press, Cambridge, Mass. 256 pp.

HUCKABEE, J. W., C. P. GOODYEAR, and R. D. JONES. 1975. Acid rock in the Great Smokies: unanticipated impact on aquatic biota of road construction in regions of sulfide mineralizations. Trans. Amer. Fish. Soc. 104(4):607-684.

JONES, J. R. 1964. Fish and River Pollution. Butterworths, London. 203 pp.

KENNEDY, J. L. 1973. Sodium hydroxide treatment of acid mine drainage. Office of Research and Monitoring, National Environmental Research Center, U.S.E.P.A. Cincinnati, Ohio. 6 pp.

KING, P. B., R. B. NEWMAN, and J. B. HADLEY. 1968. Geology of Great Smoky Mountains National Park, Tennessee and North Carolina. Geological Survey Paper, No. 587. U.S. Government Printing Office, Washington, D. C. 23 pp.

LITCHFIELD, J. T. and F. WILCOXEN. 1949. A simplified method of evaluating dose-effect experiments. J. Pharmacol. Exp. Ther. 96: 150-151.

PARSONS, J. D. 1958. Literature pertinent to formation of acid mine waters and their effects on the chemistry and fauna of streams. Illinois Academy of Science Trans. 50:49-59.

SINKS, J. D. and E. L. MORGAN. 1975. Assessment of the individual and combined toxic effects of aluminum and low pH to three aquatic organisms. Assoc. Southeastern Biologists Jour. Vol. 23, No. 2.

SKIDMORE, J. F. 1964. Toxicity of zinc compounds to aquatic animals with special reference to fish. Quart. Rev. Biol. 39(3):227-248.

STANDARD METHODS FOR THE EXAMINATION OF WATER AND WASTEWATER. 13th Ed., Amer. Pub. Health Assoc., New York, N.Y., 1966.

# THE CHEMISTRY OF THE COLORADO RIVER AND ITS TRIBUTARIES IN MARBLE AND GRAND CANYONS

Dennis M. Kubly and Gerald A. Cole[1]

## INTRODUCTION

The Colorado River Basin, with a drainage area of some 243,000 square miles in the conterminous United States encompasses a wide range of physiographic and climatic regions. By the time the river reaches Lee's Ferry in northern Arizona, it has drained approximately 107,000 square miles and has received by far the majority of water that is carried south and westward to the Gulf of California (Hely 1969). Present discharges reaching Lee's Ferry are controlled in their magnitude by regulation from Glen Canyon Dam 15 miles upstream. In contrast to the wide-scale ranges in discharge passing this point in pre-dam days, water volumes are now relatively constant. Large seasonal fluctuations have been replaced by diurnal changes in river level, reminiscent of tidal rhythms found in marine shore zones. Ionic concentration, ionic composition, temperature and sediment load, all fluctuating in response to season and discharge prior to the impoundment of Lake Powell, now show relatively little variation (USGS 1922 *et seq.*, 1941 *et seq.*)

Between Lee's Ferry (Mile 0) and the headwaters of Lake Mead, 280 miles downstream, the Colorado flows between the precipitous cliffs of Marble and Grand Canyons. River elevation falls from 3,090 feet to 870 feet, an average gradient of 7.9 feet per mile.

Many tributaries enter the Colorado in this 280-mile stretch. Some have been described in detail, but others have been hardly studied. There has been no more than cursory categorization of the springs and streams on a chemical basis, and little has been said about their relations to the main river.

It is the purpose of this short, descriptive paper to present selected data from the Colorado River and its tributaries from Mile Zero to Lake Mead, classifying the waters and discussing briefly their origins. We have assembled many data from published material, but this report will deal only with those creeks and springs that we have sampled and analyzed (Table 1). Our data were collected on six raft floats during 1975 and 1976. Chronologically, the trips were, in 1975: 22 April to 5 May, 3-12 June, 11-21 August, and 12-24 November. In 1976 there were two research trips, 1-12 March and 5 to 14 August.

## THE COLORADO RIVER

Ionic proportions in the river water at Lee's Ferry were relatively constant during the period of study. They usually showed the following relationships:

$$Ca^{++} > Na^{+} > Mg^{++} > K^{+}, \text{ and } SO_4^{=} > CO_3^{=} > Cl^{-}$$

Only during March 1976, were these proportions changed, with sodium becoming the dominant cation, although the mean values in Table 2 show sodium first. The waters are somewhat difficult to classify; cations approach a "triple" water category comparable to that proposed by Clarke (1924) for situations where the three principal anions are subequal. The Colorado River anions differ somewhat from triple water, approaching a sulfato-carbonate type. The ionic proportions differ little from month to month or as one progresses down the river (Figure 1). The small-scale fluctuations attributable to the effect of the Glen Canyon Dam, have prevailed since the completion of Lake Powell's impoundment according to subsequent chemical analyses of the water at Lee's Ferry gauging station that have been presented in USGS Water-Supply Papers since 1964.

Prior to impoundment, both chemical compositions and concentrations were correlated with river discharge (Iorns et al. 1965). High discharges were associated with comparatively dilute waters, having relatively more calcium and bicarbonate than are found at present. Low discharges produced more concentrated water than is presently found, with cations in proportions very similar to those of today, and with anions even more strongly dominated by sulfate.

Both ionic composition and concentration of the water passing Lee's Ferry today differ significantly from the average chemical features of the world's rivers presented by Livingstone (1963). He summarized the mean ionic proportions in the following sequence:

$$Ca^{++} > Mg^{++} > Na^{+} > K^{+}, \text{ and } CO_3^{=} > SO_4^{=} > Cl^{-}$$

Calcium comprised more than 60% of the cations, and carbonate over 70% of the anions, on a milliequivalent basis.

The Colorado River has a solute content fivefold greater than the reported means for the world's rivers. At Lee's Ferry the TDS mean was 605 mg/liter which was about 0.68 the conductivity expressed as micromhos/cm @ 25°C. Its silica content, however, is below the 13 mg/liter Livingstone considered the mean; it averages roughly 8 mg/liter at Lee's Ferry.

Non-filtrable solids ranged from less than one to 54 mg/liter and the water was remarkably transparent when compared with all river stations downstream. The mean vertical transmittance of light was from 57.8 to 75.4% per meter. This clarity of the water at Lee's Ferry is a post-dam phenomenon.

Other features of the Mile-Zero water, not shown in Table 2, are: annual temperatures from 7-10°C; pH values from 7.4-7.9; free $CO_2$ in excess of 100% saturation; undersaturation with respect to calcite; a phosphate mean of 0.24 mg/liter; and sums of nitrate-N and nitrite-N averaging 0.27 mg/liter. These data typify the water that the springs and tributaries enter downstream.

## THE TRIBUTARIES

Most tributaries joining the main stream in Marble Canyon and Grand Canyon fall in either one of two types described by Hamblin and Rigby (1969). They are, first, major streams having extensive drainage areas and characterized by extensive, deeply entrenched meanders. Such tributaries have relatively low gradients. Some are intermittent, varying seasonally from dry

[1]Department of Zoology, Arizona State University, Tempe.

TABLE 1. Available information on water discharge from tributaries entering the Colorado River between Lee's Ferry (Mile 0) and Pierce's Ferry (Mile 279).

| Tributary | River Mile | Average Discharge (cfs) | | Range |
|---|---|---|---|---|
| Paria River[a] | 0.5 | 30.1 | 0 - | 16,100 |
| Vasey's Paradise[b] | 31.7 | 4.0 | 0.2 - | 10 |
| Little Colorado R.[a] | 61.5 | 205 | 0 - | 24,900 |
| Blue Springs[b] | 61.5 | 223 | 217 - | 232 |
| Clear Creek[b] | 84.1 | 1.6 | 0 - | 3.0 |
| Bright Angel Creek[a] | 87.5 | 35.4 | 10 - | 4,400 |
| Shinumo Creek[b] | 108.5 | 9.1 | 5 - | 15.5 |
| Elves Chasm[b] | 116.5 | 0.2 | 0.1 - | 0.3 |
| Stone Creek[b] | 131.8 | 0.5 | 0 - | 1.2 |
| Tapeats Creek[b] | 133.6 | 100.1 | 51.4 - | 283 |
| Deer Creek[b] | 136.2 | 7.2 | 5.4 - | 8.2 |
| Kanab Creek[a] | 143.5 | 5.7 | 0 - | 4,360 |
| Havasu Creek[b] | 156.7 | 63.8 | 59.3 - | 74.5 |
| Lava Warm Spring[b] | 179.3 | 11.0 | 6 - | 15 |
| Diamond Creek[b] | 225.8 | 1.9 | 1.5 - | 2.2 |
| Travertine Falls[b] | 230.5 | --- | 0.2 | |
| Spencer Creek[b] | 246.0 | 2.7 | 1.1 - | 4.4 |

[a] Information obtained from long-term records presented in U. S. Geological Survey Water-Supply series Surface Water Supply of the United States.

[b] Information based on sporadic records of U. S. Geological Survey as compiled in Johnson and Sanderson (1968).



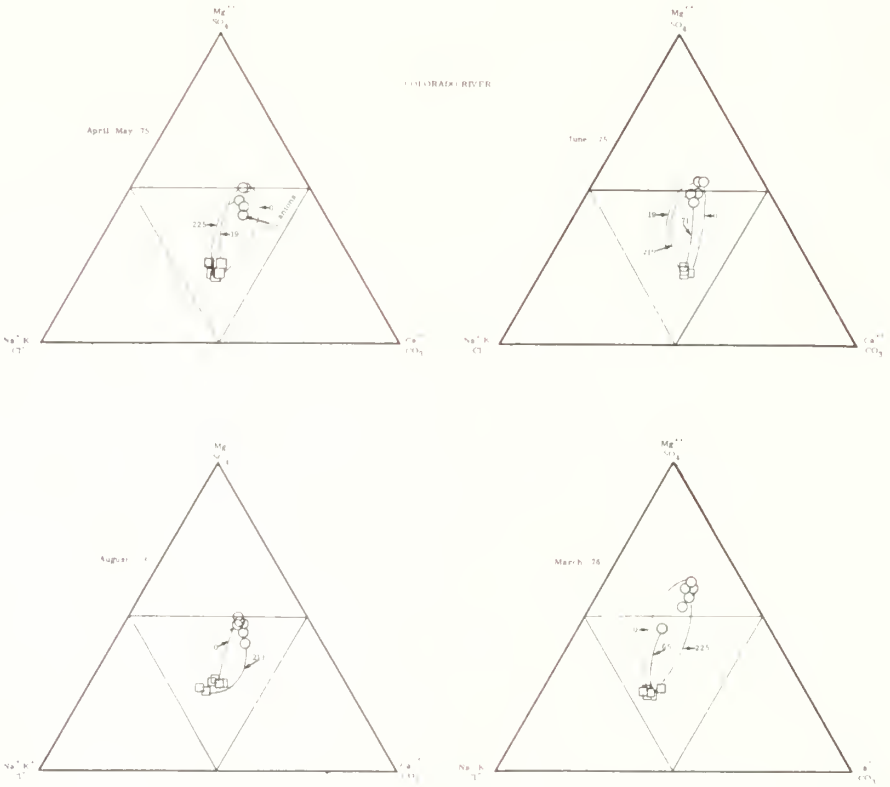


FIGURE 1. Triangular coordinate plots of the principal ions in the Colorado River on four separate raft trips; some mileages indicated. Ordinations show percentages of milliequivalents. Circles = anions; squares = cations.

TABLE 2. Means of principal ions and their sums from the Colorado River at Lee's Ferry and the dolomitic and impure dolomitic tributaries and springs. Values expressed in meq/liter.

| | $Ca^{++}$ | $Mg^{++}$ | $Na^{+}$ | $K^{+}$ | $HCO_3^{-}$ | $SO_4^{=}$ | $Cl^{-}$ | Sum |
|---|---|---|---|---|---|---|---|---|
| Lee's Ferry | 2.88 | 2.05 | 2.94 | 0.10 | 2.81 | 5.26 | 1.46 | 17.50 |
| Dolomitic Waters | | | | | | | | |
| Vasey's Paradise | 1.79 | 1.57 | 0.14 | 0.02 | 3.59 | 0.13 | 0.13 | 7.37 |
| Redwall Moss Sp. | 1.98 | 1.80 | 0.11 | 0.01 | 3.76 | 0.17 | 0.18 | 8.01 |
| Clear Creek | 1.38 | 2.47 | 0.35 | 0.03 | 3.72 | 0.22 | 0.34 | 8.51 |
| Bright Angel | 1.29 | 1.43 | 0.17 | 0.02 | 2.96 | 0.13 | 0.11 | 6.11 |
| Shinumo Creek | 1.43 | 1.28 | 0.19 | 0.02 | 2.99 | 0.12 | 0.12 | 6.15 |
| Stone Creek | 1.32 | 2.93 | 0.43 | 0.02 | 4.39 | 0.30 | 0.34 | 9.73 |
| Tapeats Creek | 1.54 | 1.31 | 0.13 | 0.03 | 3.18 | 0.08 | 0.10 | 6.37 |
| Deer Creek | 1.84 | 1.59 | 0.13 | 0.02 | 3.40 | 0.23 | 0.10 | 7.31 |
| Impure Dolomitic | | | | | | | | |
| Havasu Spring | 7.18 | 4.52 | 1.22 | | 10.19 | 1.25 | 1.50 | 25.86 |
| Havasu Creek | 2.30 | 3.46 | 1.34 | 0.12 | 5.94 | 0.75 | 1.40 | 15.31 |
| Lava Warm Sp. | 3.17 | 6.34 | 3.02 | 0.15 | 10.10 | 0.49 | 2.33 | 25.60 |
| Emory Falls | 1.56 | 3.19 | 0.83 | 0.04 | 5.00 | 0.41 | 1.39 | 12.42 |
| Three Springs | 1.23 | 5.57 | 0.87 | 0.06 | 4.50 | 1.87 | 1.41 | 15.51 |
| Spencer Creek | 1.30 | 4.65 | 1.11 | 0.06 | 6.40 | 0.68 | 1.69 | 15.89 |

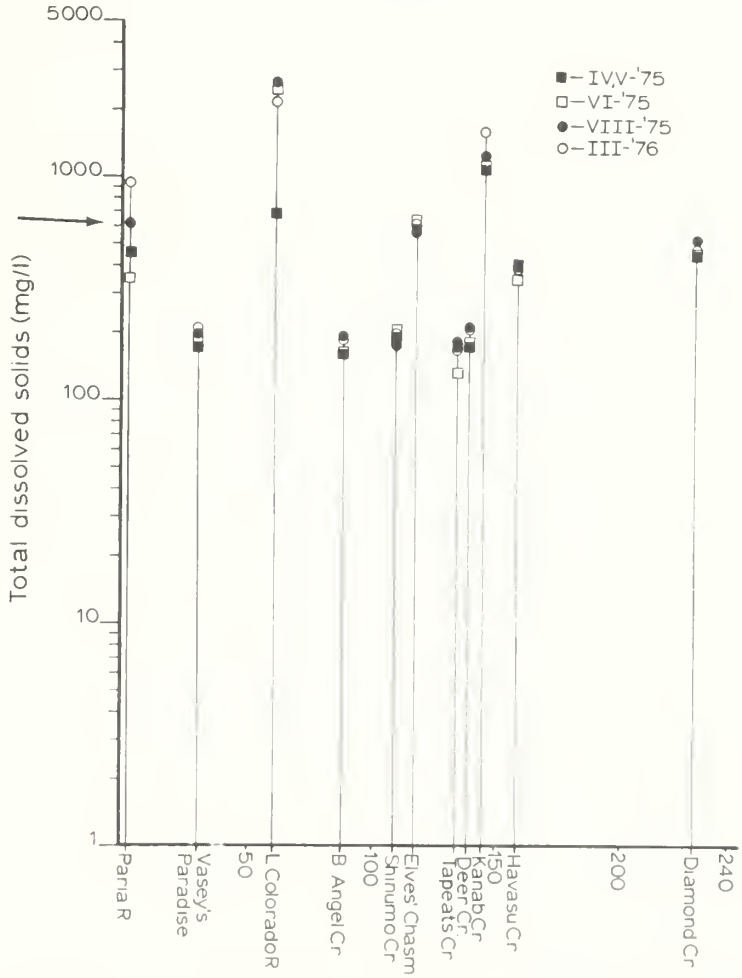



FIGURE 2. Total dissolved solids in 11 tributaries compared with the mean TDS in the Colorado River water at Lee's Ferry (arrow).

beds to swollen floods carrying enormous loads of sediment. The Paria River, Little Colorado River and Kanab Creek are good examples of this category. The second type is a short, relatively straight creek with steep gradients developed by headward erosion as the canyon deepened. Such streams carry clear water, but in times of flooding transport huge boulders to their mouths, producing many of the rapids so common in this section of the Colorado River. Most of the tributaries dealt with here are of this sort.

Table 1 presents available information on discharge rates of most of the tributaries included in this study. While some error is introduced by differences in the number and continuity of records, it is obvious that streams of the first type exhibit large-scale variations in flow compared with those of the second. This information and other discharge data from brooks in this region (Metzger 1961; Twenter 1962; Huntoon 1974) indicate that the average flow from measured streams between Lee's Ferry and Lake Mead probably does not exceed the sum of 750 cfs. This constitutes less than 10% of the mean modern discharge of the river as it passes Lee's Ferry. Thomas et al. (1963) estimated that the annual runoff of the Colorado River at Grand Canyon, Arizona, (Mile 87.4) averages about 95% of the total inflow to Lake Mead, including direct precipitation.

Figure 2 shows the total dissolved solids of 11 influent streams in relation to the average filtrable residue found in the waters of the Colorado River at Lee's Ferry. The figure points out that most waters entering the Colorado are comparatively dilute, serving to ameliorate the salt load contributed by others.

Relative ionic compositions and concentrations of the tributaries are presented in Tables 2, 3, and Figure 3, respectively. The chemistry of these streams is diverse, yet, for the most part, explainable on the basis of the lithology of their drainage systems or of the aquifers from which they arise. Very few of them have compositions like the mainstream Colorado; the Paria River and waters of Elves Chasm are closest in this respect.

### *Dilute Dolomitic Tributaries*

At least eight tributaries, all arising as springs from the Karstic groundwater system of the Kaibab Plateau north and east of the mainstream, may be placed in the category of calcium-magnesium bicarbonate waters (Table 2, Figure 3C). These streams, emerging between Mile 32 and Mile 136.2, include Vasey's Paradise, Red Wall Moss Spring, Clear Creek, Bright Angel Creek, Shinumo Creek, Stone Creek, Tapeats Creek and Deer Creek. Vasey's Paradise (Mile 32) and the nearby Redwall Moss Spring (Mile 34.5) are unusual in that they gush directly from the Redwall limestone forming the canyon walls. The entrance of other springs beneath the river's surface near Mile 32 has been documented by Moore (1925) and Lange (1956).

The fact that these waters are of the strong carbonate type with more or less equal proportions of calcium and magnesium and very low quantities of sulfate, chloride and sodium may be attributed to the geochemical nature of the Paleozoic limestone formations comprising much of the system. Chemical analyses reveal that these so-called limestones, contain much calcitic dolomite (Noble 1922; McKee and Gutschik 1969; Galbraith and Brennan 1970). Specifically, the Kaibab, Redwall and Muav limestones are the major formations in contact with the groundwater sources of these streams.

TABLE 3. Means of the principal ions and their sums from the sodium-bicarbonate, the sulfate, and the saline sodium-chloride waters entering the Colorado River. Values expressed in meq/liter.

| | $Ca^{++}$ | $Mg^{++}$ | $Na^{+}$ | $K^{+}$ | $HCO_3^{-}$ | $SO_4^{=}$ | $Cl^{-}$ | Sum |
|---|---|---|---|---|---|---|---|---|
| $NaHCO_3$ Waters | | | | | | | | |
| Diamond Spring | 2.49 | 1.73 | 0.77 | | 3.73 | 0.31 | 0.68 | 9.71 |
| Diamond Creek | 1.53 | 2.91 | 3.64 | 0.12 | 6.51 | 0.79 | 1.85 | 17.35 |
| Travertine Falls | 0.76 | 2.96 | 10.40 | 0.15 | 8.86 | 1.40 | 4.12 | 28.65 |
| Sulfate Waters | | | | | | | | |
| Paria River | 3.18 | 3.13 | 2.96 | 0.12 | 3.54 | 5.02 | 1.03 | 18.98 |
| Kanab Creek | 7.12 | 6.63 | 1.74 | 0.15 | 2.61 | 13.73 | 0.72 | 32.70 |
| Elves Chasm | 3.24 | 3.80 | 0.99 | 0.08 | 3.03 | 4.36 | 1.24 | 16.74 |
| NaCl Waters | | | | | | | | |
| Blue Sp. (source) | 13.17 | 6.50 | 22.32 | 0.59 | 15.80 | 3.06 | 22.99 | 84.43 |
| Blue Sp. (mouth) | 4.75 | 5.60 | 29.47 | 0.18 | 7.79 | 3.22 | 34.04 | 85.05 |
| Blue Sp. - L. Colo. | 2.64 | 1.15 | 5.39 | 0.11 | 4.92 | 0.62 | 6.43 | 21.26 |
| Pumpkin Sp. | 3.92 | 4.20 | 149.12 | 0.33 | 30.80 | 6.19 | 122.39 | 316.95 |

The dolomitic waters are dilute when compared with all others measured in the Marble Canyon-Grand Canyon system (Figure 2). Their rapid response to high precipitation and snow melt (Huntoon 1974), as evidenced by heightened discharge, implies a relationship between concentration and residence time. However, as Huntoon pointed out, the actual time necessary for any given particle of water to travel through this system may be years, owing to storage in the large Paleozoic aquifers.

The dolomitic streams have the highest Ca/Na, $CO_3$/Cl and $CO_3/SO_4$ ratios, and the lowest monovalent to divalent cation ratios of the entire system discussed here. Furthermore, their silica content is at the bottom of the list, and most of them have low N/P ratios; the latter are the result of both low nitrogen content and high phosphorus levels.

*Impure Dolomitic Waters*

Streams placed in this category are higher in dissolved constituents, have magnesium exceeding calcium, and contain greater amounts of sulfate, chloride and sodium than members of the previous group (Table 2, Figure 3A). All waters in this assemblage, Havasu Creek, Lava Warm Springs, Three Springs, Spencer Creek and Emory Falls, enter the Colorado River from the south rim of the Grand Canyon. They also arise from aquifers in Paleozoic formations, chiefly the Muav limestone.

Havasu Creek, one of the major sources of water supply from the south rim (Cooley 1963), arises as a series of seeps called Havasu Spring some 10 to 12 miles up a narrow canyon in the Supai formation (Moore et al. 1960). Havasu Spring and its outflow serve as an excellent example of solubility differences between calcium and magnesium compounds, the latter being far more soluble. Cole (1975) used data from Hem (1959) to show that the Ca/Mg ratio in Havasu Spring water is 1.59. Source water we have collected and analyzed had a ratio slightly greater than 2.0. By the time these waters reach the mouth of Havasu Creek, significant amounts of calcite have precipiated leaving an average Ca/Mg ratio of 0.65. Visual evidence for this precipitation exists in the blue hue of the water and the travertine deposits in the creek bed. The water is still supersaturated with $CaCO_3$ at the mouth of the stream. The change in Ca/Mg ratio is accompanied by a decrease in the $CO_3$/Cl ratio from 6.8 at the spring to 4.2 at the junction with the Colorado. Havasu Creek has a high silica content (ca. 14.5 mg/liter), which may be derived from the Supai sandstone.

Spencer Creek exits from McKee's (1945) Rampart Cave member of the Muav formation some distance from the Colorado River, while Lava Warm Spring arises from the upper part of the Muav at the mouth of Prospect Valley just above the level of the mainstream (Twenter 1962). We know of no documented evidence for the sources of Three Springs Creek and Emory Falls, but their geographic location and chemical composition suggest a Muav limestone origin.

*Sodium Bicarbonate Waters*

Diamond Creek and Travertine Falls provide examples of waters rare in Arizona--those which can be classified as the sodium bicarbonate type (Table 3, Figure 3A). Diamond Creek has its source in a group of springs exiting from the Muav limestone on the south side of the mainstream (Twenter 1962). The location and extensive travertine deposits of Travertine Falls suggest it also arises from the Muav. The soda nature of these streams is unexpected in light of the other waters emerging from the Muav. In fact, the major source of Diamond Creek, Diamond Spring, produces water of the impure dolomite type (Table 3, Figure 3A). This transition, involving a decrease in Ca/Mg ratios from 1.44 to 0.53, is probably due to a combination of factors, including: differential precipitation of calcium due to loss of $CO_2$, increase in temperature, and evaporation; inclusion of saline waters from the Tapeats Sandstone (Twenter 1962); and possibly, ion-exchange in alluvial sediments forming the channel of Diamond Creek.

Diamond Creek water carries the highest concentration of $SiO_2$ in the entire system described here. It and Travertine Falls consistently show phenolphthalein alkalinity, are extremely oversaturated with calcite and, except for the Little Colorado River and Pumpkin Spring, have the highest monovalent-to-divalent cation ratio.

*Sulfate Waters*

Tributaries having their anionic components dominated by sulfate (Table 3, Figure 3B), include two with the largest drainage systems, the Paria River and Kanab Creek, as well as the least extensive drainage, Elve's Chasm. Both the Paria and the Kanab arise in the high plateau regions of southern Utah and flow to the Colorado as meandering streams with relatively low gradients. Undoubtedly their abundant sulfate is provided by gypsiferous material common in the Jurassic and Triassic sediments which comprise considerable portions of their drainage areas (Gregory and Moore 1931); these deposits are so susceptible to erosion that they have been almost completely stripped from large portions of the Kaibab Plateau (Strahler 1948).

Elve's Chasm is somewhat of an anomaly in terms of expected vs. observed ionic components. This small tributary arises a short distance from the south bank of the mainstream, apparently from Paleozoic limestones, and flows to the Colorado as a series of falls and pools. In this respect, we would expect its waters to be of a dolomitic character, with anions dominated by carbonate rather than sulfate.

Kanab Creek is an example of gypsum water, although contaminated by magnesium (Figure 3B). The other sulfate waters are more like the Colorado River itself (see Figures 1 and 3B) and probably have less impact on its chemical make-up.

The Paria is unique in that it contributes more concentrated water when it is flooding than when its discharge is low; dilute-water springs near its confluence with the Colorado account for this. At times of flooding, however, it brings in much suspended sediment which mixes thoroughly with the Colorado River at a point somewhere more than five miles downstream. The Paria ranks first among the members of the Marble-Grand Canyon system in nitrogen and is very high in phosphorus. Its silica content is tied for third place with the other sulfate waters, Elve's Chasm and Kanab Creek ($\bar{X}$, 11 mg/liter); only Havasu and Diamond creeks carry more silica.

*Saline Sodium Chloride Waters*

The most highly concentrated waters entering the mainstream of the Colorado in the Grand Canyon are Pumpkin Spring and Blue Spring (Table 3, Figure 3B). Sodium and chloride are the dominant ions in these waters.

Pumpkin Spring is a warm spring ($32^0$C) situated near the river's edge at Mile 213. Discharge

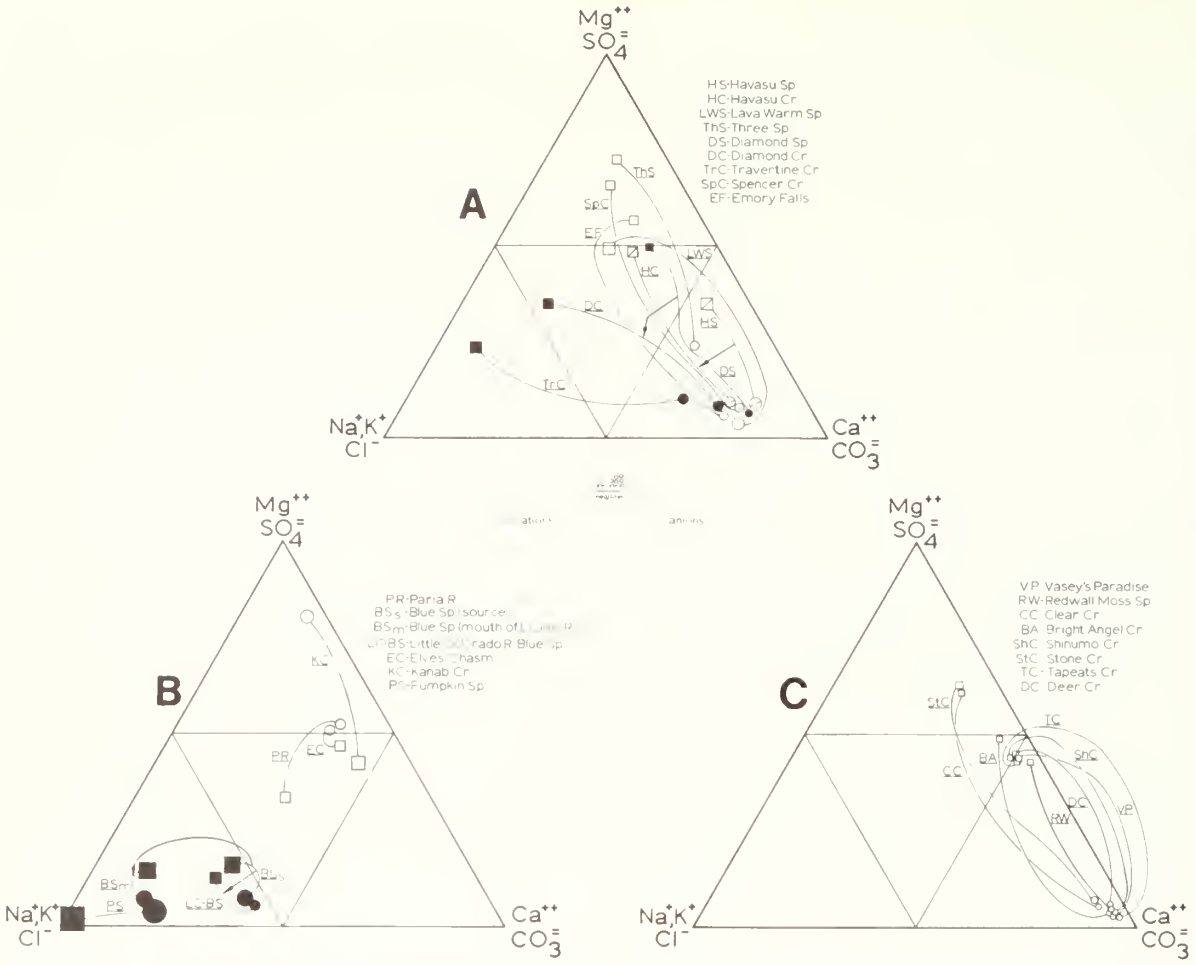



FIGURE 3. Triangular coodinate plots of the major ions in waters entering the Colorado River. Ordinations show percentages of milliequivalents. Circles = anions; squares = cations.

and, therefore, impact on the mainstream from this seep is negligible. Travertine and evaporite deposits have formed a yellow-orange bowl-shaped structure surrounding the water, accounting for the name Pumpkin Bowl. It has a great amount of carbonate also, a fact revealed by violent reaction when concentrated acid is introduced during a Winkler oxygen analysis. Its water is acid because of $CO_2$, easily seen as it bubbles from the underground source.

Blue Spring produces a relatively constant and considerable flow to the Colorado River (Table 3), giving it the infamous distinction of being the largest point-source cortributor of dissolved solids in the region (Blackman et al. 1973). The spring, actually a series of springs and seeps, arises from the Redwall limestone in the canyon of the Little Colorado River from 3 to 13 miles above its confluence with the Colorado River (Johnson and Sanderson 1968). Cooley (1963) estimated that Blue Spring serves as a discharge point for about two-thirds of the groundwater in the aquifer of the 28,000-mile$^2$ Black Mesa hydrologic basin.

Although the Blue Spring series emerges from the Redwall limestone, the major aquifer system discharging through these springs is the Coconino and De Chelly sandstones (Cooley et al. 1969). Fracturing in the Supai formation, ordinarily the major aquifer to this system, allows water movement downward to the Redwall. It is also the Supai formation, with its contained salt beds, which probably acts as the source of the high dissolved-solid content in the waters of the overlying Coconino Sandstone and ultimately of the Blue Spring issue.

Although dominated by sodium and chloride, Blue Springs waters at the origin also contain significant amounts of calcium and carbonate (Table 3, Figure 3B). Following emergence, $CO_2$ release upsets the equilibrium resulting in precipitation of $CaCO_3$; this brings about a shift to waters relatively higher in sodium and chloride (Figure 3B). It should be mentioned, however, that source water diagrammed here is from the main Blue Spring head (Hem 1959), which is augmented to a small degree by input from more saline seeps and springs in the series.

Another modification of Blue Spring water occurs with its dilution by the Little Colorado River during certain times of year. With significant input by the Little Colorado River, Blue Springs waters are carried to the mainstream with approximately the same relative composition as at the source, but with greatly decreased concentrations. This modification, illustrated in Table 3 and Figure 3B, is based on measurements made April, 1975, with the Little Colorado River discharge at approximately 950 cfs.

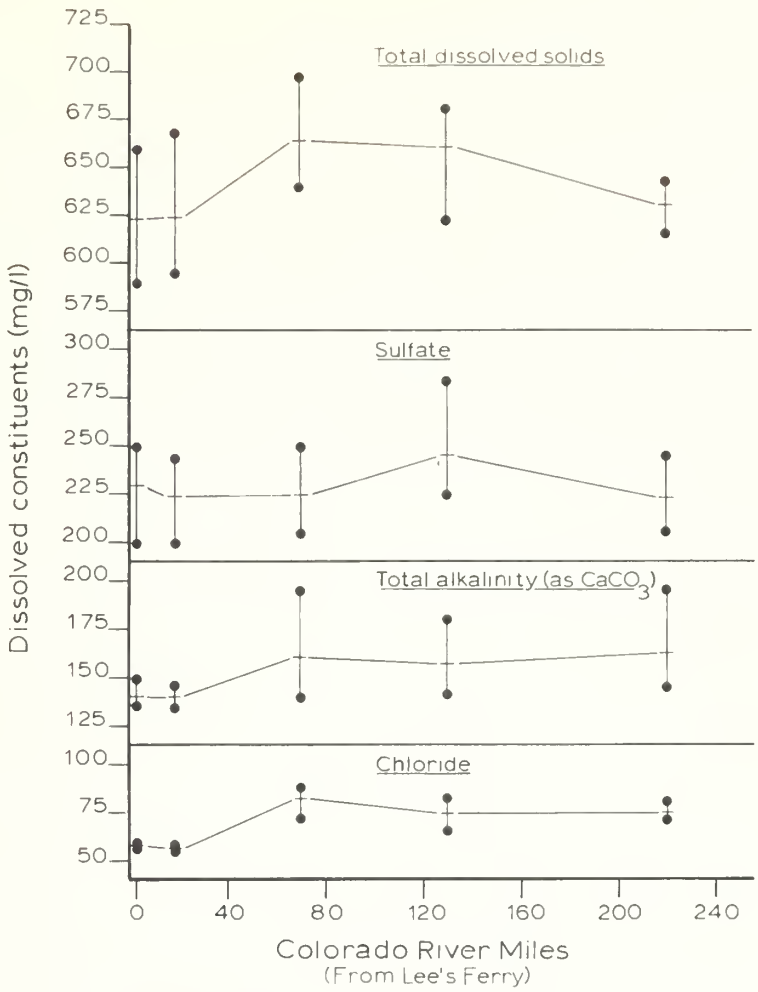



FIGURE 4. Changes in selected water chemistry--anions and total dissolved solids--from Lee's Ferry to Diamond Creek, Colorado River, 1975-76.

Figure 4 shows that there is a rise in total issolved solids in the Colorado River water be- ow Mile 61.5, where the Little Colorado enters. y the time the river reaches Diamond Creek (Mile 26), the salt concentration has diminished be- ause of the dilution effect of subsequent influ- nt streams.

The extreme turbidity introduced by the Little olorado River when flooding modifies the Colora- lo and is not noticeably alleviated by clear ributaries down stream. It reduces the trans- ission to less than 0.001 percent and this pacity persists to the upper waters of Lake Mead.

LITERATURE CITED

BLACKMAN, W. C., JR., J. V. ROUSE, G. R. SCHILLINGER and W. H. SHAEFER, JR. 1973. Mineral pollution in the Colorado River basin. Jour. Wat. Poll. Contr. Fed. 45:1517-1557.

CLARKE, F. W. The data of geochemistry. 5th ed. U. S. Geol. Surv. Bull. 770. 841 pp.

COLE, G. A. 1975. Calcite saturation in Arizona waters. Verh. Internat. Verein. Limnol. 19:1675-1685.

COOLEY, M. E. 1963. Hydrology of the Plateau uplands province. IN Annual report on ground water in Arizona, spring 1962 to spring 1963, by N. D. White and others. Water Resources Rept. 15. Arizona State Land Dept., Phoenix. pp 27-38.

COOLEY, M. E., J. W. HARSHBARGER, J. P. AKERS and W. F. HARDT. 1969. Regional hydrogeology of the Navajo and Hopi Indian Reservations, Arizona, New Mexico, and Utah. U. S. Geol. Surv. Prof. Pap. 521-A. 61 pp.

GALBRAITH, F. W. and D. J. BRENNAN. 1970. Minerals of Arizona. Ariz. Bur. Mines Bull. 181. Univ. Arizona, Tucson. 116 pp.

GREGORY, H. E. and R. G. MOORE. 1931. The Kaiparowits regions. U. S. Geol. Surv. Prof. Pap. 164. 161 pp.

HAMBLIN, W. K. and J. K. RIGBY. 1968. Guidebook to the Colorado River, Part 1: Lee's Ferry to Phantom Ranch in Grand Canyon National Park. Brigham Young Geol. Ser., 15(5):1-84.

HELY, A. G. 1969. Lower Colorado River water supply--its magnitude and distribution. U. S. Geol. Surv. Prof. Pap. 486-D. 54 pp.

HEM, J. D. 1959. Study and interpretation of the chemical characteristics of natural water. U. S. Geol. Water-Supply Pap. 1473. 269 pp.

HUNTOON, P. W. 1974. The karstic groundwater basins of the Kaibab Plateau, Arizona. Water Resources Res. 10:579-590.

IORNS, W. V., C. H. HEMBREE and G. L. OAKLAND. 1965. Water resources of the Upper Colorado River Basin--Technical Report. U. S. Geol. Surv. Prof. Pap. 441. 370 pp.

JOHNSON, P. W. and R. B. SANDERSON. 1968. Spring-flow into the Colorado River--Lee's Ferry to Lake Mead, Arizona. Water Resources Rept. 34. Arizona State Land Dept., Phoenix. 26 pp., 5 fig., 3 tab.

LANGE, A. L. 1956. Cave evolution in Marble gorge of the Colorado River. Plateau 29:12-21.
LIVINGSTON, D. L. 1963. Chemical composition of rivers and lakes, U. S. Geol. Surv. Prof. Pap. 440-G. 64 pp.
MCKEE, E. D. 1945. Stratigraphy and ecology of the Grand Canyon Cambrian, pt. 1 IN Cambrian History of the Grand Canyon region. Carnegie Inst. Washington Pub. 563. pp. 3-168.
MCKEE, E. D. and R. C. GUTSCHICK. 1969. History of the Redwall limestone of northern Arizona. Geol. Soc. Amer., Mem. 114. 726 pp.
METZGER, D. G. 1961. Geology in relation to availability of water along the south rim Grand Canyon National Park, Arizona. U. S. Geo. Surv. Water-Supply Pap. 1475-C. 138 pp.
MOORE, R. C. 1925. Geologic report on the inner gorge of the Grand Canyon of Colorado River. IN (E. C. LaRue, editor) Water Power and Flood Control of Colorado River below Green River, Utah. U. S. Geol. Surv. Water Supply Pap. 556. 125-171.
MOORE, R. T., E. D. WILSON and R. T. O'HAIRE. 1960. Geologic Map of Coconino County, Arizona. Arizona Bur. Mines. Univ. Arizona, Tucson.
NOBLE, L. F. 1922. A section of the Paleozoic formations of the Grand Canyon at the Bass Trail. U. S. Geol. Surv. Prof. Pap. 131-B. pp 23-73.
STRAHLER, A. N. 1948. Geomorphology and structure of the West Kaibab fault zone and Kaibab Plateau, Arizona. Geol. Soc. Amer., Bull. 59:513-540.
THOMAS, H. E. and OTHERS. 1963. Effects of drought in the Colorado River Basin. U. S. Geol. Surv. Prof. Pap. 372-F. 51 pp.
TWENTER, F. R. 1962. Geology and promising areas for ground-water development in the Hualapai Indian Reservation, Arizona. U. S. Geol. Surv. Water-Supply Pap. 1576-A. 38 pp.
U. S. GEOL. SURV. 1922. Surface water supply of the United States, Colorado River Basin. U. S. Geol. Surv. Water-Supply Pap. 549.
U. S. GEOL. SURV. 1941. Quality of surface waters of the United States. Colorado River Basin. U. S. Geol. Surv. Water-Supply Pap. 942.

# A LIMNOLOGICAL SURVEY OF BASS LAKE, POINT REYES NATIONAL SEASHORE, 1976[1]

Carl Widmer[2]

A description of the physical limnological parameters of this small lake serves as a reference for comparative studies of nearby natural lakes and reservoirs and of bodies of freshwater generally residing in regions of equable oceanic climate. The data also serves as a basis for studies of the lake's biology and for future assessment of park use impact. The area has been and continues to be protected from major deteriorative processes.

Previous work consists of a preliminary survey by Strohschein (1972) in which the presence of moderately sized trout in Bass Lake is documented; and a study on landslides by Clague (1969), which proposes a tectonic theory of the formation, during the past 10,000 years, of the small lake district which includes Bass Lake. The lake lies in a small graben a few kilometers west of the San Andreas fault at an elevation of 117 meters above sea level and at 38 degress north latitude. It is fed, at least in part, by two rivulets; and it drains into the Pacific Oean about one kilometer to the west.

The shores of the lake are very steep, and deep water occupies a large part of the total lake area. Riparian trees and macrophytes crowd the shores leaving almost no beach. The small areas of shallow water support a dense submerged macrophytic vegetation rooted in heterogeneously sized gravelly sand. The bottom is covered with a thick, soft layer of black mud containing entrapped gas and emitting the odor of hydrogen sulfide. The lake volume is about $4 \times 10^5$ cubic meters. The maximum depth is 17.5 meters. The surface is about 3 hectares, and the total catchment, about 66 hectares. The large ratio of catchment to lake surface suggests that the ecology of the lake might be quite sensitive to disturbance of the watershed vegetation, which consists largely of chaparral with some small groves of Douglas fir, alders and willows in the moister areas. Water inflow remained quite constant throughout the unusually dry year. No change in lake level was noted.

The water is generally of high transparency with a slate-gray color when viewed from a distance. Secchi disk depths were usually close to ten meters.

Although Bass Lake is very close to the ocean, night frost was observed in the canyons and hollows during winter. Mid-day temperatures ranged from 11 degrees in winter to 22 degrees centigrade in summer.

Bass Lake is of the warm, monomictic type. Temperature-depth profiles (Figure 1) show homothermy in early winter at slightly below 10 degrees. Thermal stratification begins in February, and a well-developed thermocline is evident in April. In late summer the epilimnion approached 22 degress. By the beginning of October cooling had set in, and the water was homothermal to almost 10 meters.

A quantity of approximatey 8,000 carlories per square centimeter of surface was gained by the lake over the warming period of January through August. These months represent times of minimum and maximum heat content, respectively. This value is very low and testifies to the moderate character of the thermal environment.

Dissolved chemical substances were determined using the Hach Direct-Reading Engineers Laboratory DR-EL/2. Electrical conductance (Table 1) indicates a slightly saline water. The salinity can be accounted for to a large extent in terms of sulfates and bicarbonates of calcium and magnesium.

Iron, manganese, hydrogen sulfide, and ammonium ion occurred in the bottom water in appreciable quantities under conditions of relatively low pH and anoxia.

Dissolved oxygen curves (Figure 2) show that this substance was well mixed into the deeper water during homothermy. As the lake became stratified, oxygen was depleted and carbon dioxide increased in the hypolimnion. With the higher concentrations of carbon dioxide lower pH values were observed (Figure 3).

The pH between 3 and 5 meters depth on February 21 reached 8.5, an exceptionally high figure. The Secchi disk reading was 3.3 meters, the shallowest for the study period. Carbon dioxide was also low in this water on that date. These observations indicate the existence of a plankton bloom.

Nitrate nitrogen was present in considerable quantities, 0.32 milligrams per liter at depths 5, 10 and 15 meters in February. By August it had fallen to 0.01 milligrams per liter at 2.5 meters and 0.13 milligrams per liter at 12.5 meters depth. The sparse data suggest that nitrate was removed slowly from the hypolimnion as autumn approached. By November nitrate nitrogen had fallen to negligible amounts in the water column.

Phosphate (Figure 4) and silica (Figure 5) data support those of dissolved oxygen and pH in demonstrating lake turnover during winter. They also show the progressive enrichment of these nutrients in the deep water at the end of summer.

Small clear inflows occur at the north and east sides of Bass Lake. The north inflow contains much more dissolved calcium and magnesium bicarbonates and sulfates, but its composition more closely resembles that of the lake water than the east inflow. The latter is strikingly lower in bicarbonate and considerably higher in silicate (Table 2). Phosphate and nitrate enter the lake through the inflowing water.

Vertical 15 meter hauls with a No. 12 mesh net were made for the collection of the abundant zooplankton. *Chaoborus* spp., *Daphnia pulex* and *Diaptomus tyrelli* are the most obvious representatives of the limnetic zooplankton. Fluctuations in their populations are not great.

---

[1]This work was financed partly by a grant from the University of the Pacific, Stockton, California 95211.

[2]Elbert Covell College, University of the Pacific, Stockton, California 95211.

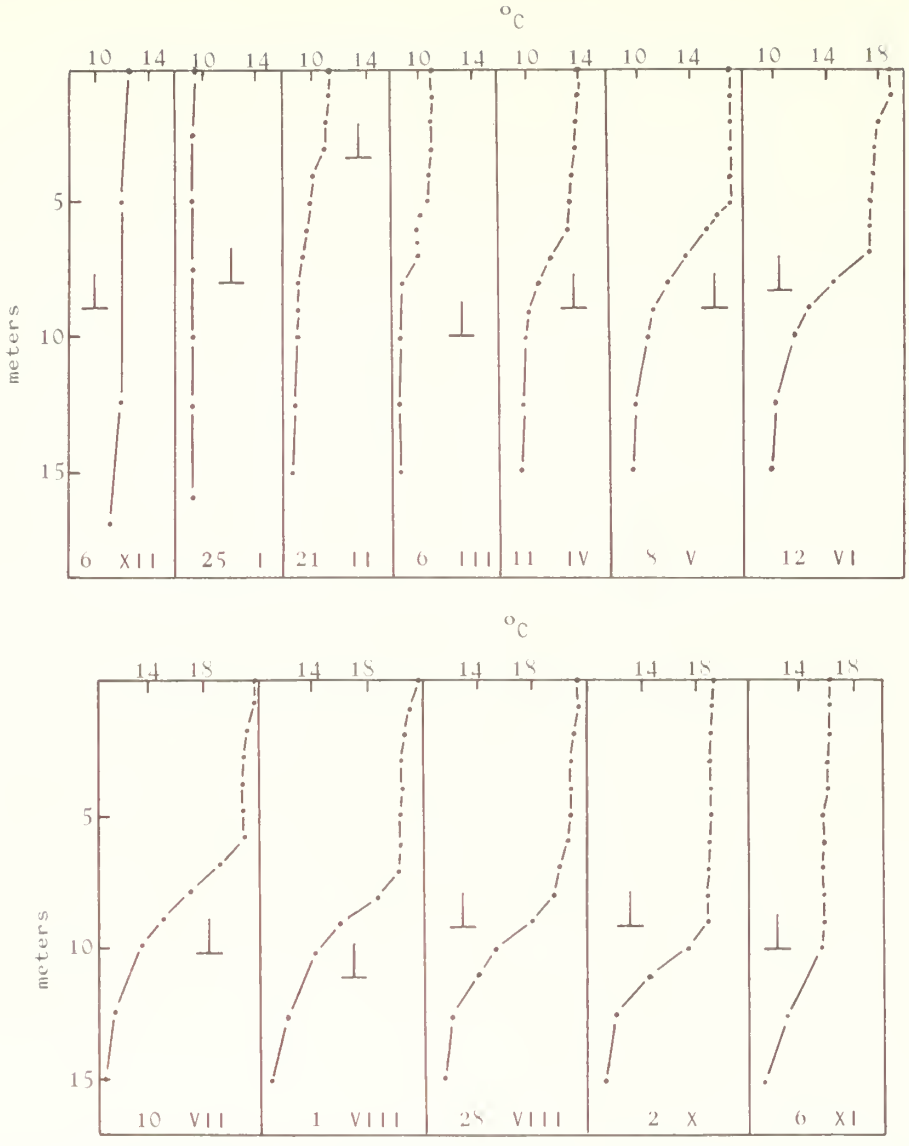



FIGURE 1. Temperature-depth profiles in degrees Celsius. Inverted T marks Secchi disk depth.

TABLE 1. Summary of chemical characteristics in mg per liter.

| | |
|---|---|
| Conductivity (µmhos/cm) | 570 |
| Alkalinity (as $CaCO_3$) | 115 |
| Hardness (total as $CaCO_3$) | 200 |
| Hardness, Calcium (as $CaCO_3$) | 85 |
| Chloride | 30 |
| Sulfate | 140 |
| Fluoride | 0.5 |

Nitrate and copper concentrations were negligible

TABLE 2. Bass Lake influents[a]

| | North Inflow | East Inflow |
|---|---|---|
| Conductivity (µmhos/cm) | 925 | 585 |
| Alkalinity (as $CaCO_3$) | 336 | 50 |
| Hardness (total as $CaCO_3$) | 356 | 200 |
| pH | 8.2 | 7.4 |
| Chloride | 30 | 35 |
| Sulfate | 172 | 186 |
| Silica | 17 | 25 |
| ortho-Phosphate | 0.27 | 0.12 |
| Nitrate-N[b] | 0.12 | - |

[a]Chemical characteristics, 12 June 1976 in mg/l

[b]2 October 1976.

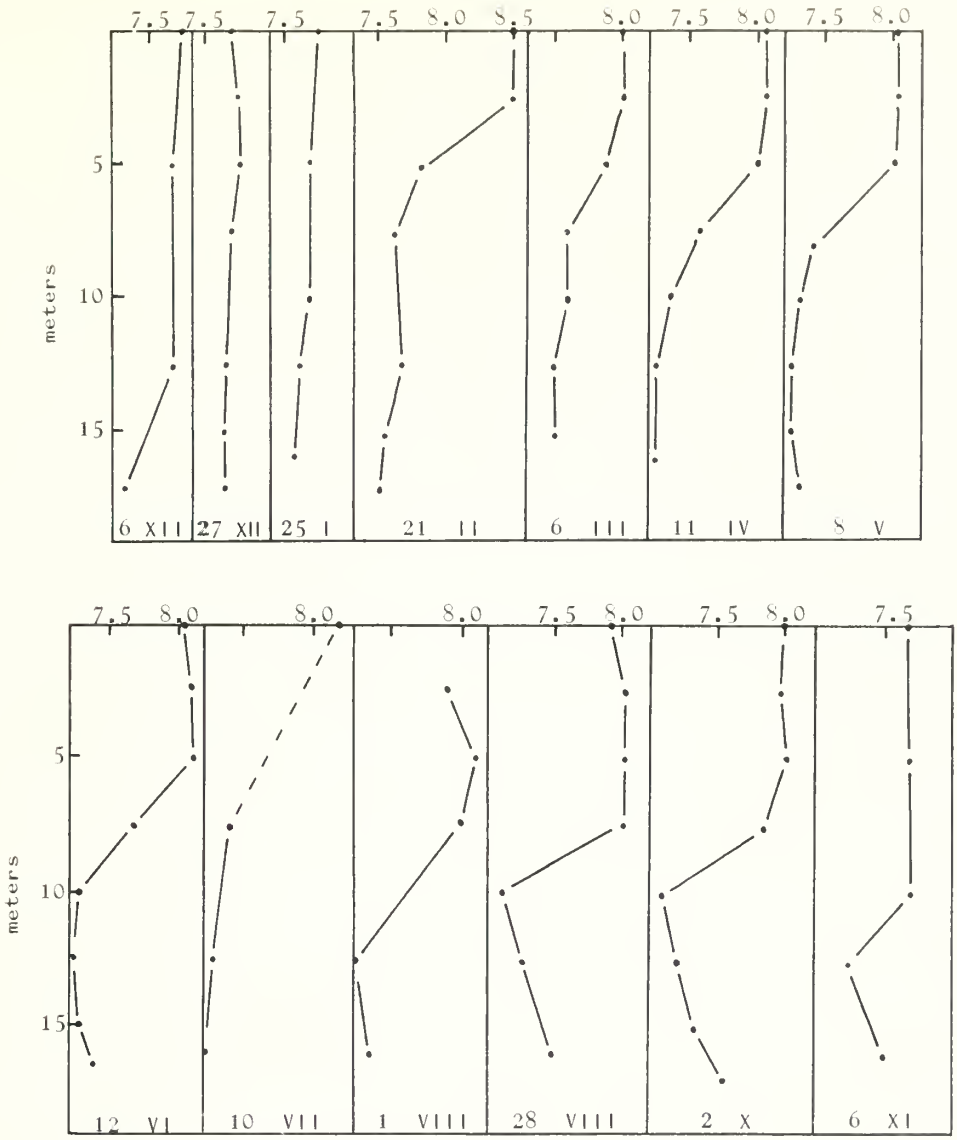



FIGURE 3. pH-depth profiles.

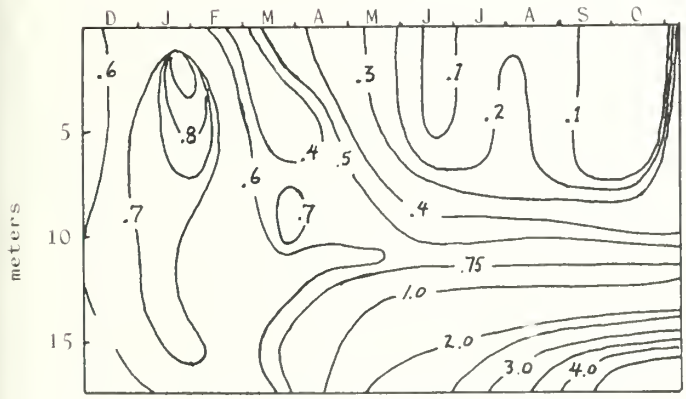



FIGURE 4. Ortho-phosphate isopleths. Concentration (mg/l):depth:month.

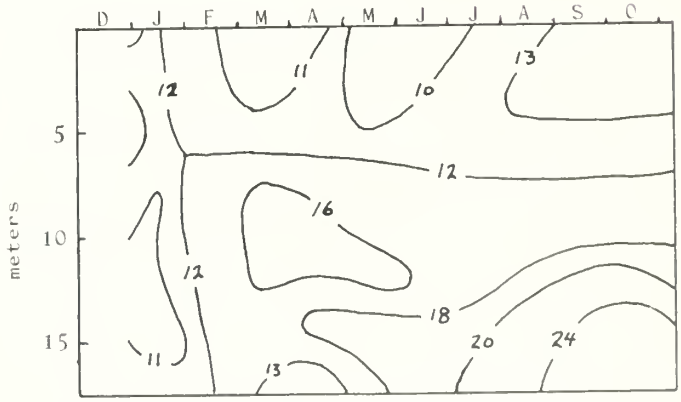



FIGURE 5. Silica isopleths. Concentration (mg/l): depth:month.

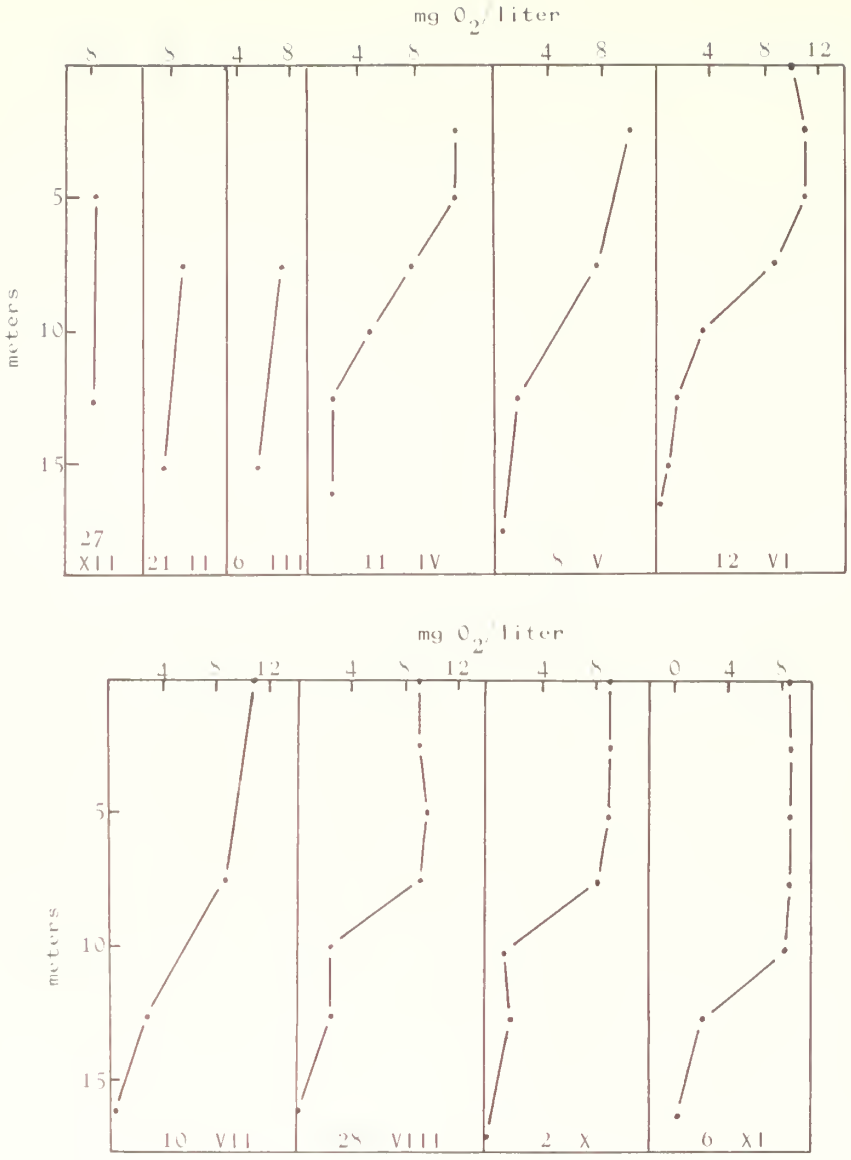



FIGURE 2. Dissolved oxygen-depth profiles (mg/l).

The phytoplankton includes species belonging to the following genera: *Anabaena, Crysomonas, Cymbella, Fragilaria, Oocystis, Schroederia, Sphaerocystis,* and *Staurasturm,* plus *Ceretium hirundinella, Elakatothrix gelatinosa,* and *Pseudokephrion conicum.*

No small planktivorous fish were observed although some catfish were seen on the shallower bottom. As a hypothesis, one might speculate that most of the energy and nutrients which enter the lake support plankton populations which sediment through a highly stable thermocline over the greater part of the year, thereby building up a thick layer of organic mud.

In summary, Bass Lake is a clear, slightly saline, slightly alkaline, warm monomictic lake of markedly equable thermal properties and showing eutrophic characteristics in terms of water chemistry.

ACKNOWLEDGMENTS

The author recognizes the orientation and background material provided by Richard Brown, park research biologist; the identification of zooplankton by Peter J. Richerson; the identification of phytoplankton by Matilde Lopez, and the assistance by Julian Widmer.

BIBLIOGRAPHY

CLAGUE, J. J. 1969. Landslides of Southern Point Reyes National Seashore, Mineral Information Service (California) 22:107-118.

STROHSCHEIN, W. E. 1972. Preliminary Survey and Management Plan for Point Reyes National Seashore Area Waters. Report, California Department of Fish and Game, Region 3.

# THE LIMNOLOGY OF FRESHWATER KETTLE PONDS IN THE CAPE COD NATIONAL SEASHORE

Michael Soukup[1]

One of the most difficult problems in natural resource management is the detection and control of human interference with natural ecosystems and their processes (such as community succession). For example, the rate of succession can be altered to hasten the establishment of a mature natural system. Although this alteration may sometimes be desirable, in the case of aquatic succession resource preservation demands that management's objective be to limit activities which accelerate the natural low rate of succession, thereby speeding the evolution of clear lakes to turbid, weedy ponds, and to eventual obliteration.

A natural pattern of succession commonly follows formation of a lake basin and its watershed. In lakes formed by glaciation, there appears to be an initial period of heavy erosion and leaching of plant nutrients from exposed soils of the watershed. Consequently, algal productivity is high in the lake basin because of the abundant supply of nutrients. As a cover vegetation becomes established, erosion is controlled; without erosion the lake's source of nutrients is ultimately the weathering of minerals, soils, and tills of the watershed, and input from atmospheric sources. The products of weathering are also largely controlled by terrestrial plant communities so that only small amounts usually enter streams and lakes, dictating limited growth of aquatic algae and plants. Thus for many temperate deep lakes the initial phase of high productivity is short-lived and may be followed by many thousands of years of stable, low levels of plant productivity (i.e., a period of trophic equilibrium (Hutchinson 1973)). Inevitably, however, and dependent on watershed characteristics and basin morphometry, the sedimentation of eroded or internally synthesized materials will fill significant portions of the lake basins. And as the basin size decreases, plant nutrients begin to accumulate in the water column and in the sediments, and recycle more efficiently, allowing higher productivity levels. Higher productivity in turn increases sedimentation of rich organic material, which accumulates in the basin, and increases oxygen demand. When dissolved oxygen is depleted in deep waters, anaerobic sediments regenerate significantly more nutrients, further favoring plant growth. Thus the process is self-enhancing, culminating in marsh and eventually woodland.

Increasingly, the extended equilibrium phase of this natural sequence is being altered by man's activities. In recent times, many lakes, especially the clear (unproductive) ones, have been sought out as homesites, campsites, recreation areas, etc., by an expanding and affluent human population. Human invasion of the watershed often disrupts the terrestrial vegetation. Weathering rates may then increase, terrestrial nutrient recycling efficiency decreases, and nutrient leakage to streams and lakes accelerates.

Often nutrients from outside the watershed are added, such as fertilizers, foodstuffs (and wastes), and phosphate-based detergents. This increase in nutrient input stimulates lake productivity either as algal (phytoplankton) growth in the open water, or as scums and algal mats, or as dense masses of aquatic weeds (macrophytes) in shallow water. Often massive outbreaks of algae ("blooms") cause harmful side effects (fishkills, odors, intestinal disorders, etc.). Macrophytes interfere with swimming, fishing, boating and visual enjoyment. The accelerated stage of rapid sediment accumulation occurs prematurely in the lake's natural cycle, rendering the lake less suitable for certain floral and faunal types, as well as for some human uses. Man's enhancement of lake aging--an acceleration of natural community succession--is called cultural eutrophication. Cultural eutrophication is a widespread problem in North America and Europe, and has received a great deal of recent attention. Since the symptoms are subtle, and gradual over long periods, it is important that management be aware of the problem long before conditions reach the level of public dissatisfaction.

Although Cape Cod National Seashore is spared the immediate environmental problems associated with industrial or heavily developed watersheds, the acceleration of nutrient input from non-point sources related to many recreational activities, and residential areas without benefit of closed sewerage systems, is a potential threat to resource preservation, and specifically to the exquisite kettle ponds within the Seashore (Fig. 1). Preliminary indications of pathogenic bacterial contamination as well as excess nutrient input (Doolittle 1974) prompted this study. Our objectives were to assess the deterioration of water quality, collect baseline water quality data, and provide supporting interpretive information for the simultaneous medical microbiological investigation of the public swimming areas (see Ortiz 1976; Ortiz, et al., this volume).

## METHODS AND MATERIALS

Early data were taken to assess nutrient levels and the amount of living algae (biomass) during the spring overturn. Subsequent observations were made to sound the ponds, describe the extent of mixing, and follow the development of thermal stratification, algal biomass, etc., were collected through the summer along with attempts to monitor phosphate additions from recreational activities. During late summer, surface water current velocities were measured. Surveys of selected characteristics were undertaken in fall and winter and another series of chemical determination (including total phosphate) were made in the spring of 1976. The summer of 1976 was given to monitoring activity on the most important ponds. Only a portion of the results are reported here.

In spring, samples were taken at ca. 1 m depth in the well-mixed, unstratified lakes. When the lakes became stratified, vertical series of samples were taken (with a Van Dorn) over the deepest points (found by depth recorder). Vertical temperature and specific conductivity profiles were also taken with a Hydrolab (or YSI) probe and 20 m cable. The Secchi transparency was measured with a 20 cm white disc. The Winkler method (APHA 1971) was used as the routine method for DO determinations.

Chlorophyll a concentrations, a rapid measure of phytoplankton biomass, were measured according to the method given by Strickland and Parsons (1972).

[1]National Park Service, North Atlantic Regional Office, Boston; and NPS Cooperative Research Unit, University of Massachusetts, Amherst.

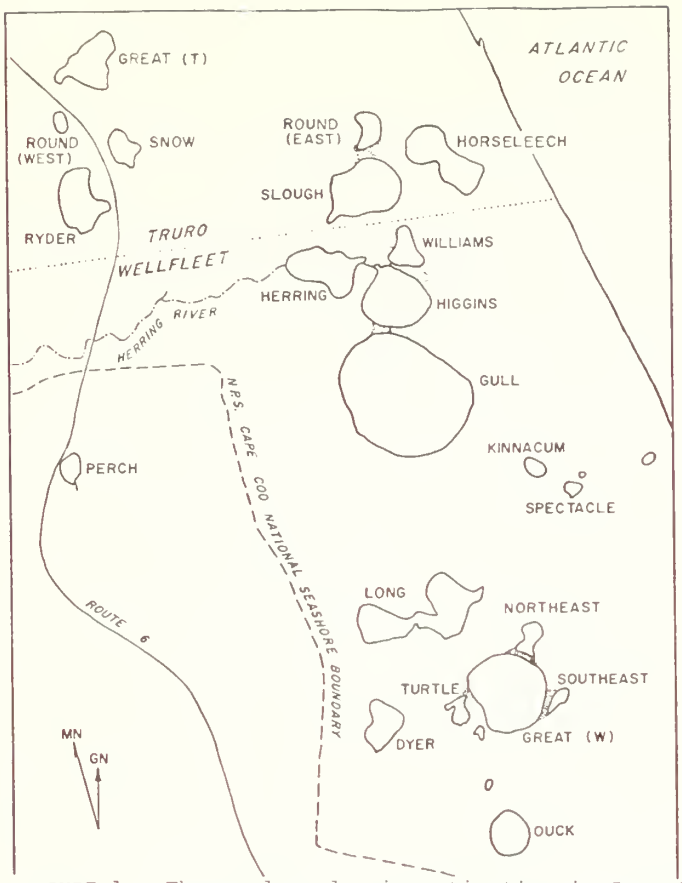



FIGURE 1. The ponds under investigation in Cape Cod National Seashore. Stippled areas indicate freshwater beach deposits, which have secondarily partitioned the original lakes (see Oldale 1968; Raisz 1938).

Selected ions were determined with a Perkin-Elmer (Model 403) atomic absorption spectrophotometer.

Soluble reactive phosphorus (SRP), which corresponds roughly to phosphorus readily available to plankton, was determined according to the method of Mullin and Riley (as described in Strickland and Parsons 1972). Total phosphorus (as P) was determined in samples which were frozen and stored. Samples were thawed overnight at room temperature before analysis. Analytical procedure follows Strickland and Parsons (1972) with the modifications proposed by Dillon and Rigler (1974).

Periodic samples from swimming areas were analyzed for soluble and total phosphorus in an attempt to detect phosphorus accumulations in waters during heavy swimming use. Soluble phosphorus determinations were done as rapidly after sampling as possible, but usually after 1-1.5 hr had elapsed. An attempt was also made to estimate the amount of phosphorus which is carried on the body surface of local swimmers, many of whom come directly from nearby ocean beaches to swim in the freshwater ponds (and thereby rinse themselves of sea-salts). The method (devised and executed by S. Danos) consisted of measuring the increase in total phosphorus in 12 liters of water used to rinse research workers as they returned from beach areas. Only 5 subjects were so treated, making the estimate (650 µg P ± 245 per swimmer) a rough one. The mean value was multiplied by the estimate of the seasonal total of swimmers at Gull Pond to arrive at a value for the relative magnitude of input of phosphorus from one recreational source.

The mass of phosphorus in Gull Pond, both at the beginning and end of summer, was calculated by measuring the volume of each 3 m interval (using a contour map plus planimeter) plus the phosphorus concentration for each water layer. An attempt to account for increases in the quantity of phosphorus between spring and late summer was then made. The accumulation in the deepest, anoxic waters was assumed to represent phosphorus regenerated from profundal sediments. Although significant input must come directly from the euphotic zone, it is impossible (and unnecessary) to distinguish the direction of input to this zone for present purposes. The phosphorus increases calculated as sediment release (0.0019 g P m-2 day-1) do not differ greatly from those found in other lakes.

An analysis of the development close to the shoreline of Gull Pond was made to arrive at an estimate of the potential phosphorus input from cottage sewerage systems. The data taken include the number of cottages close to the shoreline, mean number of occupants, period of occupancy, type of sewerage facility, presence of laundry facilities, type of detergents used, and distance of sewerage system from shoreline. These data, plus the various estimates from Vollenweider (196 on human waste contribution of phosphorus, were used to approximate phosphorus input from sewage. These calculations assume that cottages which are further away do not leach phosphorus to Gull Pond It is also assumed that there is no net loss of phosphorus associated with disposal in coarse sandy sub-surface materials (see Dillon 1974).

The contribution of the numerous gulls which res wash, and swim at Gull Pond, and from such source as swimmer excretion, aerosol transport of seawater, pitch pine pollen, and other wind-borne sources are unknown and cannot be given even broa approximations at this time.

## RESULTS

Estimates of areas, maximum depths, and spring levels of conductivity, pH, chlorophyll a, total phosphorus, and selected ions are presented in Table 1.

All ponds with depths greater than 8 m displaye stable summer thermal stratification. Several sho extensive dissolved oxygen depletion as in Gull Pond (Fig. 2).

Figure 3 shows the relationship of spring total phosphorus concentration with the maximum depth of each lake. Figures 4 and 5 show total phosphorus concentrations throughout the water column for several major lakes and also indicate the change in total phosphorus occurring over the summer of 1975.

A portion of the development along the shoreline of Gull Pond is illustrated in Fig. 6. Only those cottages situated most closely to the shoreline are included in Fig. 6 and in later calculations. Occasional indications of phosphorus increases in swimming areas can be seen in Table 2.

## DISCUSSION

The study site (Fig. 1) is underlain by old Wellfleet outwash plain deposits, which are characterized by a high content of quartzite stones (see Oldale 1968 for full description). The fine-to-coarse sandy nature of the soils (Latimer et al. 1924) and tills (Oldale 1968) creates exceptionally high permeability and results in the general absence of surface drainage in the area. Nutrient input to the kettle ponds has thus been either through groundwater seepage or atmospheric input from rain or sea spray. The lack of discrete inflows and outflow and the unknown extent and degree of basin sealing (due to accumulation of clay-size sediments within seepage lake basins)

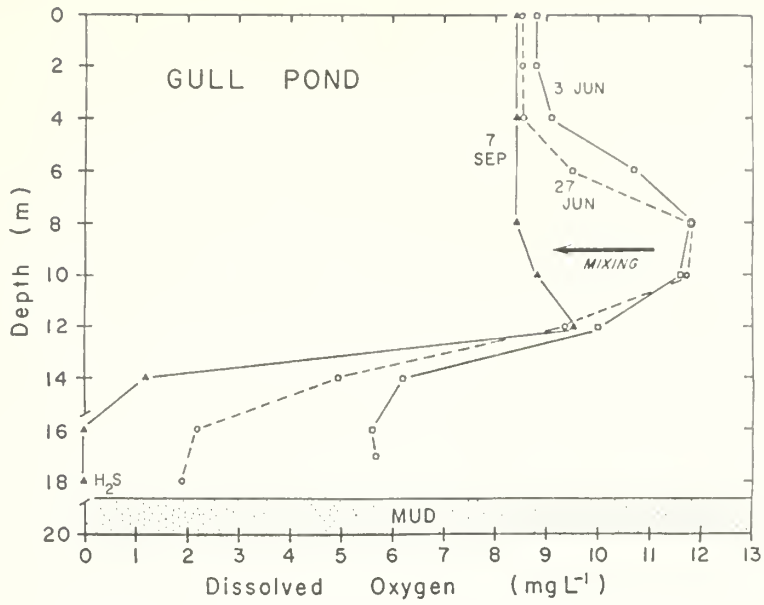



FIGURE 2. Do profiles in Gull Pond, summer 1975. Note the removal of the metalimnetic maximum by mixing in early September.

TABLE 1. Estimates of maximum depth, area, and level of pH, conductivity, total phosphate and selected ions of the Cape Cod National Seashore Ponds. (W) denotes Wellfleet ponds (T) denotes Truro. East and West is used to distinguish the two Round POnds in Truro. An asterisk denotes these ponds with public swimming areas. All levels were observed in spring 1976 except Chlorophyll a (spring 1975).

| | Max. observed depth | Area (ha) | Specific conductivity (umhos $cm^{-2}$) | pH | Chlorophyll a | Total phosphorus (as ug P $liter^{-1}$) | Ca | Fe | K | Na |
|---|---|---|---|---|---|---|---|---|---|---|
| Duck* | 18.2 | 5.1 | 63 | 5.4 | 0.1 | 4 | 1.4 | 0.05 | 0.7 | 13.1 |
| Dyer* | 10.5 | 4.8 | 55 | 5.7 | 0.9 | 8 | n.d. | n.d. | n.d. | n.d. |
| Great (W)* | 14.9 | 17.8 | 79 | 6.7 | 0.0 | 4 | 1.1 | 0.09 | 0.9 | 14.9 |
| Long* | 15.5 | 15.0 | 68 | 7.0 | 1.8 | 5 | 1.4 | 0.09 | 0.9 | 11.8 |
| Turtle | <2 | 1.6 | 63 | 6.7 | 3.6 | 16 | 1.4 | 0.09 | 0.7 | 9.8 |
| Northeast | n.d. | 1.7 | 71 | 6.6 | 1.5 | 9 | n.d. | n.d. | n.d. | n.d. |
| Southeast | 4.3 | 1.1 | 71 | 6.7 | 1.4 | 16 | 1.8 | 0.04 | 0.8 | 12.7 |
| Spectacle* | 6.8 | 0.5 | 73 | 5.8 | 2.4 | 6 | 1.2 | 0.04 | 0.8 | 13.7 |
| Kinnacum | n.d. | 0.8 | 62 | 7.0 | 5.3 | 9 | 1.1 | 0.01 | 0.5 | 9.1 |
| Gull* | 18.9 | 44.0 | 78 | 5.4 | 7.6 | 16 | 2.0 | 0.04 | 1.0 | 16.6 |
| Higgins* | 6.0 | 11.3 | 81 | 6.5 | 6.4 | 26 | 2.0 | 0.26 | 0.9 | 16.7 |
| Herring | 4.3 | 8.1 | 84 | 6.5 | 9.2 | 24 | 2.0 | 0.24 | 0.9 | 16.6 |
| Williams | 1.9 | 3.6 | 97 | 6.3 | 18.8 | 25 | 2.0 | 1.31 | n.d. | 13.1 |
| Slough | 8.2 | 11.9 | 82 | 6.8 | 1.8 | 9 | 1.4 | 0.01 | 0.7 | 15.4 |
| Horseleech | 4.6 | 10.0 | 96 | 6.4 | 2.1 | 12 | 1.5 | 0.05 | 0.9 | 16.7 |
| Round (East) | 7.8 | 2.6 | 73 | 6.2 | 2.6 | 7 | 1.2 | 0.05 | 0.8 | 14.4 |
| Ryder | 10.5 | 8.3 | 77 | 6.3 | 13.3 | 7 | 1.3 | 0.07 | 0.9 | 16.0 |
| Snow | 7.5 | 2.3 | 58 | 6.4 | n.d. | 10 | 0.8 | 0.08 | 0.6 | 10.8 |
| Round (West) | 9.3 | 0.8 | 51 | 6.1 | n.d. | 14 | 0.9 | 0.12 | 0.6 | 8.7 |
| Great (T) | 11.5 | 7.0 | 85 | 6.2 | 5.0 | 8 | 4.9 | 0.08 | 0.07 | 17.2 |

make it difficult to determine water residence times and nutrient budgets for the study ponds.

Wind energy is high in this area and is another dominating influence on the character of these ponds. Most ponds with maximum depths greater than 8 m showed stable thermal stratification in the summers of 1975 and 1976. However, Great Pond (Wellfleet), though having two deep areas (17 m), did not stratify, remaining essentially homeothermal.

Fall overturn is complete, replenishing all areas of oxygen depletion. In the winter of 1975-76, the ice cover was thin and intermittent and normal inverted winter stratification was rare and short-lived. For example, in mid-February 1976, Gull Pond was virtually homeothermal at less than 1°C (range 0.8-1.0°C) throughout the water column. It is likely that temperature stratification and ice cover patterns are highly variable year-to-year.

High wind energy, combined with easily eroded sandy till, has led to extensive changes in the shapes and numbers of these kettle ponds. Some ponds have areas of swamp deposits near their margins, and many have developed freshwater beach deposits (see Fig. 1) and become partitioned and rounded. The separation and rounding of the original basins is the result of internal wind-induced circulation patterns which tend to deposit suspended materials wherever irregularities in the shoreline occur. The ponds established secon-

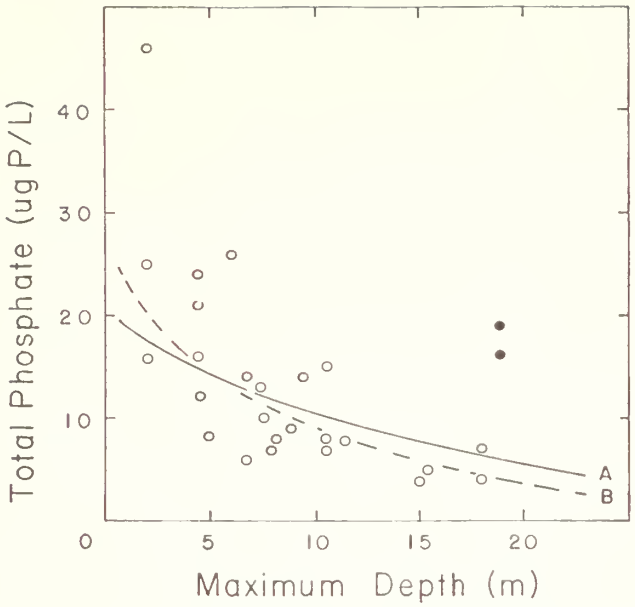



FIGURE 3. The relationship of total phosphate concentrations to maximum depth during spring overturn (1975 and 1976 data) in Cape Cod National Seashore kettle ponds. Closed circles represent values for Gull Pond. Line A generated from the equation $y = (19.5)\ e^{-0.06x}$, $r^2 = 0.28$; Line B was calculated after deleting the two Gull Pnd data points which gave the equation: $y = (24.9)\ e^{-0.1x}$, $r^2 = 0.57$.

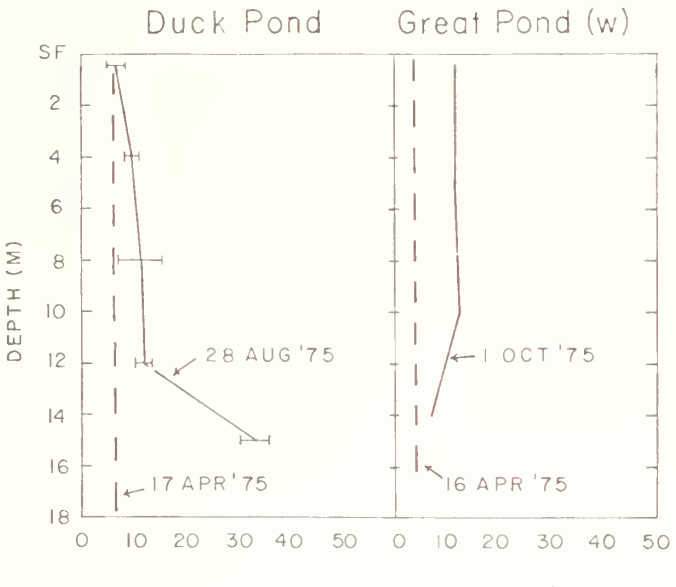



FIGURE 4. Change in total phosphate concentration over the summer of 1975 in two oligotrophic kettle ponds within the Cape Cod National Seashore.

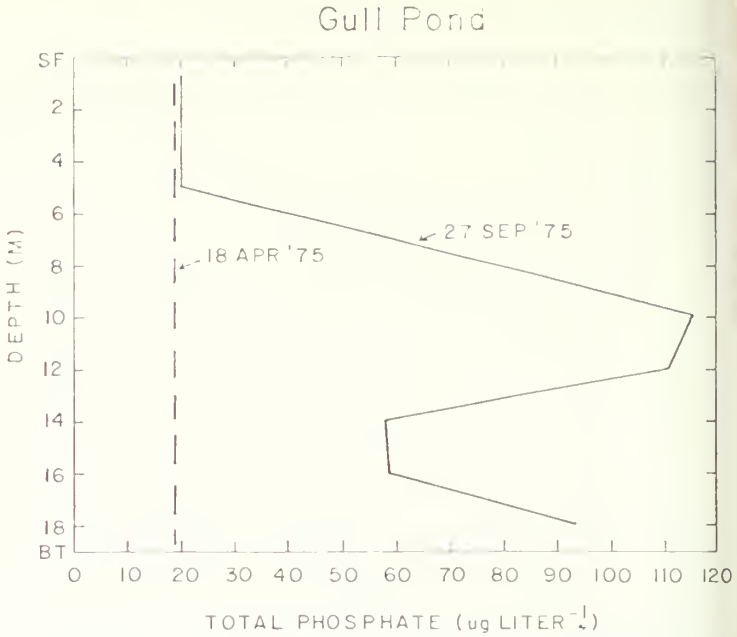



FIGURE 5. Changes in total phosphate concentrations in the water column of Gull Pond (Cape Cod National Seashore) in 1975.

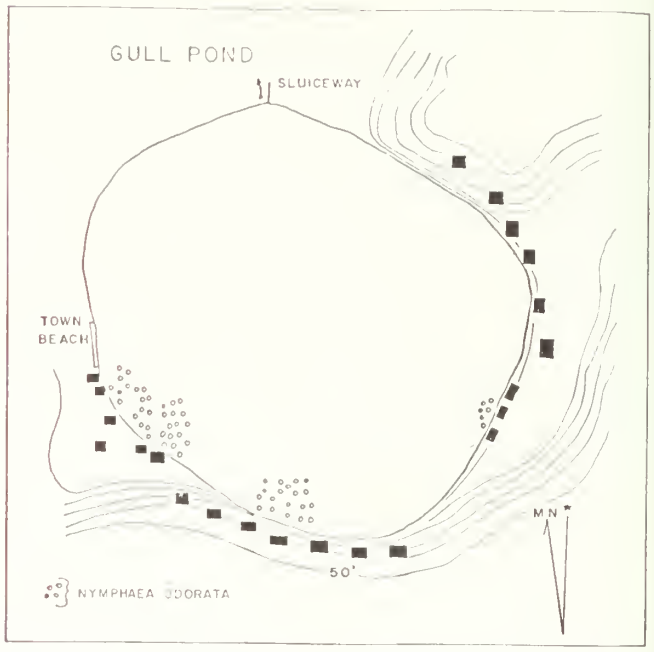



FIGURE 6. A sketch of Gull Pond showing the cottages most closely situated on its shoreline. Also noted are the locations of the major weedy areas.

darily are all small and shallow, and, as expected, tend to be more productive and weedy.

The resistant nature of the constituents of the till and outwash results in slow weathering rates and poor soils. Thus, groundwater is soft, acidic, poorly buffered, and normally low in mineral content, especially calcium, magnesium, silica, phosphate, and nitrogen. In addition, groundwater seeping into ponds becomes subject to other factors such as dilution with rain water (with higher proportion of atmosphilic elements), exchange reactions when in contact with clays, augmentation of nutrients recycling from sediments, changes in ion ratios from selective uptake by lake biota, inorganic precipitation of minerals (e.g., iron) associated with oxidizable organics, and adsorption phenomena. As a result, the ponds vary in their conductivity and chemical composition, as shown in Table 1. Horseleech Pond stands above the others in mineral content, perhaps reflecting a critical proximity to ocean spray.

TABLE 2. Monitoring total phosphate[a] is heavily swum Cap Cod National Seashore Ponds, summer 1975.

| | 19 August | | 20 August | | | 21 August | |
|---|---|---|---|---|---|---|---|
| Gull Pond | 9 a.m. | 11 a.m. | 1 p.m. | 4 p.m. | 8 p.m. | 10 a.m. | 1:30 p.m. |
| Swim area | 8.5 | 6.2 | 9.6 | 6.8 | 5.6 | | |
| Down-current of swimming area | 8.4 | 8.0 | - | - | - | Pond closed for construction | |
| Sluiceway | - | 5.1 | 32.4 | 7.5 | 6.4 | | |
| Great Pond (W) | | | | | | Extra swimming impact | |
| Swimming area | - | 5.7 | 5.4 | 6.1 | 5.1 | 5.6 | 4.9 |
| Down-current of swimming area | - | - | 6.3 | 5.1 | 2.5 | 4.2 | 12.1 |

[a]As P ug liter$^{-1}$; determination in triplicate, according to the methods of Strickland and Parsons (1972).

Overall, water quality in the 20 study ponds is high, but with a wide range of nutrient richness which may only partly reflect a range of stages in the natural succession of lakes outlined earlier. Some ponds are remarkably clear--invaluable recreational resources--while others are quite turbid and weedy.

According to the lake classification of Sakamoto (1968), the spring chlorophyll a data indicate that Williams Pond is certainly eutrophic (within the range of 5-140 mg m$^{-3}$) and Ryder, Herring, Gull and Higgins, Kinnacum and Great (T) are mesotrophic (1-15 mg m$^{-3}$). Duck, Dyer, Great (W) Ponds are oligotrophic (0.3-2.5 mg m$^{-3}$). Table 3 presents Dillon's (1974) tentative classification of lakes for potential recreational use, based on chlorophyll a levels. According to this classification, most study ponds are suitable for body-contact recreation, but Williams, Ryder, and possibly Herring Ponds are now most suitable for warm-water fisheries. Algal biomass levels appear to reflect cultural eutrophication phenomena in several ponds, most notably Gull, and to a lesser extent Duck (which still has Secchi transparencies over 11 m). Higgins, Ryder, and Great (T) ponds also appear to be adversely affected. Williams Pond has some historically significant aspects and is also naturally senescent; it will soon require management action if it is to be preserved as a pond.

Although many factors may determine levels of plant growth in these ponds, phosphorus is often a key element in controlling freshwater productivity because it is essential to life processes yet geochemically rare (Hutchinson 1973). It is also the element presently most susceptible to management. Within a nutrient-poor land area it might be expected that lake phosphorus levels are low, and related to basin size and/or depth. Phosphorus levels do vary among ponds in this fashion; a plot of spring phosphorus levels against maximum depth (Fig. 3) suggests the expected relationships of increasing nutrient concentration as depth decreases. A more suitable plot would be total phosphorus as a function of mean depth, but contour maps (and volumes) are not available for all ponds as yet. Nevertheless, a suggestion of excess phosphorus loading is present in Fig. 3, where the values for Gull Pond are noticeably higher than expected. Indeed Gull Pond, because it is the largest and deepest lake of the group would a priori be expected to be quite unproductive and clear, as is Duck Pond or Great Pond (W).

A comparison of Figs. 4 and 5 illustrates the differences in total phosphorus concentration. as well as the different magnitudes of change in total phosphorus, between two clear lakes [Duck and Great (W) ponds] and Gull Pond throughout a summer. These differences reflect significant nutrient input to, and recycling in, Gull Pond, and this aspect has been given a closer examination in Table 4 with the relative magnitude of input shown where possible.

Under the oxidizing conditions usually present in surface waters, phosphorus is absorbed on hydrous ferric oxides. This may occur at the sediment-water interface, or, most significantly perhaps, as groundwater seeps through basin sediments into the pond. This mechanism may provide a strong buffer mechanism against increasing productivity through groundwater contamination, and might account for the long-term maintenance of high clarity in many of the ponds. However, when the overlying water becomes anoxic, these ferric compounds are reduced and ferrous ions and certain associated ions (including P) are released into the water. Hypolimnetic anoxia, often a symptom of cultural eutrophication, thus accelerates recycling rates and the availability of important nutrients. The accumulation of P in deep anoxic waters may be substantial, and it is thought that most are circulated into upper layers at fall or spring overturn. Substantial DO depletions occur in the hypolimnia (lowest zone during stratification) of Gull (see Fig. 2), Round (West), Great (T), and Ryder Ponds; less extensive depletions occur in Duck Pond.

Additional loading of phosphorus may come from a variety of sources (cf. Table 5). Contamination of ground water by septic systems is probably a major source. Although no obvious septic tank "failures" were noted on any of the ponds, nutrients in sewage slowly seep down the hydrological gradient in a plume which is usually less than 1 m greater in width than the septic-cesspool facility

TABLE 3. Chlorophyll *a* levels in a tentative classification of recreational lakes. Taken from Dillon (1974).

| | |
|---|---|
| Level 1: | 2 mg $m^{-3}$; for lakes to be used primarily for body contact with recreation, adn where it is desirable to maintain hypolimnetic concentrations of oxygen in excess of 5 mg $l^{-1}$. The lake will be extremely clear with a mean SEcchi disc visibility of >5 m and will be very unproductive. (Note--The Secchi disc visibility may be lower in brown water (dystrophic lakes). |
| Level 2: | 5 mg $m^{-3}$; for makes to be used for water recreation but where the preservation of cold water fisheries is not imperative. The lake will be moderately productive and correspondingly less clear, with a mean Secchi disc visibility of 2-5 m. |
| Level 3: | 10 mg $m^{-3}$; for lakes where body-contact recreation is of little importance, but emphasis is placed on fisheries (bass, walleye, pickerel, pike, maskinonge, bluegill, yellow perch). Hypolimnetic oxygen depletion will be a common occurrence. Secchi disc will be low (1-2 m), and there is a danger of winterkill of fish in shallow lakes. |
| Level 4: | 25 mg $m^{-3}$; suitable only for warm water fisheries. Secchi disc depth <1.5 m, hypolimnetic oxygen depletion beginning early in summer, considerable danger of winterkill of fish except in deep lakes. |

TABLE 4. Analysis of the total phosphate accumulation in Gull Pond for the summer of 1975. See figure 5 and text for details of calculations.

| | |
|---|---|
| Total mass of P, spring 1975: | 80 kg |
| Total mass of P, fall 1975: | 160 kg |
| Net increase: | 80 kg |
| Approximate contributions to the net increase: | |
| Shoreline cottages (22 within 50 m of shoreline) | 22 kg* |
| Swimmers (estimated as 20,000 for this period) | |
| body surface source | 13 kg |
| metabolic wastes | ? |
| (1.3 g P capita day $^{-1}$ as urine) | |
| (0.22 g P capita day as feces) | |
| Sediment regeneration in hypolimnion (anaerobic; ca. 0.0019 g P $m^{-2}$ day $^{-1}$) | 10 kg |
| Seagulls (at hundreds of gull visits/day$^{-1}$) | ? |
| Allochthonous input (e.g., as pitch pine pollen) | ? |

TABLE 5. Estimates of the contributions of several sources of N and P.

| Source of nutrient | Mass of material (kg $yr^{-1}$) | N | | P | | Reference |
|---|---|---|---|---|---|---|
| | | kg $cyr^{-1}$ | g $cd^{-1}$ | kg $yr^{-1}$ | g $cd^{-1}$ | |
| Rainfall* | 1 X $10^6$ | 0.55 | -- | 0.0075 | -- | Miller 1955; Dillon 1974 |
| Human wastes (physiological) | | | | | | |
| a. fecal material | 48 | 0.77 | 2.1 | 0.08 | 0.22 | Van Vuran 1948; Buckstegg 1966 |
| b. urine | 437 | 4.3 | 11.9 | 0.47 | 1.3 | |
| Human wastes (household) | 275,000-550,000*** | 4.4 | 12 | 0.82—1.1 | 2.25--3** | Vollenweider 1968; Kerfoot 1975 |
| Wildfowl | | | | | | |
| a. duck (domestic) | - | 0.95 | 2.6 | 0.4 | 1.1 | Sanderson 1953 |
| b. Canada geese (x body wt = 2.56 kg) | 11.96 | 0.51 | 1.4 | 0.16 | 0.44 | Manny, Wetzell, and Johnson 1975 |

*Denotes units of g $m^{-2}$ $yr^{-1}$.
**Denotes the high range of P content of sewage which has other loadings, especially P-based detergents.
***Denotes the average rate of cesspool release, see Kerfoot 1975.
Data of Van Vuran 1948, Buckstegg 1966, Miller 1955, and Sanderson 1952 were quoted from Vollenweider 1968 and not seen.

(Kerfoot 1974). In the porous soils of the area, movement is relatively fast and sorption of nutrient such as N and P is probably minimal. Also, the use of phosphate-based detergents effectively doubles the per capita phosphorus loading (Vollenweider 1968); the recent decline in phosphate-based detergent use will be helpful but any beneficial effects will be delayed. Half of the Gull Pond residents still use phosphate-based detergents.

Another source of nutrients is related to recreational use. Swimmers can add phosphorus, and other nutrients in significant quantities by urination and defecation along the shoreline. Soluble phosphorus if added with wastes is probably taken up quickly by plankton; this source was reflected only occasionally in total phosphate levels (see Table 2). Since water currents and turbulence are efficient dispersal factors (for pathogens as well), the effect of swimmers will

be incremental, and detrimental, over a large volume of water, and thus difficult to detect. The magnitude of phosphorus transport of the body surface of swimmers is not insignificant but probably should not be a focal point of management actions.

Since only one pond (Gull) has public restroom facilities, a significant amount of human wastes is almost certainly entering other swimming ponds, some of which are used by an excess of 1000 bathers on peak days. This represents a threat to public health and to long-term preservation of water quality, and should be corrected immediately. In addition, the septic tank sanitary facility at Gull Pond should be examined to determine whether the hydrological gradient permits nutrient-rich seepage into any part of the pond. Many such facilities are constructed with only sanitation codes in mind; nutrient loading has usually not been considered.

Another source of nutrients is the large gull population characteristically seen bathing and resting on several of the ponds. Many aquatic birds do not represent nutrient sources because they feed primarily in or around the ponds. The gulls at Gull Pond and Great Pond (T) feed either on the ocean or at nearby landfills, representing an airborne route for transporting extra-watershed nutrients into the ponds. The per capita contribution of a gull, although less than that of a Canada goose (see Table 4) and somewhat proportional to body weight (Manny et al. 1975), is significant for these ponds where hundreds of gulls visit each day. Improved control of garbage availability at nearby town landfills might reduce this source of nutrient input to these ponds by reducing the number of gulls in the area.

Control of nonpoint nutrient sources is difficult and it is significant and problematic that lack of control will not lead to rapid devastation but subtle and gradual decline; only in the latter stages of cultural eutrophication do massive weed beds or algal blooms severely interfere with recreation and lead to public calls for action. However, the early lack of dramatic events does not warrant neglect. Effective and prudent management requires preventative management. As Vollenweider states (p. 141, 1968):

> There is no doubt that the elimination of local sources of pollution can bring about a considerable improvement in the overall condition of a lake, regardless of its surface area and its depth. However, it is to be feared that deep lakes in which over-enrichment is already pronounced cannot be restored to their original state, and that recourse to specific reclamation measures will do little to achieve speedy improvement of the overall condition of such lakes (i.e., as regards both the epilimnion and hypolimnion).

Management for long-term preservation of these ponds, and especially Gull Pond, should consist of minimizing watershed disturbances (e.g., from construction, development, and beach operations), minimizing septic tank seepage (at least through bans on P-based detergents, and adoption of closed-system sewage disposal alternatives), regulating the numbers of swimmers, providing sanitary facilities for each swimming area, minimizing shoreline erosion (especially from swimmer traffic), and informing the public of the vulnerability of these natural resources. The use of herbicides for weed control, at best an expensive proposition with unpredictable results and untold effects on natural aquatic systems, must by consistently avoided.

While present management options give little cause for optimism as far as corrective measures are concerned, alert preventative management will preserve park recreational waters, in many of which the level of water quality is high and problems are still avoidable.

## LITERATURE CITED


APHA, 1971. Standard methods for the examination of water and wastewater. Amer. Pub. Health Assoc. 13th ed. Washington, D.C. 874 p.

DILLON, P.J. 1974. A manual for calculating the capacity of a lake for development. Water Resources Branch, Ontario Min. of the Environment. 66 p.

DILLON, P.J. and F.H. RIGLER. 1974. The phosphorus-chlorophyll relationship in lakes. Limnol. & Oceanogr. 19:767-773.

DOOLITTLE, B. 1974. A pond study in the Cape Cod National Seashore. Unpublished Manuscript. 52 p. Dept. of Botany, Tufts University. Available from Cape Cod National Seashore, Eastham, MA.

HUTCHINSON, G.E. 1973. Eutrophication. Amer. Sci. 61:269-273.

KERFOOT, W.B. 1975. Living filters and water conservation on Cape Cod. Cape Naturalist 4:4-12.

LATIMER, W.J., E.T. MAXON, H.C. SMITH, A.S. MALLORY and O.R. ROBERTS. 1924. Soil survey of Norfolk, Bristol, and Barnstable counties, Massachusetts. U.S.D.A. Bureau of Soils, p. 1033-1120.

MACCOY, C.V. 1958. Ecology of Duck Pond, Wellfleet, Massachusetts with special reference to the vertical distribution of the zooplankton. Unpublished Manuscript, Woods Hole Oceanographic Institution, Ref. No. 58-43.

MANNY, B.A., R.G. WETZEL and W.C. JOHNSON. 1975. Annual contribution of carbon, nitrogen, and phosphorus to a hard-water lake by migrating Canada geese (*Branta canadensis* interior L.) Verh. Int. Ver. Limnol. 19.

OLDALE, R.N. 1968. Geologic map of the Wellfleet Quadrangle, Barnstable County, Cape Cod, Massachusetts. U.S. Geol. Surv. Map. GQ-750.

# THE LIMNOLOGY OF FOUR SMALL RESERVOIRS IN MISSISSIPPI[1]

Luther A. Knight, Jr.[2] and Jack Herring[3]

## INTRODUCTION

Fishing pressure on public lakes has been increasing rapidly in recent years because of higher personal incomes and more leisure time. Current thinking has created need for more understanding of conditions in such resources if they are to receive optimum utilization. Therefore, rational management of fisheries resources requires a knowledge of factors important in controlling production and understanding how these factors relate to one another. The results of limnological studies in four small impoundments within Mississippi are presented in this report.

## DESCRIPTION OF RESERVOIRS

The State of Mississippi Park Commission maintains a number of parks and recreational facilities. A number of these parks contains small fishing impoundments in which the Mississippi Game and Fish Commission advises management procedures. In addition, the Game and Fish Commission owns other small impoundments on which more comprehensive fisheries management programs are conducted. Four impoundments were included in this study: two in State Parks, Roosevelt and Clarkco; and two controlled by the Game and Fish Commission, Jeff Davis and Monroe. Locations of these reservoirs are shown in Fig. 1.

General descriptions of soil type and drainage areas are summarized (Neal et al. 1965; Murphree et al. 1966; unpublished data). Soil type for the basin and drainage area for Lake Monroe is Vaiden-Eutaw Association with poorly drained silt loam and clay sub-soil. Specific soil types are Houlka fine sandy loam, Vaiden silty clay and Vaiden and Sumpter soils. All are acid except the Vaiden and Sumpter soils which vary from acid to alkaline.

The Lake Jeff Davis general soil type is Ruston-Ora-Smithdale Association. Soils are well drained loamy soils to moderately well drained loams with specific soil types of Ora sandy loam, Mantachie fine sandy loam, Susquehanna and Boswell fine clay and Ruston fine sandy loam, all of which are acidic.

Lake Clarkco is in the Ruston-Orangeburg Association which includes several specific soil types. These are mainly Bibb and Chastain fine sandy loam and Ruston fine sandy loam with smaller areas of Boswell, Shubert and Cuthbert, Eustis sandy loam, Shubuta fine sandy loam, and Mantachie soils. These soils are strongly acid with low fertility.

Lake Roosevelt is located in the Smithdale-Ora-Boswell Association, a strongly acid low fertility soil. The majority of soil in the drainage area is Smithdale loam.

Morphology and physical features of the four reservoirs are summarized in Table 1. These impoundments are embankment types with earthen dams.

Surface areas of the impoundments range from 110 acres for Clarkco to 164 for Jeff Davis Reservoir. Watersheds in the drainage areas vary from 660 to 2800 acres and are forested in mixed hardwoods and pine.

## METHODS

One station, over deep water near the dam, was sampled six times from March 1973 through February 1974, approximately coinciding with the seasons of the year. Water for plankton samples and physicochemical analyses was collected with a 2 l Kemmerer water sampler and temperature and dissolved oxygen (D.O.) were measured at 1 m intervals.

*In situ* measurements included Secchi disk transparency, temperature profiles with a Whitney underwater thermometer, free carbon dioxide, D.O. with an oxygen meter (Yellow Springs Instrument model 54), and pH using a Hellige comparator and appropriate indicators. Conductivity and total hardness were measured in the laboratory within 24 hours after collection of samples. Analyses followed procedures outlined in Standard Methods (American Public Health Association 1971).

For identification of plankters, two samples were collected with a #20 towing net. For the study of plankton, 1 liter of reservoir water was measured in a volumetric flask, then poured into a glass-stoppered bottle. To each bottle, 20 ml of commercial formalin had been previously added for killing and perserving the organisms.

In the laboratory, the contents of the bottle were mixed by inverting the bottle several times and then this water was poured into an Imhoff Tube. To facilitate settling of bluegreen algae, Lugol's Iodine was added. After sedimentation for 24 hours had occurred, water was siphoned off to give a concentrated sample of 40-50 ml. The inside of the Imhoff Tube was washed down with tap water and this rinse water added to the sample. The water which had been siphoned was then filtered, and plankters adhering to the filter paper were washed into the concentrated sample resulting in a final sample of approximately 90-100 ml. When occasional plankton blooms occurred concentration of the samples was omitted and counts were made from the 1 liter volume.

A compound microscope, equipped with a 10X ocular and 10X objective, was used in combination with a Whipple ocular micrometer for plankton enumeration. A total count was made with a Sedgewick-Rafter Counting Cell. In general, procedures outlined in Standard Methods (APHA 1971) were followed.

A length of 300 μ represented a unit of filamentous algae, and all other plankters, including single cells and colonies, were counted as individual units. Two or three 1 ml aliquots per

[1]The authors thank Dr. Grover D. Barnes, Jackson State University and William K Anderson, Mississippi Game and Fish Commission for their helpful suggestions and critical review of this manuscript.

[2]Department of Biology, University of Mississippi, University 38677.

[3]Fisheries Division, Mississippi Game and Fish Commission, Jackson 39205.

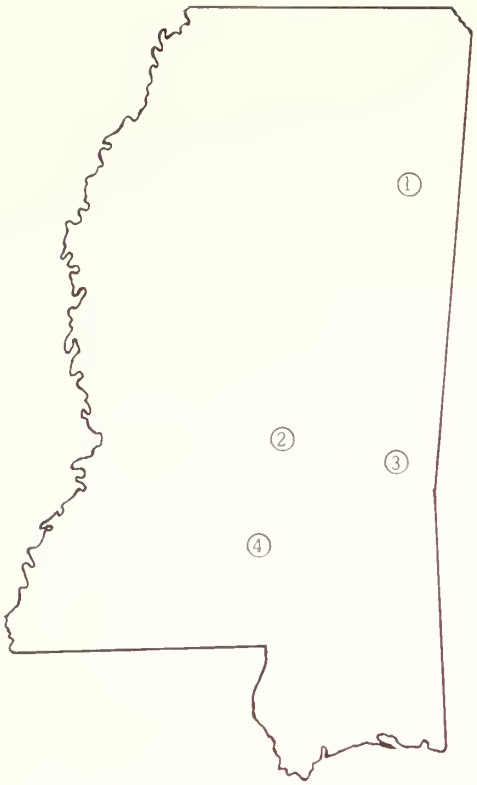



FIGURE 1. Location of study reservoirs in Mississippi. (1) Lake Monroe, (2) Lake Roosevelt, (3) Lake Clarkco, (4) Lake Jeff Davis.

sample were counted and the average number of plankters per liter calculated. Low magnification required with the Sedgewick-Rafter Counting Cell precludes identification and enumeration of nannoplankters. Qualitative examination of both live and preserved samples were made.

## DISCUSSION

Clarkco and Monroe exhibit incipient thermal stratification and when a thermocline is present no discernible hypolimnion occurred (Fig. 2). The epilimnion is shallow, seldom exceeding 1 m. Low D. O. concentrations near the bottom also imply stratification and continued low concentrations at this depth during much of the year suggest that circulation in these impoundments is incomplete. The normal sequence of events in the fall overturn is not followed in Clarkco and mixing is delayed until winter. This in part, may be due to the small size of the reservoir and protection from wind action afforded by steep, heavily wooded hillsides.

The other impoundments, Jeff Davis and Roosevelt, are sufficiently deep to have stable thermal stratification (Fig. 2). Shannon and Berzonik (1972) reported stable thermal stratification in shallow natural lakes which they attributed to size of the lakes and to other morphometric factors. Thermal stratification is well developed by the end of March in Jeff Davis and Roosevelt Lakes. The epilimnion extended down to 3 or 4 m with the thermocline 1 to 2 m thick. In Jeff Davis the hypolimnion extended from 4 m to the bottom. During periods of thermal stratification, thermoclines are well developed and hypolimnia are clearly evident. Summer bottom temperatures are 13-15° C and fall well below the usual minimum diurnal air temperatures and surface water temperatures vary between 26-31° C. Thermal stratification is not limited to summer in Lakes Roosevelt and Jeff Davis; during January stratification occurred with a thermocline between 1 and 4 m in Roosevelt and 2 and 4 m in Jeff Davis. Ruttner (1963) indicated that fall turnovers can be prevented in sufficiently deep and sheltered basins. In the winter both lakes showed decreasing D.O. toward the bottom. These two reservoirs are in the central and southern portions of the state and no doubt the warmer climate influences thermal activities and initiates thermal stratification earlier than in Lake Monroe in northern Mississippi.

Hydrogen ion concentration values for the four lakes are given in Table 2. Two of the lakes, Clarkco and Roosevelt, are acid lakes with average hydrogen ion concentrations in surface waters of 6.2 and 6.6, respectively. On the other hand, pH in Lake Monroe exceeded 7.0 during the summer and fall. Hydrogen ion concentrations of 8.4-8.6 were recorded in Lake Jeff Davis surface waters in other seasons. Verduin (1967) stated that plankton "bloom" development is accompanied by a consistent rise in pH. Increases in the plankton populations in these impoundments were closely correlated with increased pH levels.

Conductivity was low in both Clarkco and Jeff Davis Reservoirs with values in surface waters never in excess of 32 μ mho/cm. The values in surface waters of Roosevelt ranged from 11 to 73,

TABLE 1. Morphometric features of Game and Fish Commission and State Park Commission lakes in Mississippi.

| Location | Area (Acres) | Maximum depth (m) | Shoreline development[a] | Drainage area (acres) | Soil type drainage area and basin |
|---|---|---|---|---|---|
| Monroe | 111 | 6 | 4.33 | 660 | Vaiden-Eutaw association |
| Jeff Davis | 164 | 9 | 2.16 | 754 | Ruston-Ora-Smithdale association |
| Roosevelt | 125 | 7 | 2.36 | 2800 | Smithdale-Ora-Boswell association |
| Clarkco | 110 | 4 | 1.56 | 2500 | Ruston-Orangeburg-association |

[a]Shoreline development = $\frac{C_1}{C_2}$ where $C_1$ is the circumference of the lake and $C_2$ is the circumference of a circle having an area equal to that of the lake.

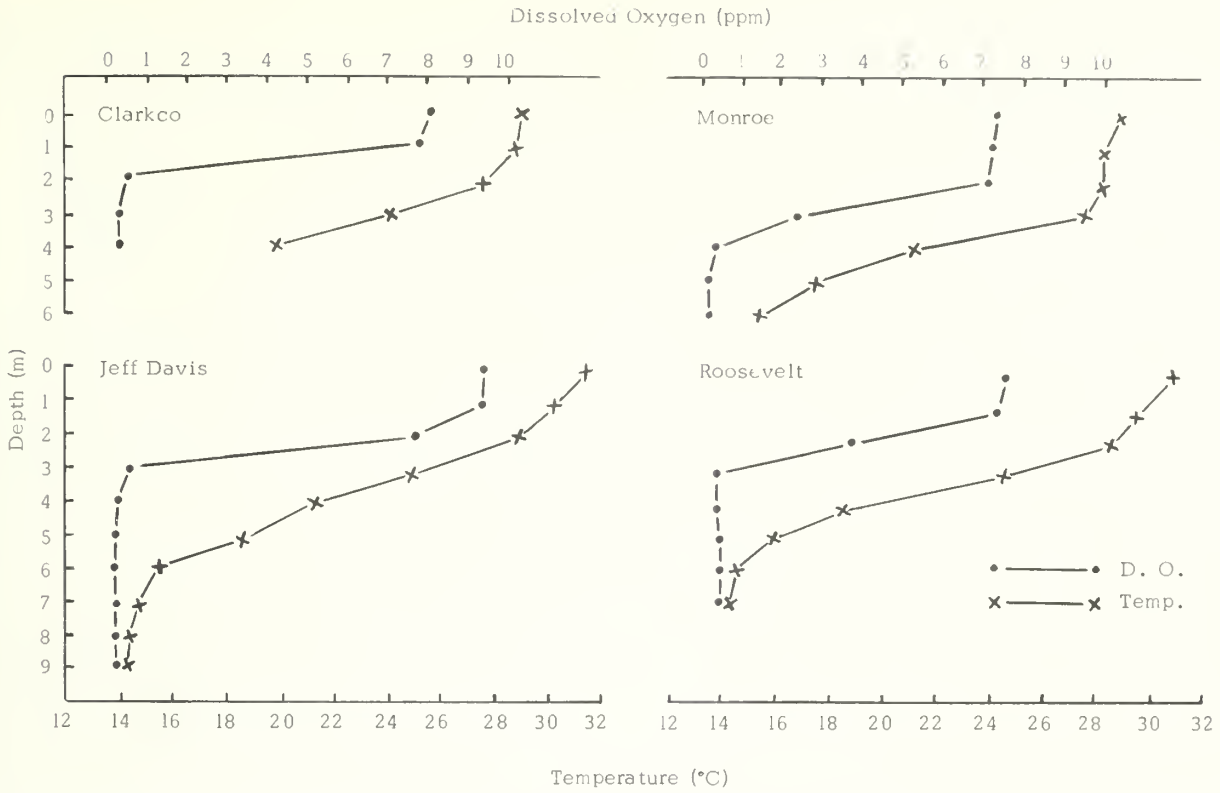



FIGURE 2. Temperature profiles and dissolved oxygen in four impoundments in Mississippi, July 9, 1973.

TABLE 2. Hydrogen ion concentration, conductivity and hardness in Clarkco, Jeff Davis, Monroe and Roosevelt Lakes, Mississippi, 1973-74.

| Reservois | pH (minimum-maximum) | Conductivity (μ mho/cm) (mean) | Conductivity (μ mho/cm) (minimum-maximum) | Total hardness (ppm) (mean) | Total hardness (ppm) (minimum-maximum) |
|---|---|---|---|---|---|
| Monroe | 6.4-9.4 | 59 | 44-72 | 20 | 12-29 |
| | 6.0-6.8 | 144 | 50-350 | 33 | 16-52 |
| Jeff Davis | 5.9-8.6 | 25 | 8-32 | 7 | 4-8 |
| | 5.5-5.9 | 45 | 17-108 | 9 | 8-12 |
| Roosevelt | 6.3-7.1 | 55 | 11-73 | 17 | 12-20 |
| | 5.7-6.3 | 76 | 14-170 | 20 | 12-24 |
| Clarkco | 6.0-6.3 | 23 | 8-27 | 7 | 4-12 |
| | 5.5-5.8 | 28 | 18-35 | 9 | 8-12 |

but the usual value was 50 μ mho/cm or more. Total hardness of stagnant bottom waters in Lakes Monroe and Roosevelt was higher than in the other impoundments. Since conductivity is related to total hardness the distributions and patterns of these parameters would be quite similar. This is verified in Table 2.

Much of the literature deals with impoundments larger than the ones in this study. Loss of plankton through discharge and replenishment from upstream must be considered if the standing crop measurements of plankton are to have more than limited value (Bensen and Cowell 1967). The reservoirs in our study receive only runoff water and that which enters from intermittent streams. Discharge is limited to rainy seasons and it is unlikely if this results in a very large plankton loss. The majority of the plankton is indigenous and only occasional or adventitious forms are transported into any of the reservoirs.

Six series of samples were collected from each lake over a period of approximately one year (March 4, 1973 to February 5, 1974). Because of the periodicity of plankton crops and the limited number of sampling dates, some organisms may be easily missed in a sampling program. However, the data on planktonic flora and fauna of these impoundments reported from this study appear to be representative.

The zooplankton populations are composed largely of rotifers, such as *Keratella* sp., *Polyarthra* sp., and *Trichocerca* sp., and to some lesser extent of copepods. In the majority of samples either *Keratella cochlearis* or *Keratella crassa* occurred. Two species of *Polyarthra, P. vulgaris* and *P. euryptera*, were found frequently throughout the water column. At least five species of *Trichocerca* were found including *T. cylindrica* and *T. similis*. Some species of rotifers usually considered limnetic species, often dwell below the surface and may constitute the majority of zooplankton near the bottom of the water column. *Kellicottia bostoniensis* is an example of this type of rotifer and numerous individuals were counted at depths below 2-3 m. The Phylum Protozoa was represented by *Difflugia, Epistylis,* and *Tintinnidium*. Microcrustacea included the cladocerans *Daphnia, Bosmina,* and *Diaphanosoma* and the copepods *Cyclops* and *Diaptomus*. Copepod nauplii were common in the majority of samples.

Roosevelt appeared to support, overall, a larger vernal population of Copepoda and Cladocera than did the other lakes although winter samples from Jeff Davis did contain large numbers of *Daphnia, Diaphanosoma, Cyclops,* and *Diaptomus*.

In three impoundments, Clarkco, Monroe and Jeff Davis, members of the Cyanophyta occurred in numbers sufficient to be considered "blooms." The usual genera included *Anabaena, Polycystis,* and *Oscillatoria*. Except for Roosevelt, *Anabaena* dominated the phytoplankton in all other impoundments. Populations reached a high of 31,650,000 units per liter in surface waters of Lake Monroe on 9/25/73. This resulted in an average count of 10,408,286 unit/l in the entire water column. Of particular interest was the dense population of *Oscillatoria* at 5, 6, and 7 m in Roosevelt Lake in October 1973. Keifer, et al. (1972), in studies of deep sub-alpine lakes, stated that deep phytoplankton maxima are common features of oligotrophic lakes. Although Roosevelt Lake certainly could not be considered deep (9 m), large numbers of these algae may be indicative of its general trophic conditions.

In addition to blue-green algae, other taxa included the diatoms *Asterionella* and *Synredra*. The green algae *Melosira* and *Staurastrum* and the euglenoids *Euglena* and *Phacus*. Lake Monroe especially contained large numbers of *Ceratium hirundinella*. A typical phytoplankton genus in Clarkco Lake was *Synura*.

Because of seasonal and geographical differences considerable differences in fauna and flora were anticipated. Actually, very little difference was found. Plankton was quite similar and differences could be attributed to variations in local conditions (i.e., runoff, bottom type, fertilization programs).

The use of plankton counts alone is not an adequate measure of productivity, but may indicate potential for production. Kalff (1972), Pavoni (1963), and Findenegg (1965) indicated that oligotrophic lakes generally have a planktonic flora containing a high proportion of nannoplankton, while eutrophic waters are dominated by net plankton. Examination of samples revealed a majority of the plankton in these four lakes is net plankton. Based upon this and the population sizes, it is suggested that these waters tend toward the eutrophic condition.

Zooplankton and phytoplankton crops generally appear to be adequate for optimum production and fish growth in these four reservoirs. However, dense blue-green algae occurring over a long period of time, particularly in Jeff Davis Lake, may inhibit fish production. The plankton of these waters was considerably denser than plankton from comparable areas of Ross Barnett Reservoir near Jackson, Mississippi. (Unpubl. data, Luther A. Knight, Jr., Dept. of Biology, U. of Miss.)

Some rotifers, cladocerans and copepods are relatively large (100 μ to 2.5 mm) and counts of individual organisms may be misleading. On a volume basis these large zooplankters provide considerably more nutritive value than would be available from large numbers of smaller phytoplankters.

Fertilization programs are important in comparing reservoir productivity. Monroe received only one application, 20-20-5, during 1973 while Clarkco and Jeff Davis were fertilized three to four times during the spring and summer. Roosevelt was fertilized once during the year with 16-16-4 plus basic slag. All reservoirs were fertilized under the direction of the park managers at a rate of 40-50 lbs. per acre. Because of the extreme variations in fertilization programs on these impoundments, no accurate assessment of effects on productivity can be made.

Lake Monroe has dense plankton although it received only one small application of fertilizer. This seems to indicate that when the trophic level of a lake is conducive to biological productivity, minimal applications of commercial fertilizers are needed.

All factors considered, shoreline development is indicative of overall productivity. Increased shoreline development increases total standing crop and sport fisheries harvest (Jenkins 1967). None of these reservoirs is large; surface areas range from 110 to 164 acres. Two of the reservoirs, Clarkco and Monroe differ in area by 1 acre (Table 1) and lend themselves to comparison. Monroe's shore is very irregular and is interrupted by several small inlets and coves. By contrast the shoreline contours of Clarkco are smooth and lack irregularities. Shoreline development of Monroe is approximately 2.8 times that of Clarkco. Plankton is recruited from stagnant, quiet and protected coves to add to the crop in

the main body of Monroe Reservoir. These additional masses of plankton, moved into the main body of the reservoir by wind and wave action, contribute considerable numbers and volume to the plankton found in the open waters of the reservoir. The poor plankton crop in Clarkco is at least a partial result of its smoother shoreline.

Monroe, in addition to its greater shoreline, has the only drainage area and basin containing limestone. Elements associated with this type soil contribute to the more alkaline pH, higher conductivity and total hardness of these waters. The increased values of these factors, as compared with those in the other reservoirs of this study, appear to be at least partially responsible for the denser plankton crop in Lake Monroe.

Summer stagnation of these impoundments is rather strong when one considers the severe oxygen depletion occurring in the hypolimnion and to a lesser extent in the thermocline. Lakes in the southern United States may have characteristics more like those of subtropical lakes than of temperate lakes. Whether eutrophic or oligotrophic, tropical lakes exhibit marked oxygen deficiencies in the hypolimnion throughout the year (Ruttner 1963). The reservoirs in our study exhibit characteristics of both temperate and tropical lakes. Oxygen depletion is caused by excessive oxidizable matter and high temperatures (Ruttner 1963) and the lack of appreciable wind action prevents disruption of stratification. Fruh (1967) emphasized that large quantities of nutrients become trapped in the hypolimnion during stratification and are not available during critical growing seasons. These conditions exist in all four of our impoundments and no doubt play a significant role in the depletion of dissolved oxygen. The lack of D.O., except in the epilimnion, creates large volumes of unproductive water and thus reduces total productivity.

Subsequent data and personal observations on these and other similar reservoirs have shown that addition of basis slag and lime increased pH and total hardness. Fertilization programs and construction of fish shelters appears to have improved catch results.

## LITERATURE CITED


AMERICAN PUBLIC HEALTH ASSOCIATION. 1971. Standard methods for the examination of water and waste water. 13th. ed. APHA.

BENSEN, N. B., and B. C. COWELL. 1967. The environment and plankton density in Missouri River reservoirs. *In* Reservoir Fishery resources symposium. Amer. Fish. Soc. April 5-7, 1967.

FINDENEGG, I. 1965. Relationship between standing crop and primary productivity. *In* C. R. Goldman (ed.), Primary productivity in aquatic environments. Univ. Calif., 1966.

FRUH, E. G. 1967. The overall picture of eutrophication. J. Water Poll. Control Fed. 39: 1449-1463.

JENKINS, R. M. 1967. The influence of some environmental factors on standing crop and harvest of fish in U. S. reservoirs. *In* Reservoir fishery resources symposium. Amer. Fish. Soc. April 5-7, 1967.

KALFF, J. 1972. Net plankton and nanoplankton (sic.) and biomass in a north temperate zone lake. Limnol. Oceanogr. 17:712-720.

KIEFER, D. A., O. HOLM-HANSEN, C. R. GOLDMAN, R. RICHARDS and T. BERMAN. 1972. Phytoplankton in Lake Tahoe: Deep-living populations. Limnol. Oceanogr. 17:718-422.

MURPHREE, L. C., J. L. ANDERSON, R. M. FERGUSON, M. C. GARBER, M. G. MARTIN, K. H. MILLER, L. H. NICHOLS and R. E. FULGHAM. 1966. Soil survey, Monroe County, Mississippi. U.S. Dept. Agr. and Mississippi Agr. Exp. Stat. Bull. 37. Series 1961.

NEAL, H. L., B. G. MOSS, C. H. WHITTINGTON, J. W. KEYES, W. W. NYE and C. H. FREEMAN. 1965. Soil survey, Clarke County, Mississippi. U. S. Dept. Agr. and Mississippi Agr. Exp. Stat. Bull. 32. Series 1961.

PAVONI, M. 1963. Die Bedeutung des Nannoplanktons im Vergleich zum netzplankton. Schweiz. Hydrol. 25:219-341.

RUTTNER, F. 1963. Fundamentals of limnology., 3rd ed. (trans.) D. G. Frey and F. E. J. Fry., U. of Toronto Press. p. 40.

SHANNON, E. E., and P. L. BREZONIK. 1972. Limnological characteristics of north and central Florida lakes. Limnol. Oceanogr. 17:97-110.

VERDUIN, J. 1967. Reservoir management problems created by increased phosphorus levels of surface waters. *In* Reservoir fishery resources symposium. Amer. Fish. Soc. April 5-7, 1967.

# THE SIGNIFICANCE OF CRATER LAKE AS A SCIENTIFIC BENCHMARK FOR LIMNOLOGICAL RESEARCH

F. O. Hoffman[1] and J. R. Donaldson[2]

## INTRODUCTION

There are essentially three basic reasons why research in the national parks should be encouraged. One reason is the need to describe the significant natural and cultural resources of the park. Another reason is the need to identify and solve problems of specific concern to park management. The third reason is the need of our present civilization to have natural, undisturbed areas from which baseline information can be derived for comparison with other similar locations (some of which may not be afforded the same degree of protection against human intervention). In so doing, national parks potentially lend themselves to functioning as scientific benchmarks.

Crater Lake has value both as a scenic resource and as a scientific benchmark for limnological research. In addition to being protected from extensive use and development, Crater Lake, despite its uniqueness, has certain characteristics which enable it to be readily used for comparative investigations. The utilization of Crater Lake for comparative research will be summarized in this paper in an attempt to illustrate its importance as a research site.

## THE CRATER LAKE ENVIRONMENT

The uniqueness of the Crater Lake environment is perhaps easier to accept than are the characteristics which make the lake an important site for comparative research. Crater Lake, Oregon, with a maximum depth of 589m, is the deepest lake in the United States. It is situated along the crest of the Cascade Mountains within the approximately 7000 year old collapse-caldera of volcanic Mount Mazama and is fed almost entirely from direct precipitation. The available land area for the collection of moisture which subsequently drains into the lake is only about 27% of the lake area. This is the lowest ratio (1:4) of terrestrial drainage basin to lake surface of any sizeable accessible lake (Volchok et al. 1970). About two-thirds of the annual water input is lost through seepage and about one-third is lost through evaporation (Phillips and Van Denburg 1968). Although several springs occur in the vicinity of Crater Lake, none of them are known to be outlets for lake water. The lake seldom freezes over because of a comparatively high summer heat income of about 30,000 g cal/cm$^2$ and because wind action is exceptionally strong during winter. Ice cover has only been known to occur three times during the recorded history of the lake (Larson 1972a).

The water of the lake is among the clearest in the world. Hasler (1938) reported a Secchi disk reading at 40m. Larson (1972a) observed a 100 cm modified Secchi disk to be visible at 44m. Extinction coeffecients were reported by Larson (1972a) and Utterback et al. (1942) to be about 0.033 per meter for blue light and 0.060 per meter for green light. These are among the lowest values recorded for fresh water lakes.

A summary of data describing the Crater Lake environment is presented in Table 1.

## THE USE OF CRATER LAKE AS A SCIENTIFIC BENCHMARK FOR COMPARATIVE RESEARCH

### *Ocean Fallout*

Oceanographic studies of radioactive fallout from nuclear weapons testing have raised the question as to whether strontium-90 disseminated into the atmosphere would be deposited at a greater rate per unit area in the oceans than onto land and whether, in the oceans, this nuclide has penetrated rapidly to considerable depths. To study this question, Volchok et al. (1970) chose Crater Lake as the site in which to perform their experiments because of the ideal natural conditions prevailing at this location. The small drainage area, the absence of outflowing streams, the presence of a large liquid surface throughout the year, and the fact that almost all the $^{90}$Sr ever deposited in the lake is still contained there (except that lost as a result of radioactive decay) made for almost a perfect situation in which to conduct such an investigation.

Volchok et al. (1970) compared the $^{90}$Sr accumulation in lake water, lake sediments, and from soils surrounding the lake with values reported for other sites in Oregon. The accumulation of $^{90}$Sr was found to be a direct function of mean annual precipitation. No evidence was found to support the hypothesis that water surfaces are more effective as a collector of dry deposited fallout or as a sink for material resuspended from terrestrial surfaces. In fact, these investigations revealed that the Crater Lake region is indicative of the average cumulative deposition of $^{90}$Sr within the 40-50° latitude band.

It is interesting to note, however, that measurements of tritium showed 20% greater concentrations in water sampled within the top 30 meters than in samples taken at lower depths. This effect was interpreted as potentially being brought about by sources of tritium production other than nuclear weapons explosions and the fact that tritium, unlike $^{90}$Sr, may contaminate the water surface through both the process of vapor exchange with the atmosphere and incorporation in rain and snow.

### *Temperature Microstructure*

Observations of irregularities in the vertical profile of temperature in the oceans have suggested that the layered thermal structure observed under certain oceanographic conditions may be produced by different rates of diffusion for salt and heat. Neal et al. (1971) chose Crater Lake as a site in which to test this suggestion because, if diffusion of heat and salt are both required for the production of layered microstructure, then this phenomenon should not exist in lakes of low salinity. With the exception of the oligohaline condition of Crater Lake water,

---

[1]Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee. ONRL is operated by Union Carbide Corporation for the Energy Research and Development Administration.

[2]Oregon State Department of Fish and Game, Portland, Oregon.

TABLE 1. Limnological data for Crater Lake, Oregon.

| | | |
|---|---|---|
| Elevation, surface (m) | 1,882 | (Byrne 1965) |
| Area ($km^2$) | 48 | " " |
| Volume ($km^3$) | 16 | " " |
| Depth, max (m) | 589 | " " |
| Depth, mean (m) | 325 | " " |
| Shoreline length (km) | 31.0 | " " |
| Shoreline development | 1.27 | " " |
| Secchi disk depth, max (m) | 44[a] | (Larson 1972a) |
| Summer heat income (g cal/$cm^2$) | 30,010 | (Kibby et al. 1968) |
| Annual mean precipitation (cm) | 170 | (Larson 1972a) |
| Annual mean air temperature ($^oC$) | 3.9 | " " |
| Light extinction coefficients ($m^{-1}$) | | (Larson 1972a; Utterback et al. 1942) |
| Blue (Schott filter, BG 12) | 0.033 | |
| Green (Wratten filter, W 61) | 0.060 | |
| Red (Schott filter, RG 1) | 0.311 | |
| Terrestrial drainage basin ($km^2$) | 20 | (Volchok et al. 1970) |
| Average water input (l/year) | $1.2X10^{11}$ | " " " |
| Annual water loss via seepage (l) | $0.8X10^{11}$ | " " " |
| Annual water loss via evaporation (l) | $0.4X10^{11}$ | " " " |
| Dissolved oxygen (mg/l) orthograde | 10 | (Larson 1972a) |
| Total dissolved solids (mg/l) | 80 | (Larson 1972b) |
| Total alkalinity (mg/l Ca $CO_3$) | 30 | " " |
| Average concentrations of chlorophyll *a* ($mg/m^2$) | 35 | " " |
| ($mg/m^3$) | 0.18 | " " |
| Average net production of phytoplankton ($mgC/m^2$ hr) | 25 | " " |
| ($mgC/m^3$ hr) | 0.15 | " " |
| Approximate depths of max production (m) | 85 | " " |
| Average concentration of zooplankton per 100 m vertical tow ($m^{-3}$) | 550 | (Hoffman 1969) |

[a]Measurement taken using a 100 cm diam Secchi disk; using a 20 cm diam Secchi disk, an average reading of 32.5 m is reported (Larson 1972a).

its depth, drainage area, and water source make it more comparable to an ocean than other freshwater lakes in the region and, thus, make it a suitable site for such a test. Using a modified expendable bathythermograph (XBT) system which had been applied in the Arctic Ocean for temperature microstructure studies, temperature profiles taken in various seasons all showed the presence of isothermal microstructure layers of at least 10 m in thickness scattered throughout the water column (Neal et al. 1972). At middepth (295 m) an isothermal layer (3.53 C) ranging from at least 10 to 40 m was found, with temperatures below this layer increasing to the bottom by 0.11 C°. The results of this study led to the conclusion that another mechanism other than the different rates of diffusion for salt and heat must be responsible for the production of the observed vertical microstructure layers in oceans.

The isothermal layer observed at 295 m in Crater Lake and the slight subsequent warming with increasing depth below this layer was interpreted by Neal et al. (1972) to indicate that vertical mixing in Crater Lake is limited to the upper 295 m. On the basis of their measurements, they believe the lake to be meromictic. However, whether or not the lake is indeed meromictic is a conclusion that awaits verficiation through further study.

### *Lake Classification*

The physical properties of Crater Lake, as well as the fact that the lake is preserved in a national park and is free of most cultural pollutants, are reasons why Larson (1972b) chose Crater Lake for testing the classification of lake oligotrophy. Comparing the net phytoplankton primary production determined for Crater Lake and three other alleged "oligotrophic" Oregon lakes with Rodhe's (1969) proposed scale for lake classification, Larson (1972b) found that Waldo Lake was the only one of the four selected oligotrophic lakes, to conform unquestionably to Rodhe's (1969) classification of oligotrophy. Crater Lake has many limnological properties, such as a high water transparency, low dissolved solids, and a low phytoplankton net production per unit volume of water (0.15 mg C $m^{-3}$ $hr^{-1}$), which conform to the classic descriptions of an oligotrophic lake (Welch 1952; Ruttner 1953). Despite this fact, the net phytoplankton productivity of about 290 mg C $m^{-2}$ $day^{-1}$ when averaged over the surface area of the lake

results in a classification of mesotrophic to near eutrophic according to the Rodhe scale (Larson 1972b).

It is interesting to note that the depth of maximum productivity of the lake from which Rodhe developed his scale of classification was at or near the surface. The depth of maximum productivity in Crater Lake was found by Larson (1972b) to be at about 85 m. Crater Lake, therefore, can be considered to be essentially morphometrically oligotrophic. The Rodhe scheme of lake classification obviously cannot be directly applied in these situations.

*Vertical Distribution of Zooplankton*

In general, vertical migrations of zooplankton are best observed in lakes that are deep, transparent, and unproductive. Therefore, Crater Lake was chosen (Hoffman 1969) as an ideal environment in which to investigate the vertical movement of zooplankton over a 24-hour period. However, even though Crater Lake is exceptionally deep and transparent, the observed vertical migrations of zooplankton were not as marked as those reviewed by Hutchinson (1967) in similar lake environments. The only noticeable major vertical migration was observed in late August of 1968 when almost the entire population of adult *Daphnia pulex* came to the surface by night after residing diurnally at a depth of 50 to 60 meters. At other dates, diel vertical migrations of zooplankton were found to be limited to a partial upward scattering during the night, but the maximum number of individual animals remained at depths of 35 to 50 meters (Hoffman 1969). Evidently true diel vertical migrations are not consistent and only occur during certain times of the year or during certain years in Crater Lake. High surface illumination appears to be the main environmental factor that determines the diurnal vertical distribution, but the factors which are responsible for determining the nocturnal distribution are as yet unknown.

Since nowhere are the exact causes of vertical migrations fully understood, Crater Lake does offer an inviting environment in which to attempt to identify the factors controlling this type of zooplankton behavior. The environmental variables are few and the species of zooplankton are primarily limited to *Bosmina longispina* and *D. pulex*. However, further studies will have to be initiated before these controlling factors are identified. The benchmark value of such investigations will be in testing the theories proposed from studies conducted at other locations.

## CONCLUDING REMARKS

Through the above examples we have attempted to show how Crater Lake has served as an ideal setting in which to conduct comparative limnological research and, in so doing, show the potential value of Crater Lake as a scientific benchmark. Currently, the U. S. Geological Survey is using Crater Lake as a part of their National Network of Hydrologic Benchmarks and is taking periodic samples of water quality and temperature. But with the exception of this work, no on-going limnological studies have been acknowledged by the Chief Scientist of the National Park Service (U. S. Department of Interior 1976). In fact, most of the present research in the park has been directed to the terrestrial environment. In light of the potential for Crater Lake to serve as a scientific benchmark for limnological research, more effort should be undertaken to encourage the utilization of this valuable park resource. The information gained from such studies will also serve to further describe the limnology of the lake as well as to contribute to the data base available to park management.

Because the lake is in a somewhat self-contained state, with direct precipitation being in equilibrium with seepage and evaporation, it should have particular value as a site of accumulation of materials deposited from the atmosphere. Volchok et al. (1970) estimated that over a 15-year period less than 5% of the total amount of $^{90}Sr$ deposited into the lake could possibly have leaked out. This has strong implications for the future use of Crater Lake as an indicator of other types of potentially hazardous anthropogenic substances which have been introduced into the atmosphere. Since the age of the caldera is known, paleolimnological studies could also be initiated to utilize Crater Lake as a site for the investigation of lake evolution. Determination of the age of the lake and locating the major sites of subsurface seepage can also lead to a further understanding of the climatology of the region. These are a few areas in which future investigations could be oriented. For long-term studies requiring several samples taken over a number of years, it is suggested that the National Park Service could explore the possibility of utilizing their field personnel to assist in the monitoring program.

Although the thrust of this paper has emphasized the value of this natural area as a research site, it must be remembered that research activities in national parks must remain compatible with the objective of natural and cultural resource preservation for the aesthetic enjoyment of park visitors. Thus, there are some restrictions as to the size and type of research activity which can be tolerated in any national park. Any activity which would seriously impair the experience of the park visitor would most likely not be permitted. For example, access to the shores of Crater Lake is currently restricted to a summer foot trail which descends 600 feet in 1.1 miles. The development of a more convenient mode of access for research purposes is not likely. Therefore, limnological investigations during the winter months can only be performed under conditions of extreme difficulty. On the other hand, attempts to increase and intensify visitor use should be scrutinized carefully in order to preserve the value of Crater Lake as a scientific resource. It should be the goal of park management to provide for visitor use and research activities without impairing either the scientific or aesthetic resources of the park.

## LITERATURE CITED


BYRNE, J. V. 1965. Morphometry of Crater Lake, Oregon. Limno. Oceanogr. 10:462-465.

HASLER, A. D. 1938. Fish biology and limnology of Crater Lake, Oregon. J. Wildl. Manage. 2:94-103.

HOFFMAN, F. O. 1969. The Horizontal Distribution and Vertical Migrations of the Limnetic Zooplankton in Crater Lake, Oregon. M.S. Thesis, Oregon State University.

HUTCHINSON, G. E. 1967. A treatise on limnology. Vol. 2. Introduction to lake biology and the limnoplankton. New York, Wiley. 1115pp.

KIBBY, H. V., J. R. DONALDSON, and C. E. BOND. 1968. Temperature and current observations in Crater Lake, Oregon. Limnol. Oceanogr. 13:363-366.

LARSON, D. W. 1972a. Temperature, transparency, and phytoplankton productivity in Crater Lake, Oregon. Limnol. Oceanogr. 17:410-417.

LARSON, D. W. 1972b. Comparative limnology and phytoplankton ecology of four "obligotrophic" lakes in Oregon, U.S.A., with emphasis on lake typology. Northwest Sci. 46:149-163.

NEAL, V. T., S. J. NESHYBA, and W. W. DENNER. 1971. Temperature microstructure in Crater Lake, Oregon. Limnol. Oceanogr. 16:695-700.

NEAL, V. T., S. J. NESHYBA, and W. W. DENNER. 1972. Vertical temperature structure in Crater Lake, Oregon. Limnol. Oceanogr. 17: 327:504.

PHILLIPS, K. N., A. S. VAN DENBURGH. 1968. Hydrology of Crater, East and Davis Lakes, Oregon. Contributions to the hydrology of the United States. Geological Survey Water-Supply Paper 1859-E. U. S. Government Printing Office, Washington, D. C. 60pp.

RODHE, W. 1969. Crystallization of eutrophication concepts in northern Europe, in Proceedings of the International Symposium on Eutrophication (National Academy of Sciences, Washington, D. C.), Madison, Wisconsin. pp. 50-64.

RUTTNER, R. 1953. Fundamentals of limnology. University of Toronto. 295pp.

U. S. DEPARTMENT OF THE INTERIOR. 1976. Annual Report of the Chief Scientist of the National Park Service CY 1975. National Park Service, Washington, D. C.

UTTERBACK, C. L., L. D. PHIFER, and R. J. ROBINSON. 1942. Some planktonic and optical characteristics of Crater Lake. Ecology 23: 97-103.

VOLCHOK, H. L., M. FEINER, H. J. SIMPSON, W. S. BROECKER, V. E. NOSHKIN, V. T. BOWEN, and E. WILLIS. 1970. Ocean fallout - the Crater Lake experiment, J. Geophys. Res. 75:1084-1090.

WELCH, P. S. 1952. Limnology. 2nd edition. McGraw-Hill, New York. 538pp.

# AN ANALYSIS OF THE DISTRIBUTION AND ABUNDANCE OF *BAETIS* IN THE KAWEAH RIVER BASIN, CALIFORNIA

Dana L. Abell[1]

The small mayfly, *Baetis*, appeared in 44 of 60 semi-quantitative collections made of macroscopic invertebrates from the Kaweah River Basin (Tulare County, California) in a study of winter faunas that was conducted in 1975-76.[2] Analysis of the distribution and abundance of this genus yields preliminary conclusions which suggest a possible role for it in studies of environmental disturbance.

Records of *Baetis* ranged from 230 m elevation at the inlet to Kaweah Reservoir to 3300 m near timber line on Alta Peak. Two or more species (tentatively identified as *B. leechi* and *B. bicaudatus*) may be present in the area, but the overlap in distribution and niche occupancy by the predominant forms appears to be sufficient that identification of the distinct species may be unnecessary for general conclusions drawn here. Refinement of identifications in later work will presumably make interpretation of the present observations to fit specific situations possible, but is not expected to alter the general picture presented here.

The species of *Baetis* which are common in the Kaweah drainage are grazers on attached microscopic algae on the upper surfaces of riffle rocks. *Baetis'* small size and good swimming ability enable it to be unusually successful in this difficult stream environment. In a very real sense *Baetis* is the characteristic macroscopic organism of this important habitat. Its numbers are useful therefore in describing conditions in this part of the stream environment.

The collections in this study were taken from a carefully defined habitat, namely current-dominated rocky beds where rubble-sized rocks predominated and currents were normally in the 20-50 cm/sec range. In very small streams the strongest available current was sought out (often only 10-20 cm/sec). A modification of the standardized hand-netting techniques of Mauch (1963) and Morgan and Egglishaw (1965) was employed, whereby rocks 8 to 25 cm in diameter were lifted immediately upstream from a 5 x 15 cm dip net (mesh 12 per cm). The net was then swept briefly through the water where the rock had been located and both rock and net were picked clean of specimens. Because this was a general faunal study, all species were taken. The procedure was continued for a period of 20 minutes. Time was available for only a single sample at most sites, so counts must be viewed at this stage in the work as general indications of abundance, expressed in the following rating scale:

| | Rating | Count |
|---|---|---|
| Abundant | (V) | 15 or more specimens |
| Very common | (IV) | 10-14 |
| common | (III) | 5-9 |
| Occasional | (II) | 2-4 |
| Rare or Accidental | (I) | 1 |

Emphasis was being placed on species diversity in the study as a whole, so taxa which could be recognized in the field were passed over during collection after 15 to 20 specimens had been taken. Thus, attention could be shifted from picking rocks and the net to finding as many forms as 20 minutes would allow. Where specimens were mixed with debris or were too small to identify with the naked eye or were simply excessively abundant, counts would be much higher. These are adjusted down to a maximum of 15. Means which were based on adjusted counts of this sort are indicated by a + sign in Table 1 which presents the results for *Baetis* only.

The general picture during the winter period is one of low numbers of *Baetis* in the smallest streams (brooks, usually first order, Abell 1961), gradually increasing numbers in the intermediate streams (creeks and small rivers, second and third order) and high numbers in the broad, exposed main stem of the Kaweah (fourth order). Streams which have their sources in areas above 2,000 meters elevation show the gradient in numbers of *Baetis* most clearly (Table 2). Both width of stream (= insolation, as the larger streams break clear of forest cover) and altitude (= temperature and, presumably, availability of nutrients) seem to be involved. Streams arising on the steep, non-glaciated upper foreslope of the Sierra (el. 1,300 to 2,000 m) start in densely shaded canyons and show a similar pattern, though data on small rivers of the montane zone and the upper foreslope cannot be separated in this study. On the lower foreslope (el. 750-1,300 m), still on the main mass of the Sierra but above the foothills, riparian cover is less dense, stream profiles are more concave and temperatures are high. Here *Baetis* appears to be abundant nearly everywhere. Data are dominated though by collections from one unusual stream (Hospital Creek, shown by the bracketed counts in Table 1).

A number of anomalously high counts (the underlined values in Table 1) can be seen in the raw data, and examination of conditions at each of these sites is of especial interest. The count of 50 in the small river category came from the Marble Fork at Marble Falls where extremes of runoff tend to be unusually high. The site is well within the main rise of the Sierra, where precipitation is high in the winter but the site is normally just below the snow line. Freshet conditions are often most severe here. Additionally, the collecting site is deficient in crevices for refuge from storm flow, for boulders and stream-polished bed rock dominate the channel, which is itself set in a rock-walled gorge. Thus, refuge sites at the stream's edge are scarce. Flow increased four-fold during such a storm three weeks prior to the collecting date, March 21, 1976.

Two of the anomalously high counts from the forest brooks were from a station on Suwanee

---

[1]The Kaweah Institute, Three Rivers, California 93271.

[2]Support was received for the study from the Sequoia Natural History Association. Facilities and supplies were provided jointly by the Association and the Resources Management and Research Scientist's offices of Sequoia and Kings Canyon National Parks. Thanks are extended to John Palmer, Maurice Zardus, David Parsons and Joyce Kelso for their assistance.

TABLE 1. Basic field data.

| Stream type | Typical Discharges | No. of *Baetis* taken in individual collections | Adjusted mean | Rating |
|---|---|---|---|---|
| Forest brook | 3-30 l/sec | 2, 0, 1, 18, 2, 0, 1, 0, 0, 12, 0, 3, 0, 10, 0, 3, 3, 12, 0, 0, 0 | 3.3+ | II |
| Canyon brook, upper slope | 3-30 l/sec | 0, 0, 1, 1, 2 | 0.8 | I |
| Canyon brook lower slope | 3-3 l/sec | 15, 27, 51, 21, 7, 8, 3, 11 | 11.1+ | IV |
| Montane creek | 30-300 l/sec | 6, 6, 3 | 5.0 | III |
| Foreslope creek | 30-300 l/sec | 9, 7 | 8.0 | IV |
| Small river | 300-800 l/sec | 3, 8, 50, 5, 1, 2, 1, 8 | 5.4 | III |
| Main stem river | 800-4000 l/sec | 22, 14, 25, 23, 14, 15 | 14.7+ | V |

TABLE 2. Counts (adjusted means) of *BAetis* by stream series.

| Order: | First | Second | Third & Fourth | Fifth |
|---|---|---|---|---|
| Flow: | 3-300 l/sec | 30-300 l/sec | 300-800 l/sec | 800-4000 l/sec |
| Montane Series | | | | |
| Type: | Forest brook | Montane Creek | Small river | Main stem river |
| Count: | 3.44 | 5.00 | 5.44 | 14.7+ |
| Rating: | II | III | III(+?) | IV(+?) |
| Upper Foreslope Series | | | | |
| Type: | Shaded canyon brook | Mid-level creek | Small river | Main stem river |
| Count: | 0.8 | 8.00 | (5.4+)* | 14.7+ |
| Rating: | I | III | III(+?) | IV(+?) |
| Lower Foreslope Series | | | | |
| Type: | Open canyon brook | Mid-level creek | | Main stem river |
| Count: | 11.1 | (8.0)* | | 14.7+ |
| Rating: | IV | III | | IV(+?) |

*These values include collections from elevations aboe the mouth of tributaries in each of these series and are presumably lower than the values that would occu in the natural sequence.

Creek, where a pulse of sand was moving as bed load past the site during much of the winter. The count of 18 on February 26 was recorded when sand depths were high. A count of 12 represents conditions on April 7, when sand depth was less and species diversity and average abundance of all species had increased, indicating some recovery.

The other two anomalously high forest brook counts were from areas of snow pack, where in one case a January thaw had recently opened the stream to full sunlight and in the second case a later unseasonal thaw had converted a stream bed trickle into a vigorous little brook. Each thaw had come approximately three weeks before the collecting date.

An additional important anomaly is bracketed in the "Canyon brook, lower slope" category. This is a series of collections taken on March 23, 1976, from Hospital Creek, a small intermittent stream which began flowing in its upper reaches in January (the three lower counts, representing populations after ten weeks of flow), with the water disappearing into the bed at about 1,000 m elevation. Initiation of flow was delayed due to drought conditions until late February in the lower half of the drainage, from which the three higher counts came. These represent the population after only three to four weeks of flow.

In each of these diverse situations anomalously high counts of *Baetis* appear to indicate an early stage in recovery from an abrupt change in environmental conditions. Later counts from the same sites, when riffle associations were well along in their development, were consistently lower.

An additional dimension on this phenomenon is provided by data from three springs on the lower foreslope (750-1,300 m), as follows:

| Flow Type | Discharge | Counts of *Baetis* | | | | Adjusted Mean | Rating |
|---|---|---|---|---|---|---|---|
| Spring | 2.5-6.0 l/sec | 5 | 0 | 3 | 0 | 2.0 | II |
| Spring brook | 2.5-6.0 l/sec | 20 | 12 | ? | 3 | 10.0+ | IV |

Counts in vertical columns are from the same water course. The last two columns represent a single spring and brook on two dates three weeks apart.

Spring brook sampling locations were 20 meters below the springs. Flow which rises under ground-water conditions faces significant environmental change at the surface and initially provides poor habitat for *Baetis*. Within 20 meters, recovery begins and counts rise to levels not unlike the anomalous highs for first order streams elsewhere in the Kaweah basin. Representative counts of *Baetis* within a kilometer or two of source points on the foreslope (i.e., stations a little farther downstream) are 0,0,1, 1,11,15,7 and 8 for an average of 6.3, suggesting a decline from the apparent high near the source points.

*Baetis* would appear, on the basis of these limited data, to offer some promise as an indicator of certain types of environmental change -- e.g., a change from allochthonous to autochthonous production, changes associated with movement of masses of relatively sterile bottom material, disturbance due to high flow, breaks in the flow regimen of small streams, and changes from ground water to surface water conditions. Effects of other changes, notably mild sewage pollution, nutrient enrichment, temperature increases and marked reduction of natural flow, remain to be explored. *Baetis* may be particularly useful as an indicator of such change due to its almost ubiquitous occurrence, its major contribution to organic drift (Waters 1962, 1965) and its amenability to simplified sampling techniques.

LITERATURE CITED

ABELL, D.L., 1951. The use of drainage analysis in biological work on streams. Verh. Int. Ver. Limnol. 16:533-537.

MAUCH, E., 1963. Untersuchungen uber das Benthos der deutschen Mosel unter besonderer Breuchsichtigung der Wassergute. Mitt. Zool. Mus. Berl. 39:1-172.

MORGAN, N.C. and H.J. EGGLISHAW, 1965. A survey of the bottom fauna of streams in the Scottish Highlands. Part I: Composition of the fauna. Hydrobiologia 25:181-211.

WATERS, T,F,, 1962. A method to estimate the production rate of a stream bottom invertebrate. Trans. Am. Fish Soc. 91:243-250.

WATERS, T.F., 1965. Interpretation of invertebrate drift in streams. Ecology 46:327-334.

# FISHES OF THE COLORADO RIVER IN GRAND CANYON NATIONAL PARK[1]

Royal D. Suttkus[2] and Glenn H. Clemmer[3]

The general decline in native fish populations in the American southwest has been documented in numerous studies (Dill 1944; Miller 1946 a,b; Wallis 1951; Minckley and Deacon 1968; Minckley 1973 and others). Isolated spring populations and residents of smaller tributaries have been particularly vulnerable to habitat losses and competition with introduced exotic forms. Species inhabiting large rivers have been similarly affected; however, their status is more difficult to ascertain. Almost 300 miles of the Colorado River through the Grand Canyon has been virtually inaccessible for ichthyological studies until recently. Float trips on large pontoon rafts have opened up the Canyon and have become increasingly popular in the past few years. This increased visitor pressure on the Colorado River and concomitant attention toward vanishing wildlife resources has stimulated our studies on the status of the fishes of the Colorado River in the Grand Canyon National Park.

Our study area extended from Lee's Ferry (which is 15 miles below Glen Canyon Dam) to the upper reaches of the Mead Reservoir at Pierce Landing (River Mile 280). Most of our 13 float trips were made in summer months; however, one trip was scheduled in mid-April and one was in late September. Most of our collecting efforts were in the mouths and lower reaches of the various tributaries.

The flow of the Colorado River through the Grand Canyon has been severely modified by the closure of Glen Canyon Dam in 1963. The seasonal floods and fluctuations of the river are now replaced with variations in water levels which correspond to the generation of electricity. The natural temperature regime has also been modified as the water is discharged from the lower portion of the dam. During our study the water temperature of the Colorado River was consistently 10°C or colder in the upper portion of the river and gradually warmed to a high of 16°C 250 miles downstream. Tributary temperatures varied with the seasons. The still waters behind Glen Canyon Dam act as a silt trap for the normally turbid river, thus the present discharge from the dam is extremely clear.

Fish collections were obtained from thirty-five different sites along 280 miles of the Colorado River in Coconino and Mohave counties in Arizona. A total of 112 collections was obtained between September 1970 and June 1976. Nineteen species of fishes were represented of which fifteen (79%) were introduced (exotics). The four native fishes were the humpback chub, *Gila cypha*, speckled dace, *Rhinichthys osculus*, flannelmouth sucker, *Catostomus latipinnis*, and bluehead sucker, *Pantosteus discobolus*. In addition to the nineteen species two different hybrid combinations were taken: the sucker hybrid *Catostomus latipinnis* x *Xyrauchen texanus* and various crosses of the rainbow trout, *Salmo gairdneri* with other species of trout. We presume the hybrid trout were artificially produced at some hatchery and then stocked in the canyon area.

In comparison to many Eastern rivers (50 to 150 species) the Colorado River could not be considered as species rich even before impoundment. Perhaps eight or as many as ten species once lived in the Grand Canyon area of the Colorado River. However few, most of the forms are unique and most occur nowhere naturally outside of the Colorado basin.

Three of the four native fishes found in the area seem to be maintaining adequate populations. Perhaps their success is due to their ability to utilize a number of small tributaries as well as the larger tributaries for spawning. These three species are the speckled dace, *Rhinichthys osculus*, flannelmouth sucker, *Catostomus latipinnis*, and the bluehead sucker, *Pantosteus discobolus*.

The flannelmouth sucker, *Catostomus latipinnis* (Figure 1, upper), is widespread in the Colorado River system and it was collected from sites throughout the Grand Canyon area, i.e., from Lee's Ferry downstream to the upper end of the Mead Reservoir. Adult, young or both were taken from fourteen tributaries and from nine sites along the main channel of the Colorado River.

The main channel of the Colorado River probably provided more spawning area prior to impoundment than it does now. Although we assume that some spawning takes place in the main stream we did not record direct evidence. All spawning activities that we observed were in the lower sections of tributary streams. In general the flannelmouth sucker spawning period extends from March to late May in the Grand Canyon area.

On February 29, 1976 reproductive condition of the flannelmouth sucker was checked at the mouth of the Paria River. Male individuals varied from a silvery color to orange-salmon color on body and fins. The silvery colored (prenuptial) individuals had slightly developed tubercles. Those males with orange-salmon breeding color had moderately developed breeding tubercles. A few of these males were ripe, i.e., they voided milt upon slight pressure but none was "running" ripe. Most females were robust but none was ripe. The Paria River was 13.5°C and the main Colorado River just off the mouth of the Paria was 7°C. The Paria is invariably turbid and thus precludes direct observations.

On April 3, 1976 collections and observations were made at the Paria River. The Paria at the collecting site was 18°C and the main Colorado was 8.5°C. One "running" ripe male *Catostomus latipinnis* was collected. It had well developed tubercles. Non-ripe females were collected although most had bright orange-tangerine color on lower fins including lower half of caudal fin.

Two ripe male flannelmouth suckers were collected on April 5, 1976 from the Paria River. These two males had better developed tubercles than the non-ripe males. No ripe female was taken although most specimens had moderately developed breeding colors. Two females were blackish or grayish without any orange coloration. The Paria

---

[1]Grand Canyon National Park, Colorado River Research Series: Contribution No. 24; and
Tulane University, Museum of Natural History: Contribution No. 10.

[2]Tulane University, New Orleans, Louisiana.

[3]M ississippi State University, State College, Mississippi.

River was 13°C at time of collection and the nearby Colorado River was 8.5°C.

Numerous ripe male flannelmouth suckers were seined from the Paria River on April 21, 1975. A single ripe female was taken. Some ripe males were golden olive in color but others had a salmon colored band along the side and bright orange-salmon colored ventral fins and lower part of caudal fin. The Paria was 20°C at the time of the collection and the nearby Colorado River was 9°C.

Two ripe males were collected on May 1, 1976 from the Paria River. No ripe female was taken although some exhibited the bright orange-salmon coloration. A number of specimens had open wounds ranging from a dime to a half dollar in size. On May 1 the Paria varied from 25°C to 13°C at the mixing zone with the river. The Colorado was 8°C. On May 2, 1976 another sample was taken from the Paria River but no ripe individuals of either sex was taken. However, one female had extensive bright coloration. The Paria River ranged from 24°C to 22°C in the collecting area and the Colorado River was 8°C. On May 3, 1976 one small male and one large male flannelmouth sucker were found to be in ripe condition. No ripe female was collected although some exhibited breeding colors. Some individuals exhibited the non-nuptial silvery coloration. Some individuals had open sores similar to the type described above. The Paria was 22.5°C on May 3 and the Colorado was 8°C.

On May 30, 1976 some of the many flannelmouth suckers were tuberculate. No ripe individual of either sex was observed. Most individuals appeared to be spawned out. The Paria River ranged from 24°C to 22°C at the site of collection and the nearby Colorado River was 10°C.

Tuberculate male flannelmouth suckers were collected on July 19, 1972 but none was ripe. The Paria was 24.5°C and the Colorado was 12°C.

A collection of flannelmouth suckers was taken from the Paria River on August 7, 1975. Two females and two males were cut open and the gonads were examined. The ova were of mixed size, small and granular. The testes were slender pinkish colored strands. Thus we interpreted both sexes to be in post spawning condition.

A collection was obtained from the Paria River on September 27, 1975. No tuberculate male was taken.

On November 15 and 16, 1975 collecting was done in the Paria River but no flannelmouth sucker was taken. At 9:15 p.m. on November 15 the Paria was 6°C and the main Colorado River 7°C. At noon on November 16 the Paria was 6°C and the main Colorado River was 10°C. The fluctuations in temperature of the Colorado are correlated with the releases from the Glen Canyon dam. We believe the flannelmouth suckers drop downstream after spawning and many move out of the Paria into the main Colorado. When the temperature in the Paria drops below that of the Colorado then most if not all flannelmouth suckers move into the main Colorado. During several different collecting and observation periods numerous individuals were observed moving upstream in the shallows above the deep pool at the mouth of the Paria. Although we did not investigate the upstream areas various hikers told us that large suckers were seen several miles up the Paria.

No specimen of the humpback sucker, *Xyrauchen texanus*, was taken during the entire study. However, we did collect three specimens of the hybrid combination *Catostomus latipinnis* x *Xyrauchen texanus* (Figure 1, lower). Our specimens agree with those described by Hubbs and Miller (1953). We believe the humpback sucker has been forced out of existence in the Grand Canyon section of the Colorado River. The low temperatures that continue to prevail because of the base releases from the Glen Canyon dam are too cold for spawning. Secondly, the humpback sucker apparently does not utilize any of the small tributaries that are available in the Canyon area. Thirdly, the dam is a barrier that prevents upstream movement to suitable spawning areas. We postulate that during the early part of the filling of the Powell Reservoir the dam acted as a barrier but water temperatures remained suitable for spawning thus hybridization took place between the two forms. After the reservoir was filled and hydro-power operation be-

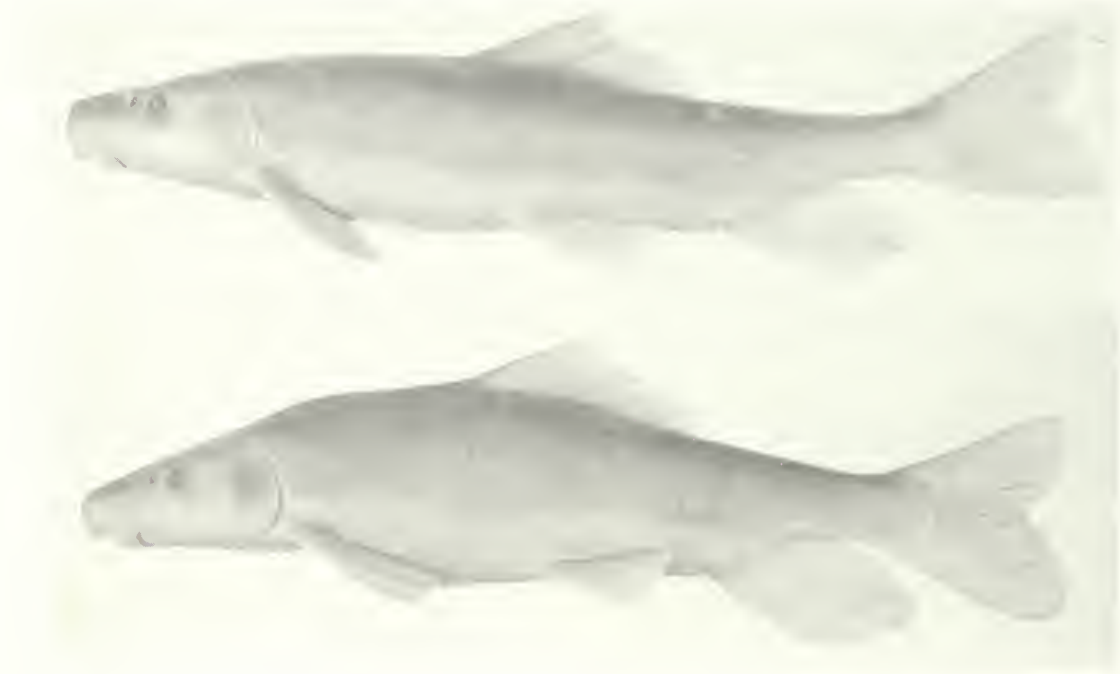


FIGURE 1. (upper) *Catostomus latipinnis* TU 97489:372 mm SL. (lower) *C. latipinnis* X *Xyrauchen texanus* TU 94377:362 mm SL.

gan the habitat became unfavorable as a spawning area for the humpback sucker. We assume that the main Colorado immediately below the Glen Canyon dam is also unfavorable for the flannelmouth sucker but because it utilizes the tributaries such as the Paria it soon greatly outnumbered the humpback sucker and is in the process of genetically swamping out the humpback sucker.

The bluehead sucker, *Pantosteus discobolus*, is highly variable in certain body proportions. Long slim peduncle forms have been collected together with short, stout peduncle forms. The upper photograph in Figure 2 is a tuberculate male with a stout peduncle. This specimen was collected on May 4, 1976 from the Paria River.

The bluehead sucker was taken from all the tributaries noted above for the flannelmouth sucker collections except for Clear Creek and Matkatamiba Creek. It was taken from the same main river sites except for River Mile 65.8, 209, and 212.5. A single specimen of the bluehead sucker was taken from Tapeats Creek on July 24, 1972. Although two different forms of bluehead sucker are recognized we treat them collectively herein.



FIGURE 2. (upper) *Pantosteus discobolus* TU 97588:200 mm SL. (lower) *Rhinichthys osculus* TU 97942: 77.1 mm SL.



FIGURE 3. *Gila cypha* TU 97918:307 mm SL, 368 mm TL.

The systematic status of this varied form and of the flannelmouth are under study and our findings will appear elsewhere.

Reproductive data were recorded for the bluehead sucker at a number of tributaries. Spawning was observed a number of times. The longest periods of observations were made at Shinumo, Kanab and Havasu creeks. Numerous ripe specimens were collected at the mouth of the Paria River but the water was always turbid which prevented direct observations.

Several ripe male bluehead suckers were collected from Crystal Creek on April 28, 1975. These ripe individuals were taken from the mixing zone of the creek and the Colorado River where the water temperature at time of capture was 15°-17°C. Upstream in the creek the temperature was 22°C and the Colorado River was 11°C. A slight pink colored band appeared on the sides of the ripe males after they were in preservative for several hours. Crystal Creek was revisited on June 6, 1975. One small group (one female and four males) was observed spawning in a small plunge pool area about a mile upstream from the mouth. Four adults (spent) were found dead along the stream between the mouth and the spawning site at the plunge pool. Three were preserved and one was discarded because it was rotten. The water temperature at the site of spawning was 22°C.

Many groups of spawning bluehead sucker were observed in Kanab Creek on May 1, 1975. Spawning was observed in a section of stream several hundred meters above the mouth of the creek. Spawning occurred in the deep plunge pools and in deep raceways. Usually several males were associated with each female. The pink lateral band was not pronounced on any of the spawning individuals. The water temperature at the site of spawning was 16°C. The Colorado River was 10.5°C.

No adults were seen or collected during a visit to Kanab Creek on June 9, 1975. Only small young and juvenile bluehead suckers were taken. Also, on June 6, 1976 only small young and juvenile specimens were collected.

Ripe males of the bluehead sucker were collected from the Paria River on May 2, 1976. A light pinkish band was developed on the sides. The Paria ranged in temperature from 22°C to 24°C in the area where the ripe suckers were taken. Several ripe males and one "running" ripe female were collected from the Paria River on May 4, 1976. The female was robust which indicated that spawning had just begun. The water temperature was 14°C at site of collection.

On May 2, 1975 several ripe male bluehead suckers were obtained from the mixing zone at the mouth of Havasu Creek. A moderately developed pink band was present on one specimen. The temperature at the mixing zone was 12°C. After collecting at the mouth the senior author climbed up on an overhanging ledge to make observations. Shortly after getting to the observation place a group of four bluehead suckers was observed going through spawning movements in the deep part of the lower creek pool which was "crystal" clear. Soon after a pair was sighted which moved over a mixed gravel and sand area at the tail end of the deep pool where it was about a half meter deep. The pair spawned four times within 10 minutes. The vibration or quivering of bodies during spawning was clearly visible.

Spawning of the bluehead sucker was observed on May 24, 1973 in Havasu Creek. Spawning was observed for nearly half an hour before we decided to collect a series of specimens. The spawning activity occurred in a pool about a hundred meters up from the mouth of the creek. The spawning groups were composed of one female and two to five males. Most of the spawning occurred over gravel and rubble, around bases of large boulders where the depth was about one meter. The ripe males had an orange-pink stripe above a black lateral band. Beneath the dark lateral band the lower side and belly were white. Silver flecks were visible on the dorsal and lateral aspects of the peduncle. These flecks seemed to flash as the fish twisted and turned.

A single ripe male was taken from the Colorado River at the mouth of Royal Arch Creek on May 23, 1973. This male had a broad light pink lateral band. An adult female was taken at the same time but was not ripe. The temperature in the river was 10°C. Later in the day several ripe male bluehead suckers were collected from the Colorado River at the mouth of Deer Creek. The water was a little over a meter in depth where the collection was obtained and was 10.5°C at the time of collection. We presume that our presence in each of the areas scared the fish out of the warmer, clear tributary water into the turbid river where we caught them.

Shinumo Creek flowing from the north rim is one of the colder tributaries in the Grand Canyon area. The temperature was 9°C on April 29, 1975 while the Colorado River at the mouth of the Shinumo Creek was 11.5°C. Nine adult bluehead suckers were collected from the creek but none was in nuptial condition. On June 7, 1975 and June 4, 1976 many spawning groups were observed. Actually hundreds of individuals were observed in the few meters between the river and the falls. The water temperature in Shinumo Creek was 17°C on June 7, 1975 and 23°C on June 4, 1976. There were various color patterns however most individuals displayed a pink stripe above a dark lateral band. We found no evidence of spawning of the bluehead sucker later than the middle of June, however, sporadic spawning may take place throughout the summer in the Paria River area where there is a comparatively large mixing zone of Paria and Colorado river waters.

As stated above spawning of bluehead suckers was observed in Kanab Creek on May 1, 1975. The seven young collected on June 9, 1975 from Kanab Creek ranged in standard length from 16.0 to 19.7 mm with an average standard length of 17.9 mm.

The speckled dace, *Rhinichthys osculus*, is the only species of the four native fishes that occurs naturally outside of the Colorado River system. It is widespread over the Great Basin area and there are numerous subpopulations recognized. The speckled dace was found in the main stream of the Colorado River in the Grand Canyon area (River Mile 0 down to River Mile 246) as well as in most of the tributaries. A variety of color patterns was found in the main river and the various tributaries. Although most specimens can be placed into either the "banded" or "unicolored" categories (Minckley 1973:130) some have intermediate patterns. Figure 2, lower, represents a unicolored specimen which was taken from the Colorado River at mouth of Royal Arch Creek, River Mile 116.5.

The speckled dace was taken from a number of very small tributaries from which neither the flannelmouth sucker, *Catostomus latipinnis*, nor the bluehead sucker, *Pantosteus discobolus*, was taken. These small tributaries are Hermit Creek (River Mile 95), Boucher Creek (River Mile 96.5), Blacktail Canyon Creek (Mile 120), Stone Creek (Mile 132) and Travertine Creek (Mile 229). Blacktail Canyon Creek and Stone Creek enter the

Colorado River from the right and the rest enter the river from the left. The variation in color patterns was not restricted to tributary samples from either side of the river.

Reproduction occurs during late spring, summer and early fall. Direct spawning observations were made on two occasions. A ripe female collected on April 28, 1975 voided numerous large eggs upon slight pressure. This female was taken from Crystal Creek (River Mile 98.2). The water temperature of the creek was 22°C at the time of collection. During the same time the Colorado River was 11°C. Nuptial coloration was apparent; the corner of mouth, the upper portion of operculum, bases of pectoral, pelvic and anal fins and lower portion of caudal fin were reddish. A ripe male was taken from Clear Creek (River Mile 84.2) on June 6, 1975. The water temperature was 20°C at the place of capture. Besides being tuberculate the male specimen had the same reddish areas as described for the female mentioned above but perhaps even brighter. Tuberculate males were taken during last of April through summer months as late as the middle of November. The November collected specimens were in postspawning condition and exhibited blunt pointed tubercles which were believed to be in a state of regression.

A sample of young taken from Boucher Creek (River Mile 96.5) on June 4, 1976 represented an early spawning. The six specimens ranged from 7.3 to 12.7 millimeters in standard length and averaged 10.3 mm in standard length. Another sample which represented a late spawning was collected from the Paria River (River Mile 0) on November 16, 1975. The thirty-four specimens ranged from 12.4 to 20.3 mm standard length with an average of 15.6 mm. For comparison, an adult speckled dace may exceed a hundred millimeters in standard length.

The original description of the humpback chub, *Gila cypha*, was based on specimens from the Grand Canyon area (Miller 1946a). We collected one adult humpback chub from Shinumo Creek on August 1, 1975. This individual was photographed and released. Four adult humpback chubs* were obtained from the Little Colorado River near its mouth on June 2, 1976. No adult specimen of the bonytail, *Gila elegans*, was taken during the survey. Positive identification of young and small juvenile specimens of *Gila* has not been made up to this time but we believe that these small specimens are *Gila cypha*. During our study young or small juvenile *Gila* were taken at River Mile 44, 61.5, 65.8, 69, 71 and 108.7. A single young specimen (35.6 mm in standard length) was taken at the River Mile 44 site on September 8, 1970. Additional attempts to collect *Gila* above the Little Colorado River (River Mile 61.5) failed to produce any more specimens. Although Holden and Stalnaker (1970) reported specimens of *Gila* from Lee's Ferry our numerous attempts with a small-mesh seine revealed no *Gila* of any size.

In addition to the adult *Gila* that was captured and released at the Shinumo Creek site, two young *Gila* were taken on September 23, 1975. One measured 32.3 mm and the other 32.8 mm in standard length. The four smallest specimens of *Gila* obtained from the mouth of the Little Colorado River were 26.0, 27.3, 27.6 and 28.2 mm in standard length. These specimens were collected on July 30, 1975. The smallest specimen taken at River Mile 69 was 27.6 mm in standard length and was collected on September 22, 1975. Two small specimens of *Gila* were obtained from the Colorado River at River Mile 71 on April 26, 1975. These two specimens measure 26.2 mm and 28.1 mm in standard length. The three smallest specimens taken during the study were obtained from the same area (River Mile 71) on September 22, 1975. These three specimens measure 24.5, 24.6 and 24.6 mm in standard length. These data are important additions to our knowledge of the chub in the Grand Canyon area and will be useful in the planning of continued studies. Unfortunately we have not observed spawning activity nor have we observed any ripe individuals. In consideration of the size of the young and the various dates of collection we believe that spawning may occur at various times during the summer months. However, the present spawning pattern may be a disrupted one which has resulted from the imposed environmental conditions.

We believe that the impoundment of the Colorado River by the Glen Canyon dam and the subsequent continuous unnatural releases of cold bottom water has had a devastating effect on the *Gila* population. We believe our samples are evidence that the distribution of *Gila* in the Grand Canyon area has been reduced to an area near and extending a few miles below the mouth of the Little Colorado. Further, we believe the continuance of the Little Colorado River in its present physical and chemical state is essential to the survival of *Gila* in the Grand Canyon. The Little Colorado River and the main Colorado River downstream to Shinumo Creek is critical habitat.

Our survey did not disclose any specimens of the Colorado squawfish, *Ptychocheilus lucius*. Numerous sampling sites should have produced young or juveniles if the species still exists and reproduces in the Grand Canyon area. We are convinced that the Colorado squawfish was extirpated from the Canyon area by impoundment and the conditions that prevailed thereafter.

The fifteen exotic species taken during the study are listed with annotations.

The threadfin shad, *Dorosoma petenense*, an exotic form presumably was introduced as a forage species for the large introduced game species. The threadfin shad was collected at Spencer Creek (Mile 246), at Emory Falls (Mile 274.3) and at Scorpion Island (Mile 279.5).

A single specimen of the coho salmon, *Oncorhynchus kisutch*, was seined at River Mile 194.5 on August 16, 1971.

The introduced rainbow trout, *Salmo gairdneri*, and various hybrid combinations were taken from many of the tributaries and various places along the main river. No young or juveniles were collected around the mouth of the Paria River and we suspect that little if any spawning is successful in that part of the river.

The carp, *Cyprinus carpio*, was as widely distributed in the Grand Canyon area as the rainbow trout. Schools of individuals were observed in the main river from Lee's Ferry down to and along the shores of the Mead Reservoir and at the mouths of all moderate to large size tributaries. For example, a group of 21 was observed at River Mile 34 on July 29, 1975 and twelve were collected from the mouth of Kanab Creek on June 9, 1975. The uppermost site for young or juvenile carp was the Little Colorado River (Mile 61.5). Young or juveniles were collected at Cardenas Creek area (Mile 71), River Mile 194.5 and at Emory Falls in the Mead Reservoir (Mile 274.3). All other collections and sightings were of adults thus indicating that the conditions prevailing in the upper stretches of the Colorado River around Lee's Ferry are not favorable spawning area even for the tolerant carp.

*_____

*_Gila cypha_ were collected under Federal Permit No. PRT 8-185-C.

A single specimen of the virgin spinedace, *Lepidomeda mollispinis*, was collected from the mouth of the Paria River on July 19, 1972.

A single specimen of the golden shiner, *Notemigonus crysoleucas*, was collected from Kanab Creek (Mile 143.5) on June 9, 1975.

The red shiner, *Notropis lutrensis*, was collected from five different sites. On August 16, 1971 five specimens were collected at River Mile 194.5 and one specimen from River Mile 212.5. Subsequently no more specimens were collected above the head of the Mead Reservoir. The red shiner was collected at Spencer Creek (Mile 246) on August 5, 1975 and June 8, 1976. It was collected at Scorpion Island (Mile 279.5) and Pierce Ferry Landing (Mile 280) on August 5 and August 6, 1975 respectively.

The fathead minnow, *Pimephales promelas*, another introduced bait fish apparently can tolerate the coldwater conditions better than the red shiner which is a native of the lower Mississippi Valley. The fathead minnow was collected from 16 different sites, the uppermost locality was River Mile 44 and the lowermost was Spencer Creek (River Mile 246). It was collected five different times at the mouth of the Little Colorado, four times at Royal Arch Creek and four times at Deer Creek.

The channel catfish, *Ictalurus punctatus*, was collected from six different sites: Little Colorado River, Cardenas Creek area (Mile 71), Shinumo Creek, Kanab Creek, River Mile 194.5, and Spencer Creek. It was collected at the Little Colorado River mouth twice, four times from mouth of Kanab Creek and once from each of the other sites.

The Rio Grande killifish, *Fundulus zebrinus*, seems to be well established at a number of tributaries. This introduced killifish was collected six different times at the mouth of the Little Colorado River, three times at the Cardenas Creek and both times that we collected at Spencer Creek. The Rio Grande killifish is abundant at Spencer Creek and during the last trip on June 8, 1976, many spawning groups were observed. The Rio Grande killifish was collected from ten different sites, the uppermost at the Little Colorado and the lowermost at Spencer Creek. Miller and Lowe (1964) reported the Rio Grande killifish from the middle part of the Little Colorado River basin where it was first noticed in 1938. Minckley (1973) repeated the above record and had no additional locality records although fish samples were taken from various sites along Little Colorado River and main Colorado River. When we examine our records in a chronological fashion we would have to say that we have witnessed a dramatic dispersion in a downstream direction from the mouth of the Little Colorado down to the head end of the Mead Reservoir.

The mosquitofish, *Gambusia affinis*, was collected at two sites: Emory Falls (Mile 274.3) and Pierce Ferry Landing (Mile 280).

A dead striped bass, *Morone saxatilis*, was observed floating in the Mead Reservoir at approximately River Mile 250. It was just under 700 mm in total length.

The green sunfish, *Lepomis cyanellus*, bluegill, *Lepomis macrochirus*, and the largemouth bass, *Micropterus salmoides*, were collected at Spencer Creek. In addition, the largemouth bass was collected at Emory Falls and Scorpion Island.

In conclusion we would like to reiterate and emphasize a message that Wallis gave in his paper of twenty-five years ago. He said, "The fauna is in urgent need of further research, because many forces are fast exterminating it". He cited references that stated similar messages before him. We believe that the humpback chub is in a precarious state, and we cannot assume that it will maintain a population in the Grand Canyon. Any form of harassment such as angling within the present known distribution should not be permitted

The study of the fish fauna should be established as a continuous long-range program.

We acknowledge the following individuals for their aid in collecting specimens: Clyde Jones, James Deacon, James Williams, Dawn Remington, Lyn Branch, Cindy Deacon, Linda Loetterle, Deborah Robertson, Margaret Mathews, Pat Moss, Leah Straub and Alice Stevenson.

All photographs were done by Jeanne Suttkus.

## LITERATURE CITED

DILL, W.A. 1944. The fishery of the lower Colorado River. California Fish and Game, 30: 309-201.

HOLDEN, P.B. and C.B. STALNAKER. 1970. Systematic studies of the cyprinid genus *Gila*, in the upper Colorado River basin. Copeia, 1970(3): 409-420.

HUBBS, C.L. and R.R. MILLER. 1953. Hybridization in nature between the fish genera *Catostomus* and *Xyrauchen*. Pap. Michigan Acad. Sci. Arts, Lett., 38:207-233.

MILLER, ROBERT R. 1946a. The need for ichthyological surveys of the major rivers of western North America. Science, 104(2710):517-519.

MILLER, ROBERT R. 1946b. *Gila cypha*, a remarkable new species of cyprinid fish from the Colorado River in Grand Canyon, Arizona. Jour. Wash. Acad. Sci., 36(12):409-415.

MILLER, ROBERT R. and C.H. LOWE. 1964. Part 2. An annotated checklist of the fishes of Arizona. *In*: The vertebrates of Arizona, ed. by E.H. Lowe. Univ. Arizona Press, Tucson, Arizona, pp. 133-151.

MINCKLEY, W.L. 1973. Fishes of Arizona. Arizona Game and Fish Department. Phoenix, 292 pp.

MINCKLEY, W.L. and J.E. DEACON. 1968. Southwestern fishes and the enigma of "endangered species". Science, 159:1424-1432.

WALLIS, O.L. 1951. The status of the fish fauna of the Lake Mead national recreational area, Arizona-Nevada. Trans. Amer. Fish. Soc. 80(1): 84-92.

# ENDANGERED AND THREATENED FISH IN THE YAMPA AND GREEN RIVERS OF DINOSAUR NATIONAL MONUMENT[1]

K.H. Seethaler, C.W. McAda, and R.S. Wydoski[2]

## INTRODUCTION

The Colorado River system of the western United States has been greatly modified during the past century, primarily by the construction of dams. The resulting alterations of the flow regimes and of water temperatures below these impoundments, and competition with introduced fish, are believed to be the major factors in the decline of four endemic Colorado River fish: Colorado squawfish, *Ptychocheilus lucius*; humpback chub, *Gila cypha;* bonytail chub, *Gila elegans*; and humpback sucker, *Xyrauchen texanus* (Vanicek, Kramer, and Franklin 1970; Minckley 1973; Holden and Stalnaker 1975b). The first two species are officially designated as "endangered" by the U.S. Fish and Wildlife Service (1973); the other two were recommended for listing as "endangered" and "threatened", respectively, by the Desert Fishes Council in 1975.

Other water development projects are in progress or planned for the upper Colorado River basin. Crawford and Peterson (1974) noted that the Colorado River, the key to development of the arid southwestern United States, is probably the most utilized, controlled, and fought over river in the world. This river annually collects less water per square mile of drainage than any other major river in the United States, yet it serves 15 million people with water for cities, irrigated agriculture, recreation, mining, and industry (Utah Water Research Laboratory 1975). This region contains some of the largest fuel deposits (coal, oil, oil shale, uranium) in the United States, and water will be a principal factor in the development of these energy resources (Bishop, Chambers, Mace, and Mills 1975). Consequently, there is manifest pressure to proceed with further alteration of this already over-allocated water resource. More development will impose additional stress on the endemic fish fauna of this unique ecosystem.

This summary of the current status of threatened and endangered fish inhabiting Dinosaur National Monument is based on a literature review and current research by the Utah Cooperative Fishery Research Unit.

## DESCRIPTION OF THE AREA

The upper Green and Yampa rivers originate as cold, clear streams in the Rocky and Uinta mountains. These headwater streams supply the main tributaries of the Colorado River Basin that flow through deserts where spectacular canyons have been carved by erosion of the soft sandstones. Historically, the main stems were warm and turbid and subject to sudden changes in volume and velocity. Flaming Gorge Dam, which was completed in 1963 and is near the Utah-Wyoming border, has changed the upper Green River. Flows that were characteristically high in spring and low in winter became much more stabilized seasonally, but may be subject to rapid daily fluctuations (Vanicek, Kramer, and Franklin 1970).

Dinosaur National Monument is in northwestern Colorado and northeastern Utah (Fig. 1). The Yampa River empties into the Green River at Echo Park, about 105 km below Flaming Gorge Dam, modifying and partly restoring the Green to preimpoundment conditions. For the next 42 km, the Green River passes alternately through canyons and meandering flats until it opens upon the Wonsits Valley in the Uinta Basin at the Monument's southwest boundary. At this point the river has largely recovered from the impact of Flaming Gorge Dam with respect to temperature and perhaps several other characteristics as well.

We note, therefore, three distinct habitat types within the study area, plus one section in which there is a gradation between these types.

*The Green River above Echo Park* - A cold-water environment under the artificial control of Flaming Gorge Dam.

*The Yampa River* - Still a relatively free-flowing, warmwater river.

*The Green River below the Monument* - A warmwater river, largely recovered from the effects of Flaming Gorge Dam, extending downstream to the confluence of the Green and Colorado rivers in Canyonlands National Park, a distance of 550 km.

*The Green River between Echo Park and the lower Monument boundary* - A region of gradation from a cold - to a warmwater environment, extending about 42 km from the confluence of the Yampa and Green rivers downstream to the southwest boundary of the Monument.

## RESEARCH ON THE FISH FAUNA IN THE WATERS OF, AND ADJACENT TO, THE DINOSAUR NATIONAL MONUMENT

In March 1963, Secretary of the Interior Stewart L. Udall requested that the Utah Cooperative Fishery Unit conduct investigations to determine the extent of changes in habitat and fish populations that occurred in Dinosaur National Monument after the closure of Flaming Gorge Dam. The conclusion of the 1963-1966 study was that the environment of the Green River was changed significantly from the dam to the mouth of the Yampa River (Vanicek 1967). Below their confluence, the Yampa River, which had retained its natural character, moderated the altered Green River sufficiently to allow the continued existence of all species of fish present before impoundment. The large native fishes disappeared from the 105 km reach below Flaming Gorge Dam because of the cold water discharge from the dam and were replaced by introduced rainbow trout

[1]This study was supported by U.S. Fish and Wildlife Service Contract No. 14-16-0008-1140. The funds that enabled the senior author to attend the First Conference on Scientific Research in the National Parks were granted by the Ecology Center, Utah State University, Logan.

[2]Utah Cooperative Fishery Research Unit, Utah State University UMC 52, Logan, Utah 84322. The Utah Cooperative Fishery Research Unit is jointly sponsored by the Utah Division of Wildlife Resources, Utah State University, and the U.S. Fish and Wildlife Service.

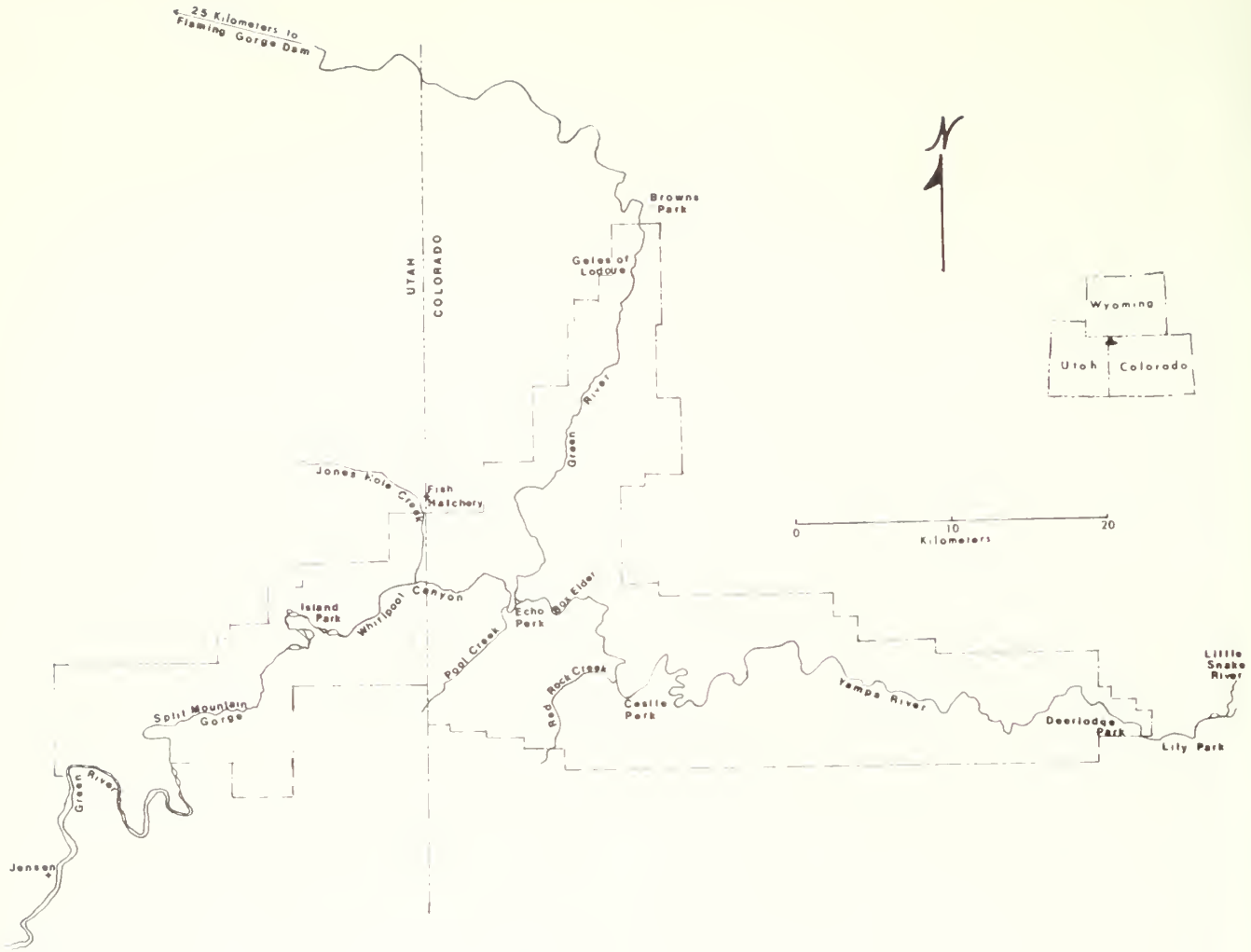



FIGURE 1. Dinosaur National Monument study area.

*(Salmo gairdneri)* (Vanicek, Kramer, and Franklin 1970).

Between 1968 and 1972, the Utah Cooperative Fishery Research Unit assessed the distribution and relative abundance of fish throughout the upper Colorado and Green Rivers, including major tributaries (Holden 1973). Between 1974 and 1976, the Unit investigated the movement, habitat, and possible spawning areas for the Colorado squawfish and humpback sucker in the lower Yampa and upper Green rivers. These studies by the Unit have indicated that these four indigenous fish species are declining in abundance. In most areas, only large adults have been captured, suggesting a lack of reproduction.

## FISH FAUNA

The native fish fauna of the Colorado River basin is unique, in that 74% of the native species occur only in this river system (Miller 1959). This high degree of endemism is linked to a long period of isolation reflected in the geologic history of the basin. The Colorado River Wildlife Council listed 20 species (40%) as native to the river and 30 species (60%) as introduced (Richardson 1976). Holden and Stalnaker (1975a) recorded 10 native fish species (34%) and 19 introduced species (66%) in the main stems of the upper Colorado River system. In the present study we have updated the list of fishes to reflect conditions as we now perceive them in the vicinity of Dinosaur National Monument.

Holden (1973) found all 10 of the native species and all but 4 (15 of 19) of the introduced species in the lower Yampa. Our recent observations were similar to his, although we did not find largemouth bass *(Micropterus salmoides)*, bluegill *(Lepomis macrochirus)*, green sunfish *(Lepomis cyanellus)*, or walleye *(Stizostedion vitreum)*. Holden considered these fish to be occasional or rare. More significantly, we failed to collect any specimens of the native bonytail chub. We collected three introduced species from the Yampa River that were not documented previously: One plains killifish *(Fundulus kansae)* was captured near Red Rock Creek in July 1975; one Utah chub *(Gila atraria)* was collected at Box Elder in April 1976 (see Fig. 1 for locations); and sand shiners *(Notropis stramineus)* were seined in Lily Park and in the Little Snake River just above the Monument boundary. Researchers from Colorado State University have also collected this species at Lily Park and points further upstream in the Yampa River.(C.G. Prewitt and D.E. Snyder, personal communication).

In the Green River we collected one smallmouth bass *(Micropterus dolomieui)* at Horseshoe Bend (about 40 km below the Monument) in October 1975, and the Colorado Squawfish Recovery Team captured one northern pike *(Esox lucius)* below Horseshoe Bend in May 1976. Indeed the species composition of the fish population in the Green River below the Monument appears to differ from that of the Yampa in several notable respects: The centrarchids and walleye, only occasionally found in the

Yampa River, are common in this portion of the Green; the red shiner *(Notropis lutrensis)* is rare in the Yampa, but is abundant in the lower reaches of the Green River in the Monument and downstream. We collected two juvenile squawfish in the Green River at Jensen, Utah, in October 1975 and the Squawfish Recovery Team captured several below Jensen in May 1976. Thus, conditions appear suitable for at least limited reproductive success downstream from the Monument, but not upstream. The species composition appears to reflect the differences in the habitats that were described above.

## CURRENT STATUS OF ENDANGERED AND THREATENED ENDEMIC FISH OF THE UPPER COLORADO RIVER SYSTEM

The decline of the four endemic fish species of the upper Colorado River may be attributable to various factors. The following outline lists some of the possible causes contributing to the decline of these species.

I. Stream Alteration

A. Dams

1. Physical obstructions to movement and migration.

2. Flow Patterns - more stable on annual basis, less stable on a daily basis.

a. Loss of the scouring effect from peak flows.

b. Loss of flows that may elicit spawning migration or behavior.

c. Effect on other habitat characteristics such as changes in substrate, river morphology, and riparian vegetation.

3. Temperatures - cooler in summer, warmer in winter.

4. Turbidity - reduced downstream.

5. Reservoirs

a. Not suitable for successful reproduction of large-river fish.

b. Favor other species.

B. Irrigation

1. Increased leaching of the soil resulting in increased salinity through return flows.

2. Changes in water quality due to the addition of fertilizers, pesticides, and other materials.

C. Dewatering (transmountain diversion, evaporation from reservoirs, irrigation, industry, municipal water use, etc.).

1. Reduces flow (volume and velocity)

2. Concentrates dissolved solids, increasing salinity.

D. Channelization

1. Eliminates slow-moving backwaters and eddies.

2. Alters species composition.

3. Substrate becomes unstable, adversely affecting invertebrates that may serve as a food supply.

E. Unstable Banks (caused by livestock grazing, roads, and other activities of man) alter river morphology.

II. Competition and predation are increased by introduction of non-native fish species.

III. Pollution and Eutrophication

A. Industrial, agricultural, and municipal wastes that may be toxic may increase.

B. Water quality may change --in particular salinity and sedimentation may increase.

IV. Other Factors

A. Parasites may be introduced by exotic fish species.

B. Food organisms may change in species composition and abundance with changes in stream habitat.

C. Fishing pressure may be too heavy on large, adult Colorado squawfish and the bonytail and humpback chubs, which are very vulnerable to sport fishing.

*Colorado squawfish* - Whereas this species was once abundant throughout the Colorado River system, with a range extending from Wyoming to the Gulf of California, it is now rare and restricted to parts of the upper basin (Fig. 2). A few squawfish may exist below Lake Powell, but the existence of self-sustaining populations is doubtful. The occurrence of this species in the San Juan River is also uncertain. It is no longer found in the now clear, cooler waters of the Green River above the confluence with the Yampa River, but adults were collected in the lower Yampa in 1968-71 and 1974-75 during July and August after water temperatures reached 20-21 C (Holden 1973, McAda and Seethaler 1975). Most captured squawfish have been males; no ripe females have been collected. However, several squawfish believed to be spent females were collected in the Yampa between Cross Mountain and the confluence of the Little Snake River, and a fisherman reported to us of catching a ripe female in early August 1975 at this same location. These suspected females were captured in deeper water than most of the males, which tended to congregate in shallow eddies near the bank.

It has been assumed that the movement of squawfish into the Yampa River during the summer is a spawning migration. It is also commonly assumed that this migration is triggered by some seasonal factor or factors such as temperature, turbidity, flow, photoperiod, or water chemistry.

Spawning has not been observed in the turbid river waters. At Willow Beach National Fish Hatchery, Arizona, spawning of captive Colorado squawfish occurred but was not directly observed.

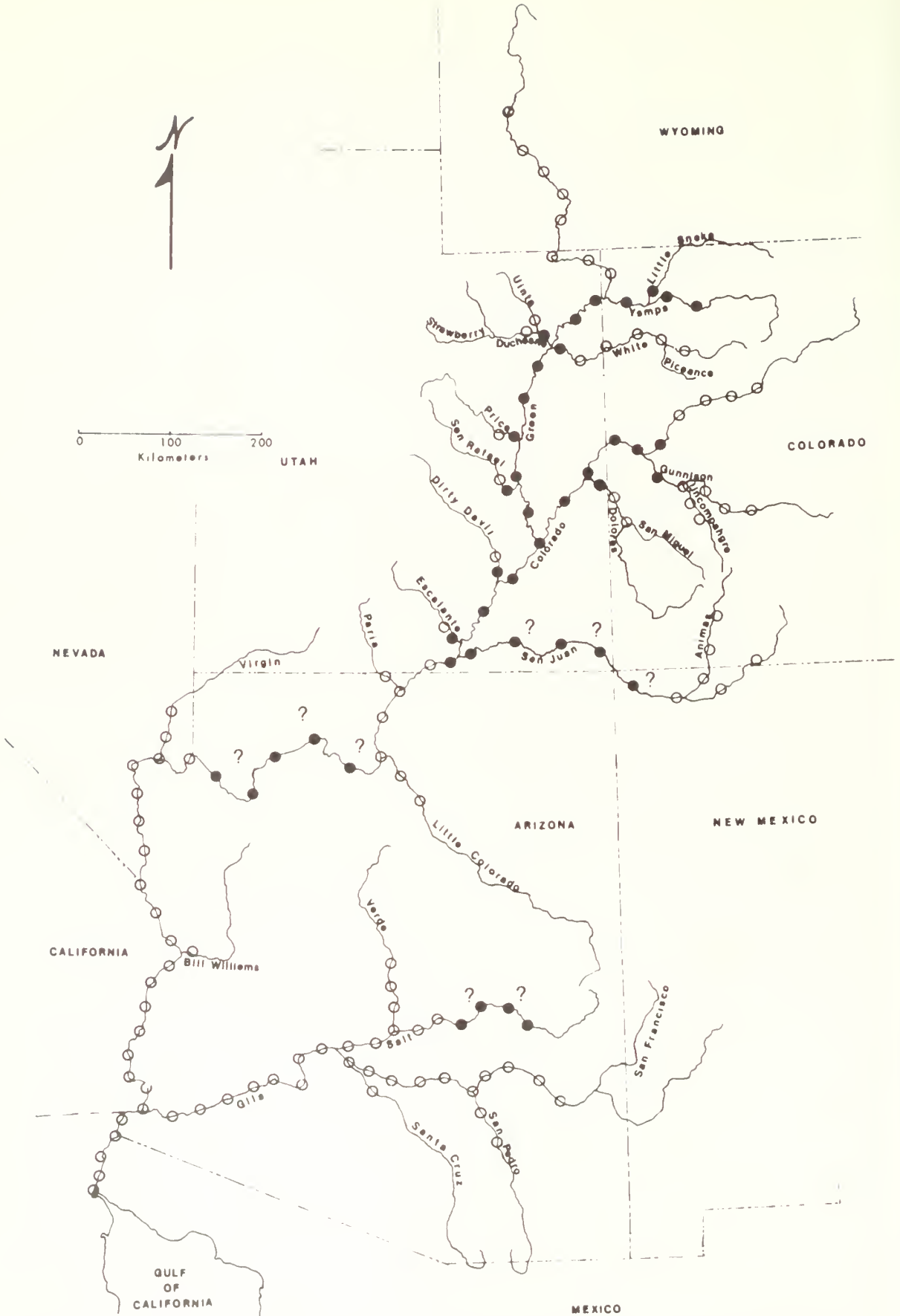



FIGURE 2. Historical distribution (all circles) and present distribution (solid circles only) of the Colorado squawfish in the Colorado River basin based on published reports and recent collections. (The question marks indicate uncertainty in present fish distribution.)

On 1 July 1974, two months after the water temperature had reached 18 C and after the fish had been injected with hormones, eggs were found attached to rocks and gravel at the head of the raceway, where water percolated through the gravel. (D. Toney, Hatchery Supervisor, personal communication; Toney 1974).

In addition to providing potential spawning locations, the high water levels of the Yampa River in early summer provide habitat and food. As the Yampa recedes in late summer, habitat and food are greatly reduced and the fish apparently return to the Green River where conditions are more favorable. A few squawfish may remain in the deeper pools of the Yampa throughout the winter; although our attempts to capture them in the late fall and early spring were unsuccessful, local residents reported observing them in winter in the deeper ice-covered pools.

Squawfish are piscivorous, being a top carnivore in the Upper Colorado River. Vanicek (1967) found that squawfish as short as 50 mm (total length) had eaten fish. As the squawfish grow, fish increase in importance as food, comprising substantially the entire diet of squawfish longer than 200 mm. The fish are opportunists, however, and also eat other food items such as frogs and mice.

Squawfish reproduction has declined steadily since the 1960's. Vanicek (1967) determined that year classes were strong in 1959, 1961, 1963, 1964, and possibly 1966, but weak in 1962 and 1965. He collected 275 young of the year in 1964, 42 in 1965, and 560 in 1966. Holden (1973) found young of the year in Desolation Canyon in 1971 and in the Green River at Canyonlands National Park in 1970 and 1971. He considered juvenile squawfish to be abundant at Echo Park in 1968, but found very few in 1969 and none in 1970. We collected young squawfish (about 75 mm TL) in the Green River at Jensen, Utah in 1975 where conditions still appear to be suitable for successful reproduction. The decline in successful reproduction can be correlated with the impoundment at Flaming Gorge and concurrent changes in composition of the fish fauna. Conditions in the river which favor exotic species may be detrimental to the native species.

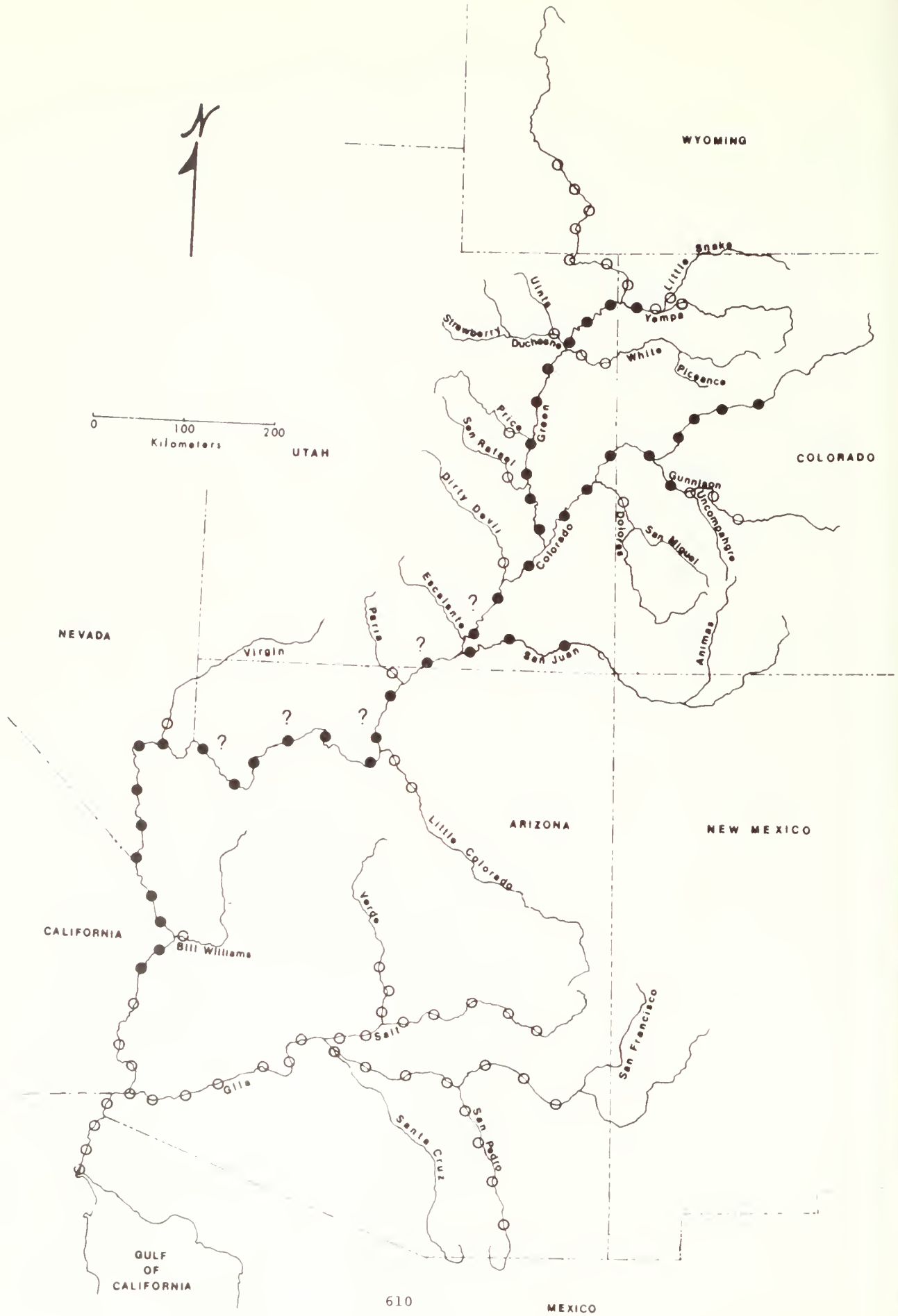
We determined that sexual maturity for squawfish occurs when the fish reach a minimum total length of 420 mm, at about age VII. Squawfish once attained much greater size than they do today. It is not known whether this greater size was due to longevity or whether conditions in the past favored faster growth. The larger fish in the past may have had a greater reproductive potential than the smaller fish that are present today. Perhaps lower fecundity today, coupled with high mortality of young squawfish, is resulting in fewer offspring in this species. These factors may have yet other implications for the reproductive potential that are not fully understood.

*Humpback sucker* - The range of this unique fish has been drastically reduced in the Colorado River system (Fig. 3). The species has been completely extirpated from the Gila River system of the lower Colorado River basin, where it was once abundant (Minckley 1973). In 1949, a commercial fisherman in Sahuaro Lake (Salt River, Arizona) had a spawning season catch of more than six tons of this species (Hubbs and Miller 1953). However, not one specimen was found when Sahuaro Lake was drained in 1966 (Minckley and Deacon 1968). Humpback suckers were also relatively common in Colorade River reservoirs during the 1940's and 1950's (Dill 1944; Wallis 1950; Douglas 1952; Jonez and Sumner 1954). This species is still found in Lakes Mojave and Mead, but is declining in numbers and appears to be approaching extinction below Lake Mojave (Minckley 1973).

Although the humpback sucker is more widespread in the upper basin, it has been considered to be rare by all investigators (Vanicek, Kramer and Franklin 1970; Miller 1972; Holden and Stalnaker 1975a, 1975b). During the present study (1974-76), humpback suckers were considered to be relatively common, but not numerous, at two locations in the upper basin: at the mouth of the Yampa River during early spring and late fall, and in a flooded gravel pit (Walter Walker Wildlife Area) that is connected to the Colorado River near Grand Junction, Colorado, during all seasons. Humpback suckers are captured primarily in quiet water areas except during the spring, when they congregate in swift water over gravel bars for spawning.

Evidence of successful reproduction has been lacking in recent years (Vanicek, Kramer and Franklin 1970; Minckley 1973; Holden and Stalnaker 1975a, 1975b). In the spring of 1975, ripe male and female humpback suckers were collected over a gravel bar in the Yampa River about 400 m upstream from its mouth. One of these females (tagged at Island Park) had traveled 21 km upstream to Echo Park (Fig. 1) in 3 weeks. Another spawning bar was located about 2.5 km upstream at Box Elder Park (Fig. 1) on the Yampa River. This is the farthest

FIGURE 3. Historical distribution (all circles) and present distribution (solid circles only) of the humpback sucker in the Colorado River basin based on published reports and recent collections. (The question marks indicate uncertainty in present fish distribution.) ►


N
WYOMING
Snake
Little
Yampa
Uinta
Strawberry
Duchesne
White
Piceance
Price
San Rafael
Green
Dirty Devil
Colorado
Gunnison
Uncompahgre
Dolores
San Miguel
Animas
COLORADO
UTAH
0
100
200
Kilometers
Escalante
Parria
Virgin
San Juan
NEVADA
?
?
?
?
Little Colorado
ARIZONA
NEW MEXICO
Verde
CALIFORNIA
Bill Williams
Salt
San Francisco
Gila
Santa Cruz
San Pedro
GULF
OF
CALIFORNIA
MEXICO

penetration up the Yampa River documented during the present study, although humpback suckers were reported 18 km upstream at Castle Park (Fig. 1) during a previous investigation (P.B. Holden, unpublished data).

Humpback suckers were also attempting to spawn along the shoreline of the gravel pit of the Walter Walker Wildlife Area and on gravel bars in the Colorado River near Grand Junction, Colorado. Neither young of the year nor juvenile humpback suckers were captured at any location, despite many attempts.

During the spawning period, water temperatures in the Yampa River increased from 6 to 10 C and turbidities increased from 600 to 1000 Jackson Turbidity Units (JTU). The temperature of the Colorado River averaged 12 C during this time, and turbidities exceeded 1000 JTU. Temperatures in the gravel pit were approximately 17 C and turbidities were slightly more than 100 JTU. The spawning bars consisted of large cobble-sized rocks at depths of 0.5 to 1 meter, and water velocities averaged 1 m/s. The shoreline of the gravel pit at the Walter Walker Wildlife Area is composed of similar sized rocks and was often agitated by wave action. Douglas (1952) described the spawning of humpback suckers in Lake Havasu on the lower Colorado River. However, spawning was not observed during the present investigation, primarily because of the high turbidity at most potential spawning locations.

Hybrids of the flannelmouth sucker *(Catostomus latipinnis)* and the humpback sucker were observed during the present investigation and were also reported in other studies (Hubbs and Miller 1953; Vanicek, Kramer and Franklin 1970; Holden and Stalnaker 1975a). The incidence of hybridization appears to be increasing (Holden and Stalnaker 1975a), as would be expected in an altered system where one fish is considerably more abundant than another closely related fish, both having similar reproductive requirements. We collected 8 *X. texanus* x *C. latipinnis* hybrids during 1974-76. Humpback suckers also appear to be hybridizing with the introduced Utah sucker *(C. ardens)* in the lower basin (Gustafson 1975), and these hybrids may soon appear in the Upper Colorado River Basin.

*Humpback chub* - This species was previously found in the Flaming Gorge basin of the upper Green River, but only a few (26) were captured in Dinosaur National Monument in 1968-71--usually from eddies adjacent to fast currents (Holden 1973). Only recently discovered (Miller 1946), humpback chubs have never been known to be abundant. In 1973 the Colorado Division of Wildlife found a population of this species in the Colorado River in deep glides near the border between Colorado and Utah (G. Kidd, personal communication). We collected 12 specimens, including possible hybrids with other species of the genus *Gila*, from an eddy about 3.2 km upstream from Castle Park in 1975, 5 on the Yampa near the cutoff channel to the Green at Echo Park in 1975, and 1 at Lily Park in 1976 (see locations in Fig. 1). Although our nets were set in eddies and were near or at the surface, they were adjacent to or in water 4-5 meters deep. We postulate that humpback chubs may be present in the denser pools of the Upper Colorado River system.

*Bonytail chub* - Although formerly abundant, the numbers of this species have been drastically reduced since the closure of Flaming Gorge Dam. Vanicek (1967) found that the 1959, 1960 and 1961 year classes of bonytail chubs were more numerous than the closely related roundtail chubs *(Gila robusta)*. Since then, the bonytail chub has virtually disappeared, while the roundtail chub remains rather common and in no apparent danger of extinction. Only a few bonytail chubs have been found recently (1968-71) in the lower Yampa and Green rivers in Dinosaur National Monument and a few in Desolation Canyon and Canyonlands National Park (Holden 1973). No bonytail chub was collected in 1974-76 in Dinosaur National Monument. An occasional bonytail chub is collected in the lower Colorado River basin (Lake Mohave, Arizona; D.P. Toney, personal communication). Indeed, this species appears close to extinction.

## PROBLEMS ASSOCIATED WITH DEFINING "CRITICAL HABITAT"

In December 1975, the Colorado Squawfish Recovery Team, composed of members from various federal and state agencies, held its first meeting in Las Vegas, Nevada. Several meetings have been held by the Team since then and a draft "Recovery Plan" for preservation of the Colorado squawfish has been prepared. One of the problems that confronted the Team was defining "critical habitat" for this species.

The Endangered Species Act of 1973 -- P.L. 93-205 (U.S. 93rd Congress, 1973) -- with amendments in the Federal Register requires that the "critical habitat" for endangered species be defined so that the potential effects of future alterations to ecosystems can be identified and alternatives sought that would minimize the impacts on fish and wildlife.

The defining of "critical habitat" for aquatic organisms is not as simple as for terrestrial organisms. Water quality and quantity, in addition to the physical environment, are important for aquatic organisms. Alterations (e.g., in water temperature, or dissolved oxygen) that occur upstream can affect the aquatic organisms far downstream. In addition, the streamflow requirements for the endemic fish in the Colorado River are not known. Ohmart, Deason, and Freeland (1975) showed that the backwater marsh habitat of the lower Colorado River, although never extensive, was extremely important for various species of wildlife. Vanicek and Kramer (1969) reported that young squawfish and chubs were commonly captured in backwater habitats in the upper basin. The natural flushing action of the spring runoff may be necessary to keep these habitats from becoming filled with silt and organic material. The historic annual peak flows in the upper Colorado River have been reduced by reservoirs and may result in a reduction of the critical nursery areas that are used by young endemic fish.

## IMPORTANCE OF THE WATERS IN DINOSAUR NATIONAL MONUMENT FOR THE CONTINUED EXISTENCE OF ENDEMIC FISH

The Yampa River may provide a refuge for some, if not all, of the large-river endemic fish that are now threatened or endangered. However, we believe its major contribution to the continued survival of threatened and endangered fish is its amelioration of the Green River below their confluence. Our concern is that any alteration of the Yampa River or its tributaries could have a serious negative impact on this ameliorating effect. Although some comprehensive plans (e.g., Water Resources Council 1971) have been made for the management of the upper Colorado River, fish and wildlife have not been considered adequately in these plans. Information needed for such planning is widely scattered in the literature but is being compiled for reference in future management (R.S. Wydoski, K. Gilbert, K.H. Seethaler, and C.W. McAda, in preparation).

The rationale and moral obligation for man to protect threatened and endangered species has

been summarized in various papers (e.g., U.S. Fish and Wildlife Service 1969; Pister 1976). Decisions regarding alterations to the environment must be based on sound ecological principles if water development is to be compatible with the ecosystem. Often certain species of our native flora and fauna serve as "environmental barometers" of the quality of land and water. When these species begin to disappear, it is a warning that something has changed in the ecosystem that may also affect man. In addition, the U.S. Fish and Wildlife Service (1969) has taken the position that the true value of any wildlife species grows greater as its numbers decline, for in a few individuals are concentrated all the worth of one small but valuable part of our environment.

Natural areas that are within federal refuges, monuments, or parks can provide suitable habitat for threatened or endangered species if the habitat can be protected. Interpretive programs in geology are being used by the National Park Service at Dinosaur National Monument. Although these programs help to interpret the geological evolution that has occurred in these areas, other interpretive programs could be developed to describe the dynamic evolution as in endemic fish species that is occurring in the Monument today.

## LITERATURE CITED


BISHOP, A.B., M.D. CHAMBERS, W.O. MACE, and D.W. MILLS. 1975. Water as a factor in energy resources development. Water Res. Lab., Utah State Univ., Logan, PRJERO28-1. 104 pp.

CRAWFORD, A.B., and D.F. PETERSON. 1974. Environmental management of the Colorado River basin. Utah State Univ. Press, Logan. 313 pp.

DILL, W.A. 1944. The fishery of the lower Colorado River. Calif. Fish Game 30(2):109-211.

DOUGLAS, P.A. 1952. Notes on the spawning of the humpback sucker, *Xyrauchen texanus* (Abbott). California Fish & Game 38(2):149-155.

GUSTAFSON, E.S. 1975. Early development, adult sexual dimorphism, and fecundity of the razorback sucker, *Xyrauchen texanus* (Abbott). Final Rep. to U.S. Fish Wildl. Serv., Contract No.14-16-0002-3585. 43 pp.

HOLDEN, P.B. 1973. Distribution, abundance, and life history of the fishes of the upper Colorado River basin. Ph.D. Thesis, Utah State Univ., Logan. 58 pp.

HOLDEN, P.B., and C.B. STALNAKER. 1975a. Distribution and abundance of mainstream fishes of the middle and upper Colorado River basins, 1967-1973. Trans. Am. Fish. Soc. 104(2):217-231.

HOLDEN, P.B., and C.B. STALNAKER. 1975b. Distribution of fishes in the Dolores and Yampa River systems of the upper Colorado basin. Southwest. Nat. 19(4):403-412.

HUBBS, C.L., and R.R. MILLER. 1953. Hybridization in nature between the fish genera *Catostomus* and *Xyrauchen*. Pap. Mich. Acad. Sci. Arts Lett. 39(1952):207-241.

JONEZ, A., and R.C. SUMNER. 1954. Lakes Mead and Mohave investigations. Nevada Fish and Game Commission, Reno. 187 pp.

MCADA, C., and K. SEETHALER. 1975. Investigations of the movements and ecological requirements of the Colorado squawfish and humpback sucker in the Yampa and upper Green rivers. Prog. Rep. (June 1, 1974-Oct. 31, 1975), U.S. Fish and Wildlife Service Contract No. 14-16-0008-1140, Utah Coop. Fish Res. Unit, Utah State Univ., Logan. 38 pp.

MILLER, R.R. 1946. *Gila cypha*, a remarkable new species of cyprinid fish from the Colorado River in Grand Canyon, Arizona. J. Wash. Acad. Sci. 36(12):409-413.

MILLER, R.R. 1959. Origin and affinities of the freshwater fish fauna of western North America. Pages 187-222 *in* C.L. Hubbs, ed., Zoogeography. Am. Assoc. Adv. Sci., Publ. 51.

MILLER, R.R. 1972. Threatened freshwater fishes of the United States. Trans. Am. Fish Soc. 101(2):239-252.

MINCKLEY, W.L. 1973. Fishes of Arizona. Arizona Game Fish Dep., Phoenix. 293 pp.

MINCKLEY, W.L., and J.E. DEACON. 1968. Southwestern fishes and the enigma of "endangered species". Science 159:1424-1432.

OHMART, R.D., W.O. DEASON, and S.J. FREELAND. 1975. Dynamics of marsh land formation and succession along the lower Colorado River and the importance and management problems as related to wildlife in the arid Southwest. Trans. N.A. Wildl. Nat. Resources Conf. 45: 240-251.

PISTER, E.P. 1976. A rationale for the management of nongame fish and wildlife. Fisheries 1(1):11-14.

RICHARDSON, W.M. 1976. Technical committee minutes. Colorado River Wildlife Council, Las Vegas, Nevada (February 19, 1976):12-18.

TONEY, D.P. 1974. Observations on the propagation and rearing of two endangered fish species in a hatchery environment. Proc. West. Assoc. State Game Fish. Comm. 54:252-259.

U.S. FISH AND WILDLIFE SERVICE. 1969. The right to exist. U.S. Fish Wildl. Serv., Resour. Publ. 69. 12 pp.

U.S. FISH AND WILDLIFE SERVICE. 1973. Threatened wildlife of the United States. U.S. Fish Wildl. Serv., Resour. Publ. 114. 289 pp.

U.S. 93RD CONGRESS. 1973. Endangered species act of 1973 - Public Law 93-205. Senate and House of Representatives of the United States of America Congress, 93rd Congress, Public Law 93-205. December 28, 1973.

UTAH WATER RESEARCH LABORATORY. 1975. Colorado River regional assessment study. Utah Water Res. Lab., Utah State Univ., Logan. 4 vol. Various pagination.

VANICEK, C.D. 1967. Ecological studies of native Green River fishes below Flaming Gorge Dam, 1964-66. Ph.D. Thesis, Utah State Univ., Logan. 124 pp.

VANICEK, C.D., and R.H. KRAMER. 1969. Life history of the Colorado squawfish, *Ptychocheilus lucius*, and the Colorado chub, *Gila robusta*, in the Green River in Dinosaur National Monument, 1964-1966. Trans. Am. Fish Soc. 98(2):193-208.

VANICEK, C.D., R.H. KRAMER, and D.R. FRANKLIN. 1970. Distribution of the Green River fishes in Utah and Colorado following closure of Flaming Gorge Dam. Southwest. Nat. 14(3): 297-315.

WALLIS, O.L. 1951. The status of the fish fauna of the Lake Mead Recreation Area, Arizona-Nevada. Trans. Am. Fish. Soc. 80(1950):84-92.

WATER RESOURCES COUNCIL. 1971. Upper Colorado region comprehensive framework study. Upper Colorado Region State-Federal Inter-Agency Group, Pacific Southwest Inter-agency Committee, Water Resour. Council, Main Rep. and 18 appendices. Various pagination.

# SPECIES RELATIONSHIPS AMONG FISHES OF THE GENUS *GILA* IN THE UPPER COLORADO RIVER DRAINAGE[1]

Gerald R. Smith[2], Robert Rush Miller[2], and W. Daniel Sable[3]

Taxonomic treatment of the chubs of the *Gila robusta* complex (family Cyprinidae) that inhabit the Colorado River basin and certain rivers in north-western Mexico (Figure 1) is problematical and requires study of the entire group for final resolution. It is intended to do this, but in this paper we present data demonstrating that there are three species of this complex in the Colorado River and its major tributaries, from the Grand Canyon region upstream. These chubs are the most extreme members of the genus in their specialization for life in the unique big-river habitat of the Colorado River.

Our objectives are (1) to determine the validity and relationships of the roundtail, bonytail, and humpback chubs in the big-river habitat; (2) to determine their relationships to other populations of *Gila* in the middle and upper Colorado River basin; and (3) to find characters useful for identifying young and adult *Gila robusta* Baird and Girard, *G. elegans* Baird and Girard, and *G. cypha* Miller, and possible hybrids. We do not at this time treat the complex representatives of *Gila* in the Gila River basin (see Rinne, 1976), except to note that *G. intermedia* (Girard) may be a separate evolutionary line, secondarily related to *G. robusta*.

Misinterpretation of the patterns of variation in the nuchal hump and lack of decisive, objective evidence has been the main cause of disagreement among those studying the *G. robusta* complex. The nuchal convexity has never been measured precisely or quantitatively related to other characters. For example, Holden and Stalnaker (1970) used subjective code values for the form of the nuchal hump, and coded continuous morphometric variables (23.1 15.8, etc.) into discontinuous states ("A", "B", etc.), thus losing much of the resolving power of the measurements. The clustering illustrated by them shows only the level at which specimens join clusters; it does not show intermediacy, and it cannot display the morphological relationship of a specimen between other specimens. Thus there is no way to evaluate the supposed "intergrades" cited by Holden and Stalnaker: in their paper the "intergrades" may appear as a result of the method of coding data. They were unable to determine whether the so-called intergrades were part of one variable complex or two incompletely separated species. In contrast, we find that there are very few intermediates, in the Green River at least, and that most specimens, including the "intergrades" shown by Holden and Stalnaker (1970: Figure 4), can be assigned to one of the two species *cypha* or *elegans*.

Our analysis consists of two parts. First, principal components analysis of 34 meristic and morphometric characters, not including a direct measure of the nuchal hump, is used to establish clear evidence of morphological segregation of the large-river specimens into three distinct clusters. It is important to establish that the segregation is not based on the nuchal hump or other subjective characters, but on a broad range of body proportions, fin-ray counts, and vertebral numbers, presumably with a broad genetic basis. Second, after establishing the existence of three separate populations, with little or no overlap, at least within the unmodified, large-river habitat, individual discriminating key characters are developed for identification of these fishes in the laboratory and field. Such characters are critically needed to end the confusion that has clouded attempts to formulate a sound management policy for these endangered or threatened fishes. The population analysis and the development of key characters were conducted separately by us in order to avoid circular taxonomic logic and to enable the two systems to serve as useful tests of one another.

Principal components analysis, a multivariate statistical method enabling taxonomic use of combined (correlated) information from many characters, was applied to 34 characters of 140 specimens. These characters are: dorsal, anal, pectoral, and pelvic fin-rays (rays from both paired fins recorded); standard length, head length, eye diameter, snout length, preanal length, head depth through eye, head depth at occiput, interorbital width, occiput to tip of snout, dorsal-fin basal length, anal-fin basal length, predorsal length, pectoral-fin length, pelvic-fin length, upper jaw length, mouth width, body depth over pelvic insertion, caudal-peduncle depth, anal origin to caudal base; number of vertebrae; pharyngeal arches, total length, width, length of anterior limb, and length of posterior limb, of both left and right arches (eight characters). This analysis discriminated the populations in question (Figures 2-5) showing the major trends in variation, the characters dominant in the trends, and the characteristics of typical as well as intermediate individuals.

A graph of 140 individuals plotted according to their scores on principal components I and II,

[1]Completion of this paper was delayed by closure of upper Green River to scientists other than federally funded personnel during the five-year period 1963-1967. Considerable aid was received from a number of organizations and individuals. Included are research grants to R. R. Miller from the Horace H. Rackham School of Graduate Studies (1950), the National Science Foundation (G-15914, 24129, 24465, GB-3271, 4854, 6272X), and the National Park Service (1975), with cooperation from the various western states for collecting permits. Frances H. Miller recorded and calculated data, helped prepare the distribution map, and criticized drafts of the manuscript. Jeffrey N. Taylor prepared the original plots for Figure 1. Loans of specimens were received from the U.S. National Museum (E. A. Lachner, S. H. Weitzman, W. R. Taylor, Susan Karnella), Arizona State University (W. L. Minckley), Bell Museum of Natural History (Samuel Eddy, H. B. Tordoff, C. W. Huver), and the Museum of Northern Arizona (S. E. Carothers). Mark J. Orsen (of the Museum of Zoology) and Karna M. Steelquist (of the Museum of Paleontology) prepared the drawings and other illustrations, except Figure 10, taken by Bruce J. Turner. Abbreviations are: UMMZ (University of Michigan Museum of Zoology) and USNM (U.S. National Museum of Natural History).

[2]Museum of Zoology, University of Michigan, Ann Arbor, MI 48109.

[3]Wisconsin State University, Whitewater, Wisc. 53190.

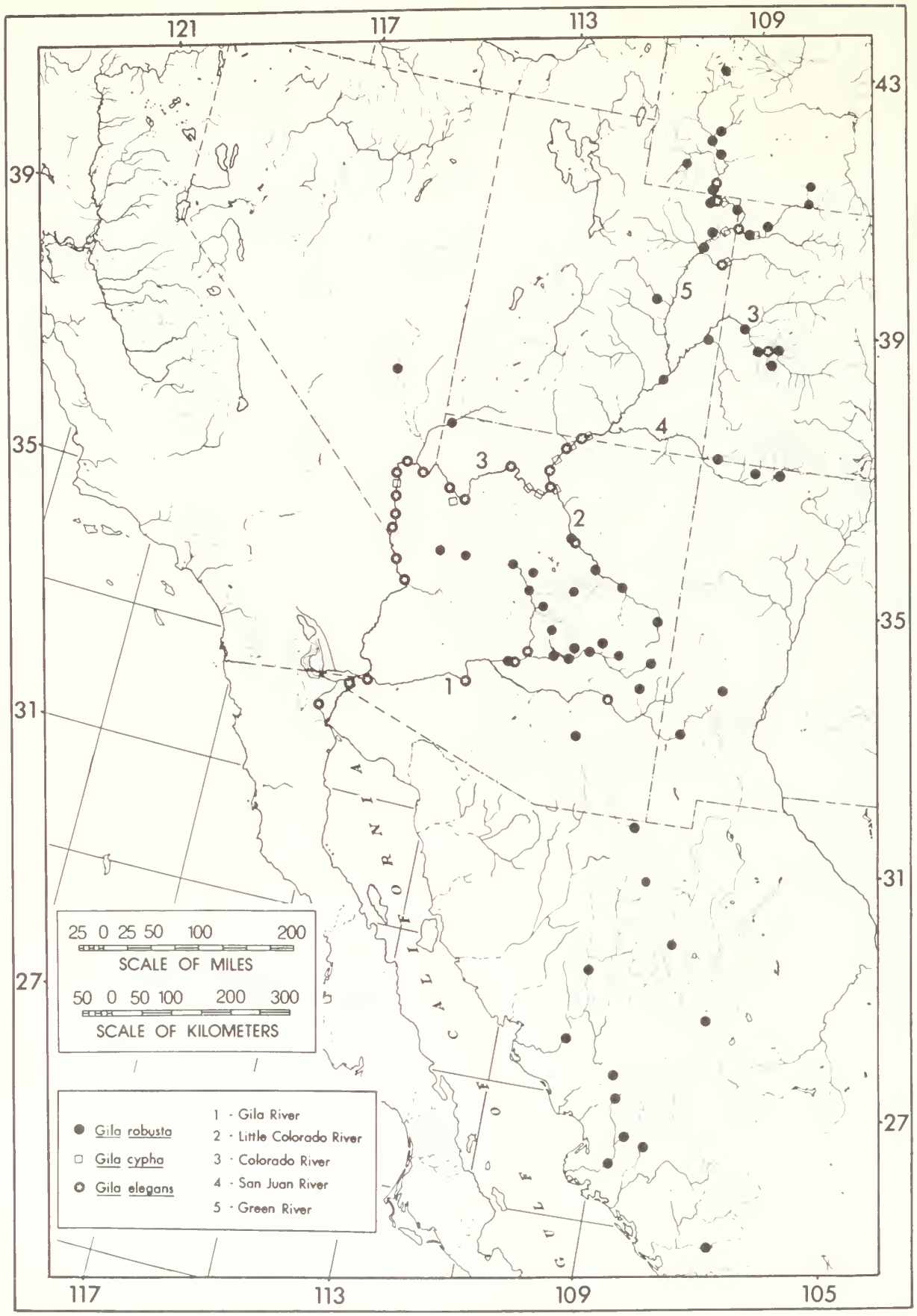



FIGURE 1. Distribution of *Gila robusta*, *Gila elegans*, and *Gila cypha*. See Rhine (1976) for distribution of allied forms in the Gila basin.

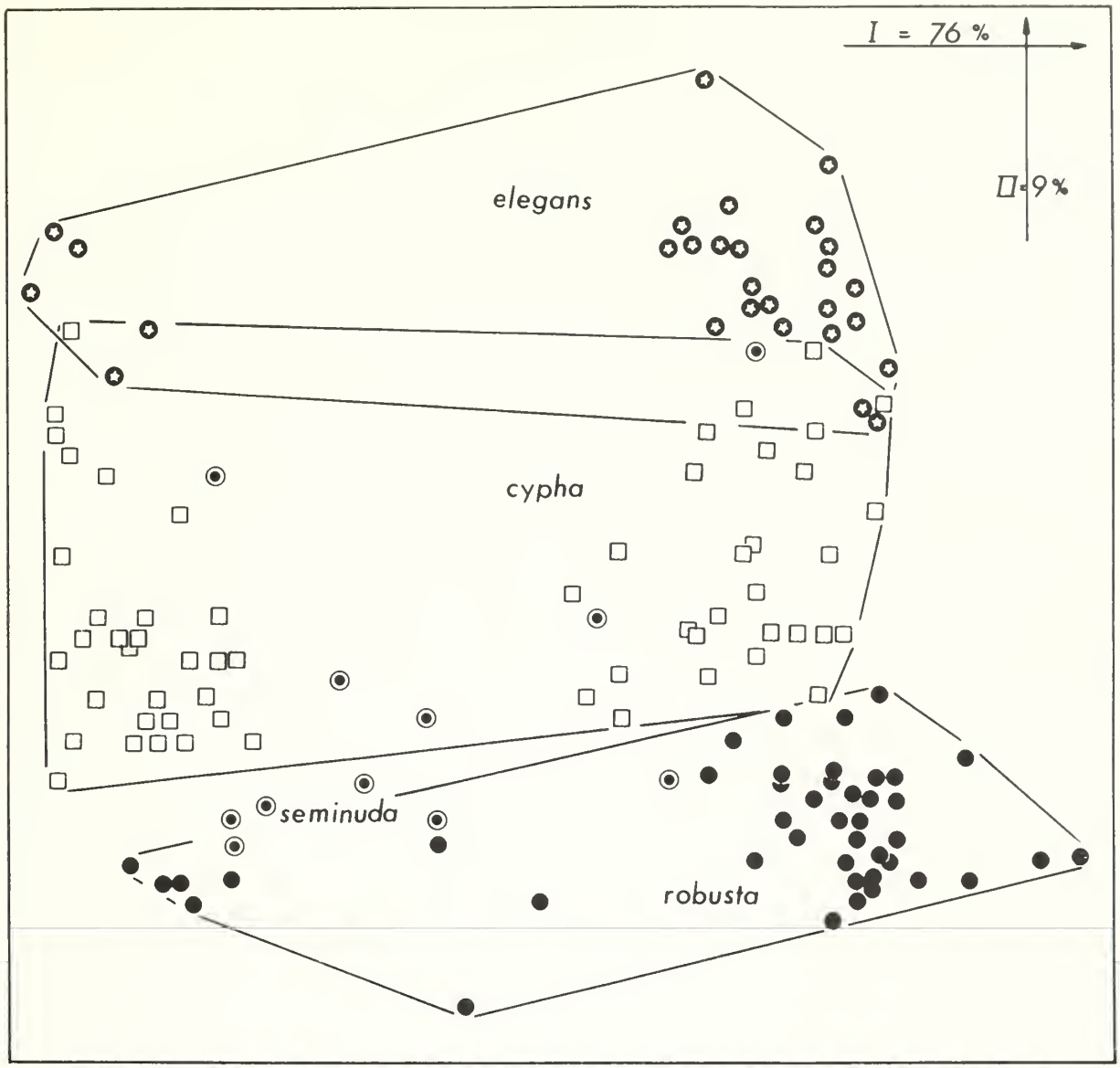



FIGURE 2. Principal components analysis, components I and II, of four forms of *Gila*. *G. robusta robusta*, *G. elegans*, and *G. Cypha* are discriminated by the combination of projections shown in Figure 2 and 3. *G. r. seminuda* is scattered through the other clusters. Percentages indicate the proportion of the total variation accounted for by each component.

TABLE 1. Development of nuchal hump in Colorado River chubs, Genus *Gila*.[a]

| Species | Ratio (range) | S.L.range (mm) |
|---|---|---|
| *cypha* (31) | 6-13 | 206-328 |
| *elegans* (20) | 15-29 | 245-412 |
| *r. robusta* (17) | 28-207 | 211-309 |
| *r. seminuda* (4) | 31-121 | 175-247 |

[a]Expressed as ratio: $\frac{P_{1}\text{-}P_{2}\text{ distance}}{\text{Depth frontal depression}}$.

Figures in parentheses indicate number of specimens measured.

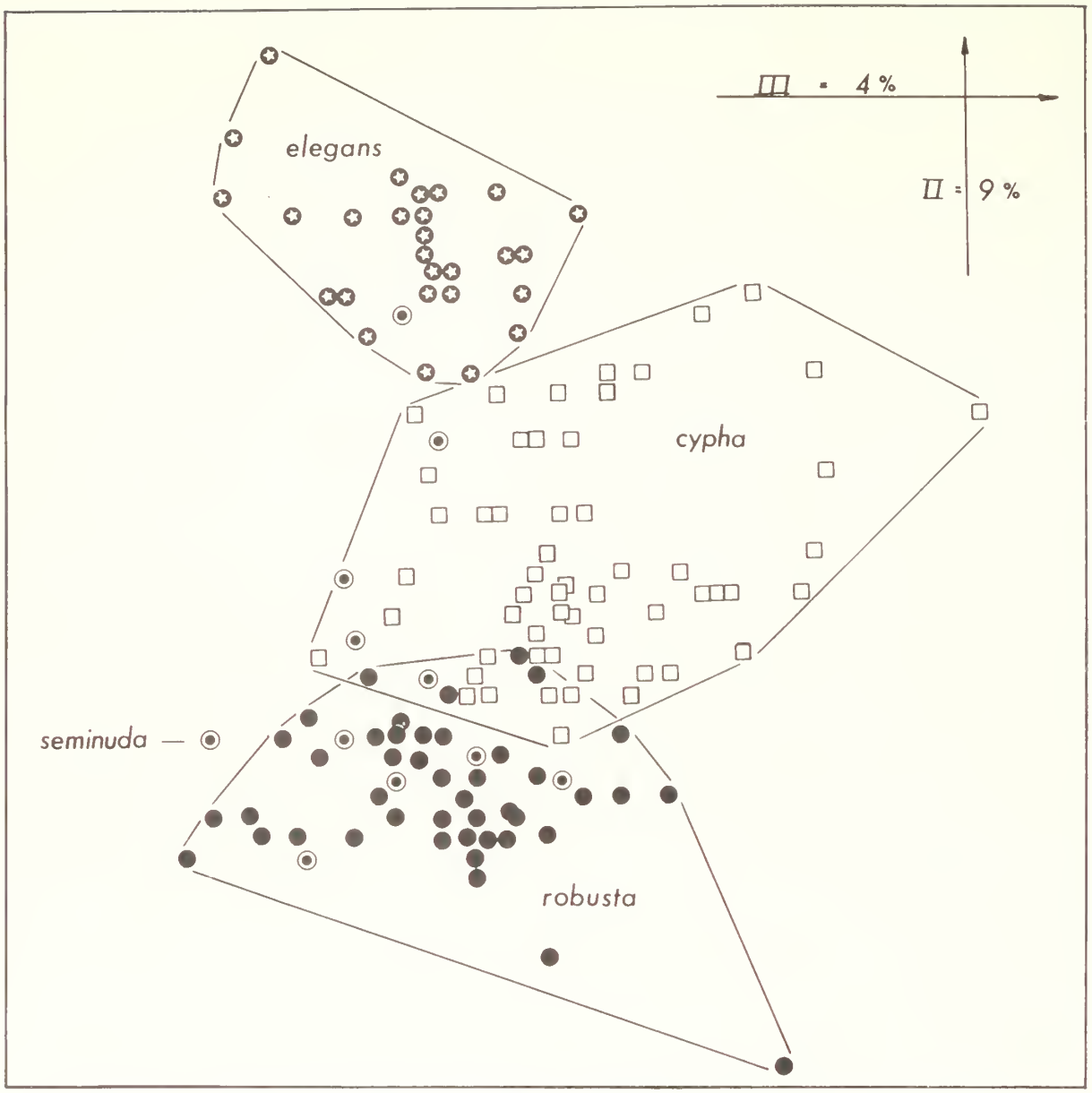



FIGURE 3. Principal components analysis, components II and III, of four forms of *Gila*. Compare with Figure 2.

TABLE 2. Number of gill rakers on second arch in three species of *Gila*.

| Taxon | No. of gill rakers | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | No. | $\bar{X}$ |
| *G. r. robusta* | 8 | 13 | 21 | 1 | | | | | | | 43 | 13.35 |
| *G. r. seminuda*[a] | | | | 4 | 9 | 6 | 4 | 1 | | | 24 | 16.54 |
| *G. cypha* | | 4 | 13 | 17 | 16 | 4 | | | | | 54 | 15.05 |
| *G. elegans* | | | | 1 | 2 | 8 | 5 | 5 | 3 | 1 | 25 | 17.96 |

[a]Including the five syntypes, USNM 16975.

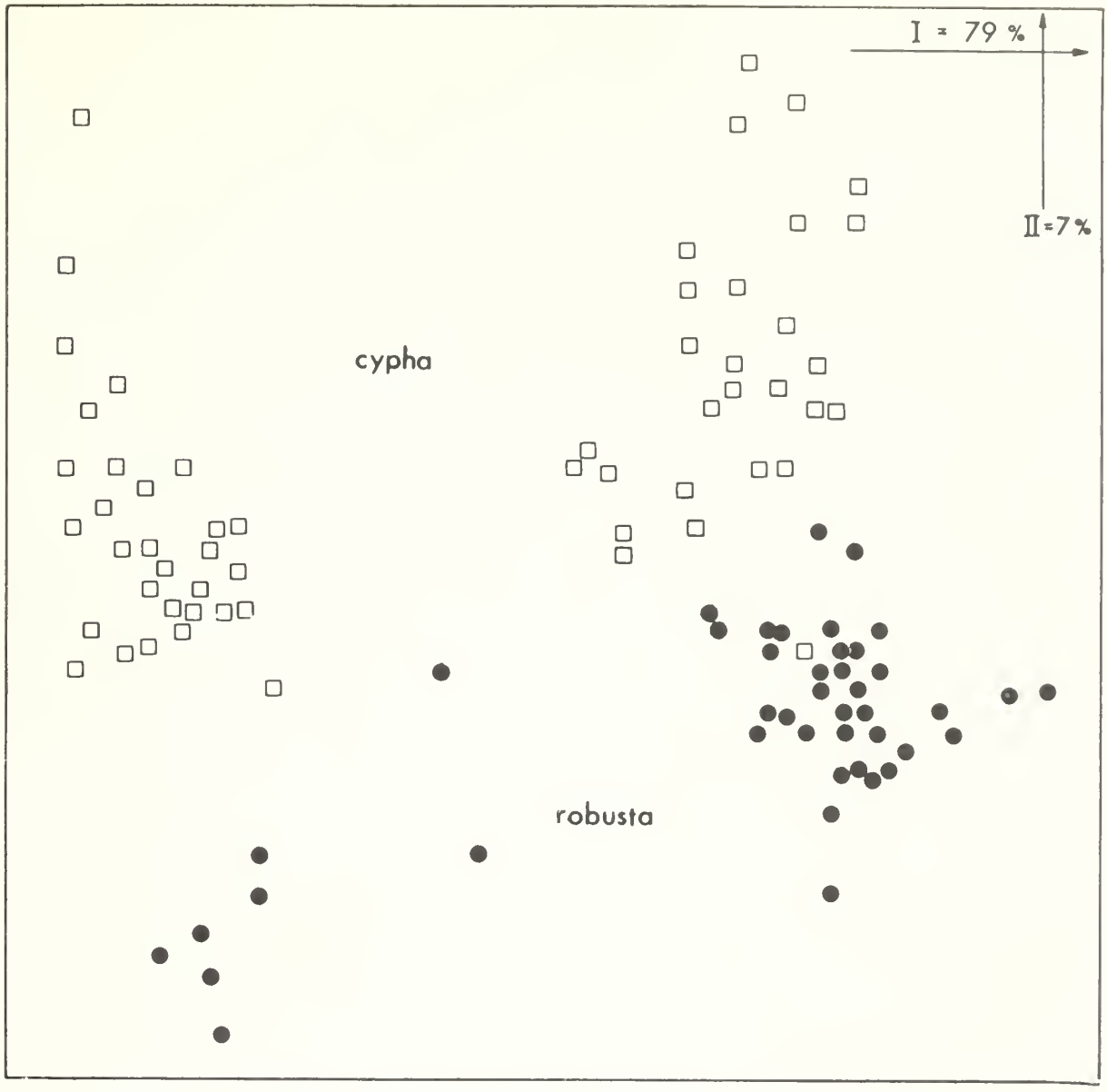



FIGURE 4. Principal components analysis, components I and II, of *Gila cypha* and *G. robusta*. See text for discussion of the specimen of *cypha* in the *robusta* cluster.

TABLE 3. Precaudal vertebrate in Colorado River chubs, Genus *Gila*.

| | Number of precaudal vertebrates[a] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Taxon | 18 | 19 | 20 | 21 | 22 | 23 | 24 | No. | $\bar{X}$ |
| *G. r. robusta* | 7 | 43 | 29 | | 4 | | | 83 | 19.36 |
| *G. r. seminuda* | | 2 | 6 | | 15 | 10 | | 33 | 21.00 |
| *G. cypha* | 26 | 41 | 25 | | 2 | 1 | | 95 | 19.06 |
| *G. elegans* | | | 1 | | 12 | 26 | 9 | 1 | 49 | 21.94 |

[a]Excluding those in the Weberian apparatus.

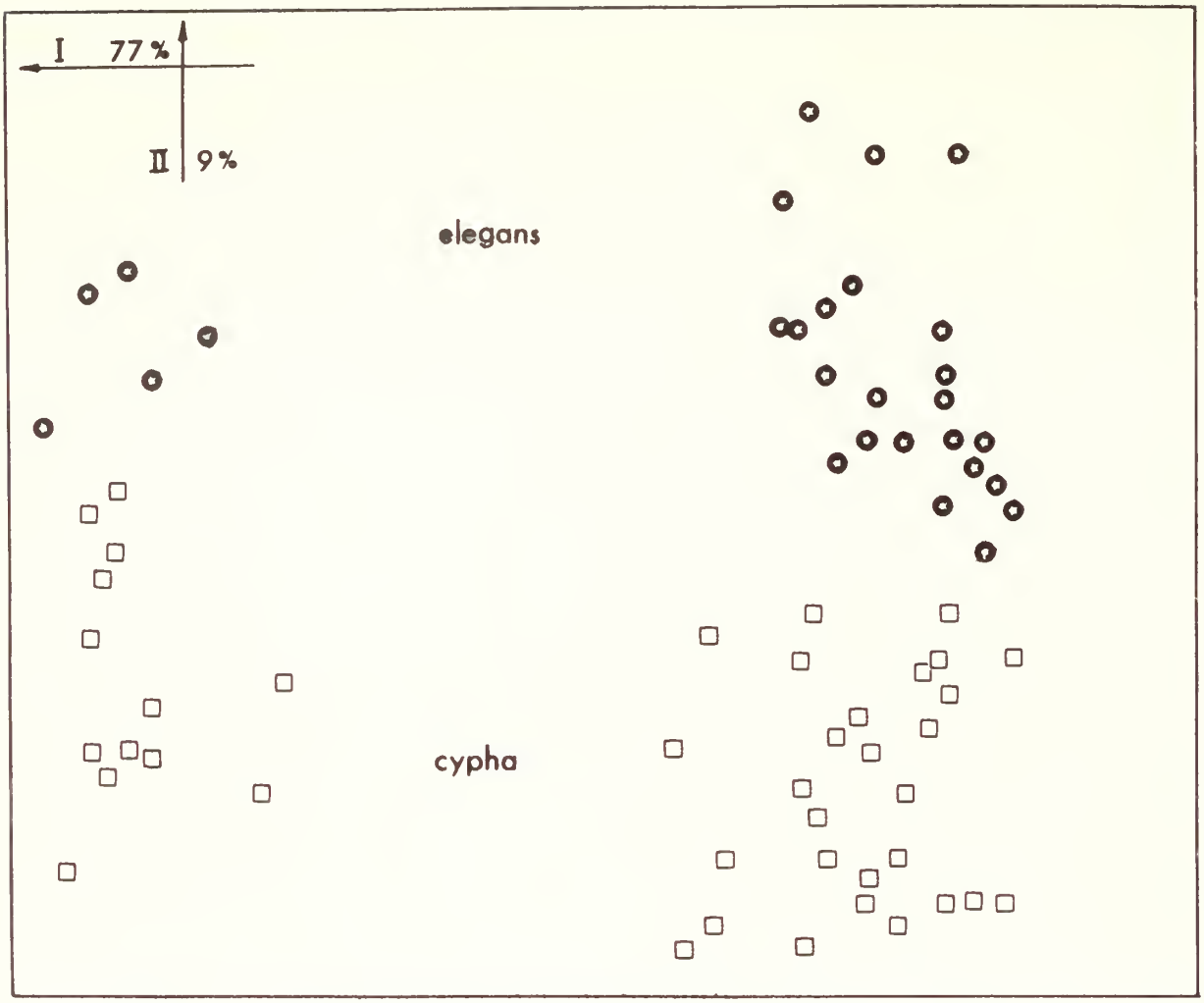



FIGURE 5. Principal components analysis, components I and II, of *Gila cypha* and *G. elegans*.

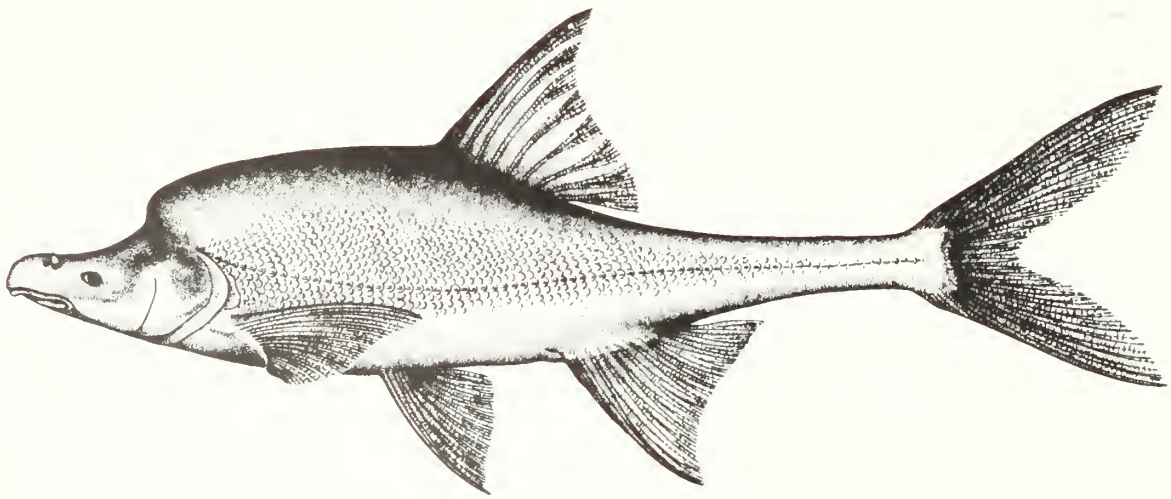


FIGURE 6. *Gila cypha*, holotype (USNM 131839), adult (eviscerated), 305 mm S.L., Colorado River, Grand Canyon National Park, at or near the mouth of Bright Angel Creek, Arizona.

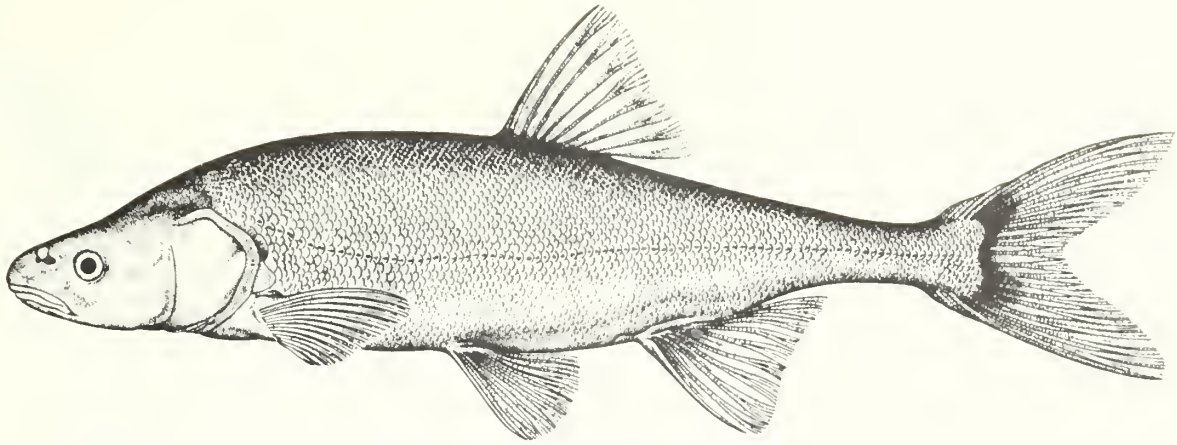


FIGURE 7. *Gila robusta seminuda*, adult female (UMMZ 141666), 189 mm S.L., Virginia River at Littlefield, Arizona.

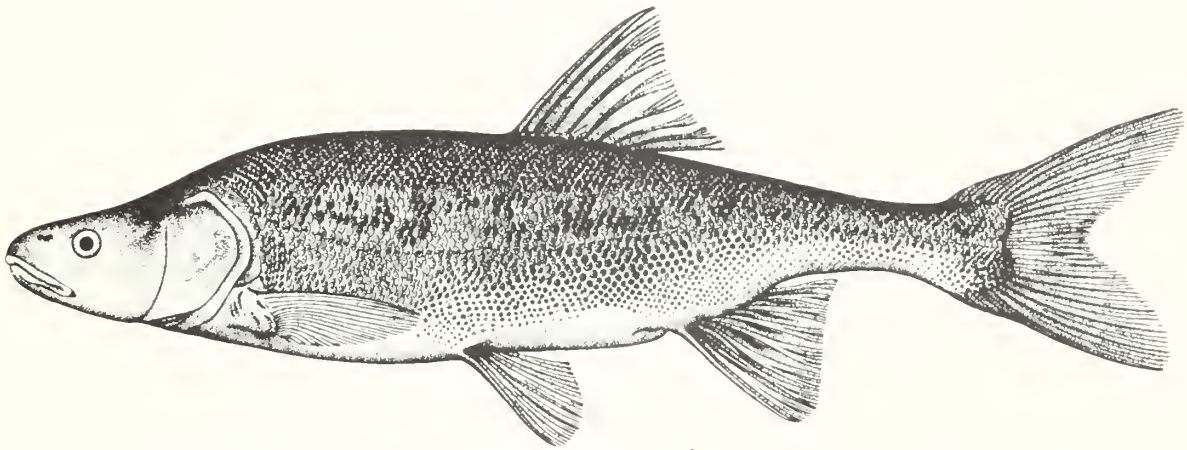


FIGURE 8. *Gila r. robusta*, adult female (UMMZ 182499), 305 mm S.L., Green River about 13 km south of Big Piney, Wyoming.

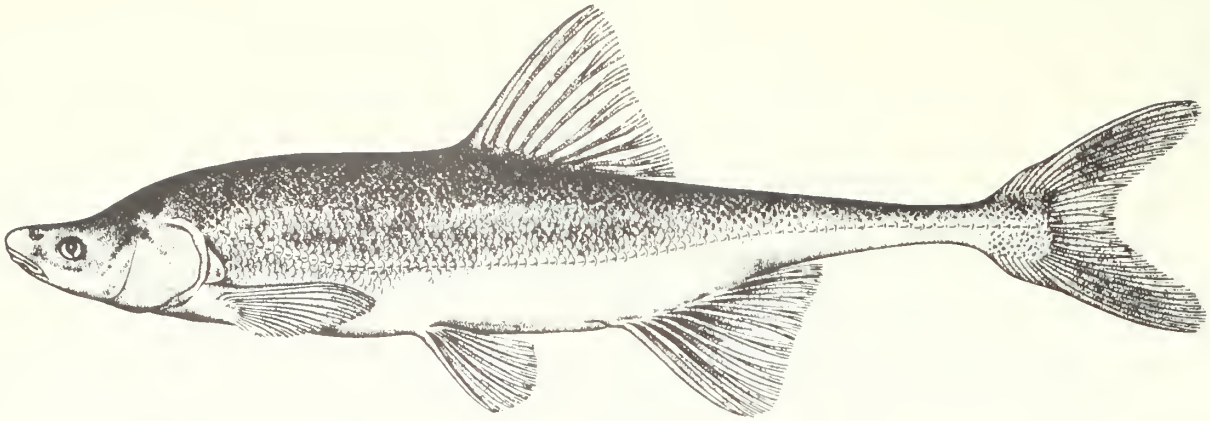


FIGURE 9. *Gila elegans*, post-spawning female (UMMZ 179581), 314 mm S.L., Green River in pool below Flaming Gorge Dam (when under construction), Utah.



FIGURE 10. Juveniles of three species of *Gila*. (above) *G. r. robusta* (UMMZ 161782), 57 mm S.L., Ashley Creek, tributary to Green River, 16.1 km SE of Vernal, Utah. (middle) *G. cypha* (UMMZ 180090), 58.3 mm S.L., Spencer Creek, tributary to Colorado River, 914 m above mouth, Mohave Co., Arizona. (below) *G. elegans* (UMMZ 94865), 65.3 mm S.L., Gila River below Dome,Arizona. Note snout, concave frontals, small eyes, and intermediate peduncle depth in *cypha*. Note slender peduncle of *elegans*. Counts of fin rays, gill rakers, and vertebrate confirm discrimination of young and adult specimens (see text).

excluding direct measurement of the nuchal hump, is shown in Figure 2. Component I reflects general size; II is especially correlated with numbers of vertebrae, dorsal rays, anal rays, and gill rakers. Figure 3 shows the plot of components II and III of the same analysis. Component III is uncorrelated with II, but is highly correlated with counts of fin rays and gill rakers as well as pectoral length and eye diameter. In the combination of the three axes, which represent summaries of the three major trends in the original 34 characters, *robusta*, *elegans*, and *cypha* are discriminated with almost no overlap.

Because the status of *cypha* has been most controversial, it was analyzed separately with *robusta* and *elegans*. The discrimination of *robusta* and *cypha*, when these are considered without *elegans* (Figure 4), and of *elegans* and *cypha* alone (Figure 4), shows complete separation for the latter and only a one-specimen overlap between *robusta* and *cypha*. This fish (UMMZ 181281, spec. 2) falls into the *robusta* cluster because it has 9 anal rays (a character of *robusta* weighted strongly by this multivariate analysis) and several other traits that lean toward *robusta*; it is noteworthy that this is the only specimen that did not fall into its own cluster and, when discriminated with key characteristics such as nuchal-hump development (which yielded a 9.2 ratio--see Table 1), it is typical of *cypha*. Moreover, when treated with the other two species together, (Figures 2-3) it also was identified with *cypha*. We cannot be sure, however, that the several traits aligning it closely with *robusta* may not indicate that some *robusta* genes were present in this specimen.

Thus, although some of the individuals falling at or within the borders of clusters (Figures 2-5) could possibly be interpreted as hybrids, the clusters are quite distinct, indicating genetic differentiation and strong reproductive isolation among the three populations in the big-river habitat. The differentiation and isolation are probably facilitated by different ecological roles and habitat preferences within the complex big-river habitat, although insufficient data are available to be certain at this time.

The characters that contribute most to the above clustering are dorsal- and anal-ray number, gill-raker and vertebral-number, and depth and length of the caudal peduncle. *Gila robusta* and *cypha* separated primarily on counts of fin rays, vertebrae, lateral-line scales, gill-rakers, and post-anal length (II). *Gila cypha* and *elegans* separated on correlation patterns dominated by the same characters, excluding pelvic rays and post-anal length, but including snout, eye, and caudal peduncle dimensions. These characters can be used as key characters, but it is interesting that when used alone they do not provide as complete discrimination as do all 34 traits.

Figures 2 and 3 show the position of eleven specimens of *Gila robusta* from the Virgin River, plotted with the clusters of *robusta*, *elegans*, and *cypha* to demonstrate the nature of overlap of peripheral populations. The Virgin River population is clearly a single variable population with individuals that span some of the variation shown by *robusta*, *elegans*, and *cypha*. None of the Virgin River specimens have distinct humps, yet their body proportions may be similar to those of members of the other populations in analyses excluding the hump character. This is interpreted as indicating that environmental conditions in the medium-sized tributaries are selecting for some kind of variable average of the three morphotypes present in the large-river habitats, but that the range of heterogeneity of habitat in the medium-sized river is not sufficient to support three separate species. The populations in the medium-sized rivers, for example, the Virgin and the San Juan, are interpreted as adapted to their local environments, and not as intergrades (in the introgressed sense), though limited introgression over the past tens of thousands of years cannot be ruled out. When gill-raker number is considered (Table 2), the Virgin River chub separates well from populations of *Gila robusta* inhabiting the main river.

The results of the above analyses suggest that three populations in the main Colorado River are morphologically segregated and are behaving as reproductively isolated species. Exceptional circumstances exist in peripheral tributaries, for example, the Virgin River, as mentioned above, and possibly in disturbed habitats, such as artificial Lake Powell. These will be mentioned again in the discussion.

The search for key characters to discriminate the above populations involving univariate analysis of a larger sample of 261 individuals. The development of the nuchal hump, as expressed by means of a special ratio (see below), was analyzed in 72 individuals.

One of the impediments to key discrimination of these fishes is the variability and lack of complete discriminating power of the nuchal-hump and caudal-peduncle characters. These traits are obvious and striking and one would like to be able to use them to discriminate the populations, but difficulties in quantification of the nuchal-hump characters have heretofore prevented its effective use. Previous multivariate analyses have included subjective scores for nuchal-hump development, raising the question of subjective influence on the final results.

We have circumvented this dilemma by adapting an instrument described by Eschmeyer and Poss (1977). It provides a direct, repeatable measurement, accurate to 0.1 mm, of the development of the nuchal hump in association with the depressed (often concave) dorsal surface of the skull, features most conspicuous in *Gila cypha* (Figure 6). A ratio derived by measuring the depth of the frontal depression (the maximum distance between a straight line from highest part of nuchal hump and dorsal tip of snout, and dorsal surface of skull) and dividing this figure into the distance between the insertion of the pectoral and pelvic fins, provides an effective means for distinguishing adults of the three chubs of the middle and upper Colorado River basin (Table 1).

Number of precaudal vertebrae (Table 3) proves to be useful, along with gill-raker number (Table 2), in discriminating *Gila robusta seminuda* Cope (Figure 7), from the typical subspecies, *G. r. robusta* (Figure 8). Counts of these vertebrae provide a better separation than the total number which (excluding Weberian vertebrae) varies from 40 to 45, modally 42, in *seminuda*, and 39 to 44, modally 42, in *robusta*. *Gila r. seminuda* is closest to *G. elegans* (Figure 9) in number of precaudal vertebrae, as well as in gill-raker number, but separates well from that species on the basis of nuchal hump development (Table 1) although more and (especially larger) individuals need to be examined to verify this. Modally, *G. robusta* has nine dorsal and anal rays; *G. cypha* usually has nine dorsal and 10 anal rays; and *G. elegans* has 10 dorsal and 10 or 11 anal rays. *G. r. seminuda* tends to be intermediate.

## DISCUSSION

Our analyses indicate that *Gila robusta*, *cypha*, and *elegans* coexist as three separate, reproductively isolated species in the main channels of

the Colorado and Green rivers. This conclusion cannot be confidently applied to certain populations that we have available but have not fully studied from Lake Powell, however. Furthermore, populations of *Gila robusta* from certain tributaries were *elegans* and *cypha* are absent parallel these species in many characteristics. We choose a taxonomic treatment of this situation that emphasizes the specific distinction of the three populations in the big-river habitat, but admit the possibility that the species isolating mechanisms may break down under disturbed (reservoir) conditions and that the populations in tributary streams may not be completely independent or isolated from the three central forms. We refer to the entire complex as the *Gila robusta* superspecies, including *robusta, cypha,* and *elegans* as defined above, and including subspecies or races of *robusta, seminuda* of the Virgin River, a similar population in the San Juan River, and a number of isolated populations in northern and western Mexico. The complex in the Gila River basin includes *Gila intermedia* and forms intermediate between that species and *robusta,* i.e., *G. r. "grahami"* (cf. Rinne, 1976). *Gila intermedia* is inferred to be a part of the *robusta* superspecies on the basis of shared characters and possible gene exchange through *"grahami",* but may be a sister phyletic line by its origins, as indicated by its similarity to several of the large-scaled, small-finned subgenera of *Gila* (cf. Miller, 1945).

In spite of the uncertainty regarding peripheral populations, it is clear that *robusta* (s.s.), *elegans,* and *cypha* have diverged in a number of characters, and can be discriminated on the basis of counts of fin rays, vertebrae, and gill rakers, the relative depth and length of the caudal peduncle, snout shape, fin position, and form of the nuchal hump. The multivariate analysis shows that *cypha* is intermediate between *robusta* and *elegans* in general, but is extreme in several respects. This suggests the possibility that *cypha* and *elegans* were derived from *robusta* by separate speciation events. *Gila robusta* shows the most primitive characters of the three, and the separate ways in which *elegans* and *cypha* are extreme suggest that neither is likely to be ancestral to either of the other two.

The lack of coexistence of the three species in smaller tributaries is in accordance with the expected relationship between diversity and spatial heterogeneity. The species seem to be omnivorous carnivores with specializations related to habitat --chacters associated with food processing (jaws, teeth) are similar, except that *robusta* has fewer gill rakers and *elegans* more (Table 2). In small tributaries, such as the Virgin and possibly the San Juan, a single species with intermediate morphology seems to be selected for; in the larger tributary systems of the Gila River, a bewildering mosaic of generalized forms occur (Rinne, 1976), where in former times *robusta* and *elegans* lived in the main channel.

The close apparent control of habitat size and diversity over morphology and species diversity suggests that if the habitat could be experimentally changed, the populations should show predictable responses. Rather unfortunately, the destruction of main-river habitat by Glen Canyon Dam has created such an experiment. Early indications are that the two more specialized species will not exist in the Lake Powell environment. The three species seem to be breaking down locally by hybridization. We predict that a single-species of mixed origins and generalized characteristics will appear. Given long enough, some re-oriented diversification would develop, but the reservoir is apparently silting in too rapidly for the necessary stability to persist.

In a period of controversy following the poisoning of the upper Green River in 1962 (Miller 1963b), erroneous statements about the classification, biology, and distribution of Colorado River chubs appeared which have been destructive to the understanding and management of these fishes, and require correction. For example, Stroud (1963:7) irresponsibly claimed that the construction of Flaming Gorge Reservoir resulted in making available "large numbers" of humpback chubs, all of which were supposedly males. The agency (U.S. Bureau of Sport Fisheries and Wildlife) that "confirmed the presence and ready availability of numerous humpback chubs in [the Green River below Flaming Gorge Dam] . . ." subsequently reported (Vanicek 1967; Vanicek et al. 1970; Holden and Stalnaker 1975) the absence of *Gila cypha* in the area indicated and great rarity of this species below the mouth of the Yampa River; only three specimens were taken in 1963, and none during 1964-1966, in the Green River in Colorado and Utah (Kramer 1967:Table 2; Vanicek et al. 1970:Table 4).

Vanicek and Kramer (1969:194-195) stated, ". . . criteria are not available for distinguishing between young fish of the two morphological variants" (i.e., between what were then called *Gila r. robusta* and *G. r. elegans*). "Consequently, specimens shorter than 200 mm total length were combined in the present study under the general taxon, Colorado chub." Collections of *Gila robusta* and *G. elegans* at The University of Michigan, containing young as small as 22 to 40 mm S.L., were identified as early as 1926; by 1968, humpback chubs as small as 43 mm S.L. had been determined. By the criteria reported here, we have identified *Gila robusta robusta* (UMMZ 162818) to 20 mm, *Gila cypha* (UMMZ 182415) to 54 mm, and *Gila elegans* (UMMZ 162846) to 22 mm in total length. Juveniles of three species are shown in Figure 10. Holden and Stalnaker (1975) (citing Minckley and Deacon, 1968, as authority) reported Colorado squawfish (*Ptychocheilus lucius* Girard) in the Grand Canyon, but the two specimens actually came from between Glen Canyon Dam and Lees Ferry, well above Grand Canyon. The only valid record (based on preserved material) known to us of this species from the Colorado River in Grand Canyon is represented by an adult (about 320 mm S.L.) caught in 1975 by an unknown fisherman at the mouth of Havasu Creek (ASU 7087). However, squawfish formerly moved up the Little Colorado River in Grand Canyon to the base of Grand Falls (Miller, 1963a:1, ftn.1).

In our distribution map of the *Gila robusta* complex (Figure 1), the record for *G. elegans* in the Little Colorado River (at base of Grand Falls) is based in part on the statement referred to above, in part on our conclusion as to the true type locality for *Gila elegans* (and *Gila robusta*), and in part on the absence of the bonytail from the Little Colorado River above Grand Falls. The holytype (USNM 251), as well as the three syntypes of *Gila robusta* (USNM 246), were said to have come from the "Zuni River, New Mexico" (Baird and Girard, 1853, 1854; Girard, 1858:286-287). However, at the time of collection during the summer (rainy season) of 1852, Zuni River was described ". . . as a mere rivulet, and not entitled to the name of river; in most parts of our country it would not be dignified with that of creek" (Sitgreaves, 1854:5). This is hardly the habitat of *Gila elegans* and, moreover, that species is unknown from the Little Colorado River basin (to which Zuni River is tributary in floods) above Grand Falls, an impassible barrier 56 meters high (Dryer, 1965). Furthermore, careful examination of the channel of Zuni River in New Mexico convinced us that (at least in recent centuries)

this river did not provide a suitable habitat for the bonytail (W. L. Minckley, who has also studied the channel, concurs--pers. comm. 1976). Study of Sitgreaves' report and map shows that his last station in the basin of the Little Colorado River (No. 13) was at Grand Falls. We thus assume that this is the correct type locality for *Gila elegans* and *G. robusta* (of which the third species taken, *G. gracilis*, is a synonym). Incidentally, the genus *Gila* was named for the river of that name on the mistaken idea that the Little Colorado River was tributary to Salt River of the Gila River basin.

The perpetuation and management of *robusta*, *elegans*, and *cypha* depends on the maintenance of large sections of unspoiled, natural, main-channel habitat. Dams threaten these species primarily by destroying the swift-water habitat above the obstruction and drastically decreasing the temperature and turbidity below. Introduced exotic competitors and predators (on young) are a threat, especially in these modified areas. The most important current need is research on the habitat, food, reproduction, recruitment, and hydrodynamics and energetics of these forms of *Gila*, both for the purpose of sound management and for the reason that such information is one of the valuable benefits that man can derive from these unique species.

Key to species of *Gila* in the Main-channel Habitat of the Upper Colorado River Basin*

1a. No nuchal hump, frontals nearly straight (Figures 8,10 above), dorsal and anal rays usually 9, distance from anal origin (base of first ray) to caudal base (bases of rays, internally) much less than distance from anal origin to opercle . . . . . *robusta*.

1b. Nuchal hump present in specimens over 150 mm (Figures 6,9), frontals concave above eyes in lateral profile (Figures 6,9,10 middle and below), dorsal rays 9 or 10, anal rays 10 or 11, distance from anal origin to caudal base about equal to or greater than distance from anal origin to opercle . . . . . 2.

2a. Nuchal hump abrupt (Figure 6), dorsal rays usually 9, anal rays usually 10, in young less than 150 mm the eye diameter less than 2/3 caudal peduncle depth, snout overhangs upper lip (Figure 10 middle). . . . . *cypha*.

2b. Nuchal hump not abrupt (Figure 9), dorsal rays usually 10, anal rays 10 or 11, in young less than 150 mm the eye diameter greater than 2/3 caudal peduncle depth, snout not overhanging upper lip (Figure 10 below) . . . . . *elegans*.

*Supplemental characters in Tables 1-3 aid identification, especially for difficult specimens and possible hybrids. Hybrids tend to have several characteristics distinctive of each parent and several intermediate. Specimens may be sent to The University of Michigan Museum of Zoology for identification.

LITERATURE CITED


BAIRD, S. F., and CHARLES GIRARD. 1853. Descriptions of some new fishes from the River Zuni. Proc. Acad. Nat. Sci. Phila. 6:368-369.

BAIRD, S. F., and CHARLES GIRARD. 1854. Fishes, pp. 148-152, pls. 1-3. *In:* Sitgreaves, Capt. L. Report of an expedition down the Zuni and Colorado rivers. U.S. Senate, 33rd Cong., 1st Sess., Exec. Doc., Washington.

DRYER, I. 1965. Grand Falls of the Little Colorado. Nat. Parks Mag. 39(212):10-12.

ESCHMEYER, W. N., and S. G. POSS. 1977. Review of the scorpionfish genus *Maxillicosta* (Pisces: Scorpaenidae), with a description of three new species from the Australian-New Zealand region. Bull. Mar. Sci. 26(4):433-449.

GIRARD, C. 1858. Fishes. *In:* General report upon the zoology of the several Pacific railroad routes. U.S. Pac. R.R. Expd. and Surv. 10(4):i-xiv, 1-400.

HOLDEN, P. B., and C. B. STALNAKER. 1970. Systematic studies of the cyprinid genus *Gila*, in the upper Colorado River basin. Copeia 1970 (3):409-420.

HOLDEN, P. B., and C. B. STALNAKER. 1975. Distribution and abundance of mainstream fishes of the middle and upper Colorado River basins, 1967-1973. Trans. Amer. Fish. Soc. 104(2): 217-231.

KRAMER, R. H. 1967. Introduction, pp. 1-9. *In:* Green River fishes and invertebrates. Spec. Repot., U.S. Bur. Sport Fish. and Wildlife, Utah Coop. Fish. Unit, Logan, Utah.

MILLER, R. R. 1945. A new cyprinid fish from southern Arizona, and Sonora, Mexico, with the description of a new subgenus of *Gila* and a review of related species. Copeia 1945(2):104-110.

MILLER, R. R. 1963a. Distribution, variation, and ecology of *Lepidomeda vittata*, a rare cyprinid endemic to eastern Arizona. Copeia 1963(1):1-5.

MILLER, R. R. 1963b. Is our native underwater life worth saving? Nat. Parks Mag. 37(188): 4-9.

RINNE, JOHN N. 1976. Cyprinid fishes of the genus *Gila* from the lower Colorado River basin. Wassman J. Biol. 34(1):65-107.

SITGREAVES, CAPT. L. 1854. Report of an expedition down the Zuni and Colorado rivers. U. S. Senate, 33rd Cong., 1st Sess., Exec. Doc., Washington, 198 pp.

STROUD, R. H. 1963. Green River humpbacks. Sport Fish. Inst. Bull. 141:7.

VANICEK, C. D. 1967. Ecological studies of native Green River fishes below Flaming Gorge Dam, 1964-1966. Ph.D. Thesis, Utah State Univ. Issued as Spec. Rept., U.S. Bur. Sport Fish. and Wildlife, Utah Coop. Fish. Unit, Logan, 124 pp.

VANICEK, C. D., and R. H. KRAMER. 1969. Life history of the Colorado squawfish, *Ptychocheilus lucius*, and the Colorado Chub, *Gila robusta*, in the Green River in Dinosaur National Monument, 1964-1966. Trans. Amer. Fish. Soc. 98(2):193-208.

VANICEK, C. D., R. H. KRAMER, and D. R. FRANKLIN. 1970. Distribution of Green River fishes in Utah and Colorado following closure of Flaming Gorge Dam. Southwest. Nat. 14(3):297-315.

# REPRODUCTIVE ECOLOGY OF THE QUITOBAQUITO PUPFISH FROM ORGAN PIPE CACTUS NATIONAL MONUMENT, ARIZONA

Boyd Kynard and Robert Garrett[1]

## INTRODUCTION

Quitobaquito is a unique spring-fed oasis within Organ Pipe Cactus National Monument, Arizona (Fig. 1). The pool which receives the spring waters is approximately 90 m wide and 100 m long and has a surface area of .22 hectares. When it was deepened in 1962, water depth was established at a fairly uniform 90 cm and the pool banks became vertical except for the sloping shallows on the east and northeast sides. Even though the spring waters emerge at 24.5°C, their flow into the pool 100 m distance is so reduced that they do not affect pool water temperatures. *Chara* and *Potamogeton* form a dense growth of aquatic vegetation that covers almost the entire bottom of the pool. Various aspects of water quality can be found in Cole and Whitesides (1965) and Kynard (1976).

The pupfish in Quitobaquito are a disjunct population of the desert pupfish, *Cyprinodon macularius*, which inhabits the Rio Sonoyta 1.2 km to the south in Mexico (Miller 1943). A connection existed between the springs at Quitobaquito and the Rio Sonoyta as recent as the early 20th century (Lumholtz 1912). Today the separation between these populations is complete and probably has been for 50 years.

The Quitobaquito pupfish is the only known population of *C. macularius* that is located on public lands where their chance of long-term survival is good. This study was initiated to establish a knowledge base from which to better understand the population and their critical habitat requirements. It examined population demography and reproductive ecology. The study of population demography involved determination of (1) population size, especially during the breeding season (2) age and growth, particularly age at reproduction, and (3) sex ratio, particularly during reproduction. Although Cox (1966) described courtship and general breeding behavior of these fish, only cursory examination was given to reproductive ecology. The present study documents (1) breeding season length and the role of temperature (2) the location of breeding males relative to habitat types and water quality (3) changes in the number and location of territorial males during the breeding season, and (4) experimental evidence of breeding habitat preference of males.

### *Population Demography Methods*

Population size was estimated using the Peterson Mark-Recapture Method after Deacon (1967). Population enumeration was conducted on October 22, 1975, June 10, 1976, and November 11, 1976. Fish were captured in 20 standard metal minnow traps that were covered with window screen wire. Those fish >22 mm were marked by a 1/5 removal of the pectoral fin tip and were returned to the various pool locations where they were caught. Traps were reset 24 hr later and the number of marked fish and unmarked fish (>22 mm and <22 mm total length) were counted. A population estimate was calculated using the formula

$$N = \frac{MC}{R}$$

and 95% confidence limits were placed on the estimate (Everhart, Eipper, and Young 1975; Clopper and Pearson 1934).

A sample of 203 fish taken June 11, 1976 (a few weeks after reproduction began) was examined for age, growth, and sex ratio of breeding sized adults, i.e., those >32 mm. Individual fish were aged by the scale method since Jester and Terry (1976) had shown this method was amenable to pupfish. Mean growth of each year class was determined and length frequencies of the population from the two fall samples (October 22, 1975 and November 11, 1976) and June 10, 1976, were compared for changes in age (size) structure. Sex ratios during breeding and post breeding were compared using the June and November 1976, samples.

### *Reproductive Ecology Methods*

General observations were made of breeding season length (as indicated by the presence of <1 cm young) during monthly trips. The presence of young was noted in relation to data from a 45-day Ryan Thermograph. This constant recording temperature device was located in the warm, shallow, northeast cove in 15 cm of water. During the breeding season, young pupfish were always abundant in this area.

To determine the period when most males bred, a monthly count of territorial males was made in a 4 m x 4 m index area in the shallow northeast cove. A territorial male was easily identified by his dark irridescent blue body. Early in the breeding season (May 20) and later (July 15), the entire pool was surveyed by boat and the occurrence of territorial males relative to geographical location and aquatic habitat was recorded. Areas where territorial males were found were monitored for 24 hr water quality (temperature/dissolved oxygen). A yellowsprings Instruments model 57 field meter was used to determine water quality.

Both laboratory and field experiments were used to gather evidence about the preferred breeding habitat of male pupfish. Male choice tests of soft vs solid substrate and open vs sheltered breeding sites were conducted at the University of Arizona in a large 6.6 m diameter pool. Twenty-five territorial males and 8 females were captured from the Blankenship refugia at Organ Pipe National Monument, transferred to Tucson, and introduced into the experimental pool. Water depth was 45 cm with one-half of the bottom covered with 3 cm of alluvial silt. The location of each male's territory was noted relative to substrate type and distance from the pool wall i.e., shelter.

Quitobaquito males were given a choice of shallow or deep breeding habitat on June 10-11 and July 8-9, 1976. On these dates several 19.2 cm x 38.4 cm x 5 mm sheets of plywood were anchored in place in Quitobaquito pool to form 10-15° inclined planes from the surface to the bottom of the pool. Sand and bottom debris were sprinkled over the boards to give them a natural appearance. Boards were placed at various locations about the pool. Twenty-four hours after placement, they were checked periodically and the

[1]School of Renewable Natural Resources, University of Arizona, Tucson.




FIGURE 1. Location of Quitobaquito, Arizona.

depth of territorial males was recorded.

*Population Decography Results and Discussion*

The population size of the pupfish in Quitobaquito fluctuates seasonally, see table below:

| Date | $\hat{N} = \frac{MC}{R}$ | Number Markable Size Fish With C.I. Limits | Total Population Estimate |
|---|---|---|---|
| Oct. 22, 1975 | $\hat{N} = \frac{(1802)(591)}{146}$ | 6,228 - 7,294 - 8,589 | 7,986 |
| June 10, 1976 | $\hat{N} = \frac{(675)(888)}{178}$ | 3,073 - 3,367 - 3,996 | 3,592 |
| Nov. 10, 1976 | $\hat{N} = \frac{(300)(310)}{40}$ | 1,667 - 2,325 - 3,333 | 4,558 |

Population Size cycled seasonally with the greatest abundance occurring in the fall after breeding recruitment and the lowest abundance occurring after a winter and/or spring mortality. This may be the annual pattern for many desert Cyprinodon populations since this pattern existed for *C. nevadensis pectoralis* from Saratoga Springs (Deacon 1967) and for a warm spring population, Indian Spring (Soltz 1974). The winter and/or spring mortality was of such magnitude that only about one-half of the Quitobaquito population survived from October 22, 1975 to June 10, 1976. A similar winter mortality occurred in Tucson in outdoor experimental pools that were free of insect and bird predators so the mortality would not seem to be related to predation. The population estimate of November 1976 indicated a good recruitment from breeding although the fishes size was smaller due to the later initiation of breeding (Fig. 2). The smaller size of the fish in the fall of 1976 is also reflected in the population estimate where the submarkable size fish were 49% of the total population. Submarkable size fish were only 6% in the fall of 1975. Also, there was a very poor carryover of $I^+$ and $II^+$ year classes during the summer of 1976 and their abundance was reduced approximately one-half that from 1975 (Fig. 2). Thus, the pupfish population in the fall of 1976 was composed almost entirely of 0 age fish. The cause of the drastic decline in abundance of I and II year fish wasn't revealed from monthly observations on the fish population or from monthly water quality samples.

Quitobaquito pupfish live a maximum of 3 years (Fig. 2). For June aged fish, growth had been rapid the first year and I's averaged 29.6 mm total length. Age II fish were 40.2 mm TL ( a $\bar{x}$ increase of only 8.7 mm) and III's averaged 48 mm TL or a $\bar{x}$ increase of 7.8 mm. Growth was very rapid for the first year but very slow and approximately the same during the second and third year. In June, 1976, 78% of the population was in age class I (wintered one year); 18% in II; and 4% in III. Since territorial males were >32 mm TL, it is probable that males breeding in June were II and III year classes plus some larger I's. Smaller non-territorial males were observed attempting to steal an egg fertilization but none were seen with territories.

In June, 1976, the sex ratio of males:females among breeding sized fish (>32 mm, N = 154) favored females 43%:57%. Even though there were more females than males, the difference was not significantly different from 50:50, $x^2 = 3.14$ $p > .15$. In November, 1976, sex ratio of >32 mm fish was approximately equal (N = 145, 48%:52%).

*Reproductive Ecology Results and Discussion*

Fish fry were first seen in 1975 on April 29 at a noon temperature of 24.5 C in the shallow northeast cove. None was present earlier on March 20 when the noon water temperature was 18.0°C. In 1976, first fry were observed on May 20 when the noon temperature was 28.3°C. None had been present earlier on April 28 when the daily maximum in the shallow northeast cove was 26.0°C. Cox (1966) found breeding fish on 24 April 1964 in water of 23-27°C. He found first fry of 1965 on May 6 but presented no temperature data. Thus, successful breeding, as indicated by the presence of fry, appears to begin in late April or early May. The Ryan thermograph data indicated this is probably when the daily temperature maximums in 1976 began to consistently exceed 24°C (75 F) (Fig. 3). Since the spring of 1976 was cocler than 1975, reproduction in 1976 was delayed and breeding began later probably during the first two weeks of May. This model predicts that since breeding was later in 1976, the age structure of the new recruits in the fall would be showed to a smaller mean size. This point has previously been discussed and the empirical data conformed to the expected results. During 1975, breeding ceased between July 14 and August 28. In 1976, a few males were still breeding on August 5 but none was observed on September 9. Thus, the breeding seasons of 1975 and 1976 were approximately 2.5-3.5 months in length. Although there was several weeks variation in the initiation of breeding between 1975 and 1976, termination dates were similar. Thus, the delay of breeding in 1976 was not compensated for by extending the breeding season.

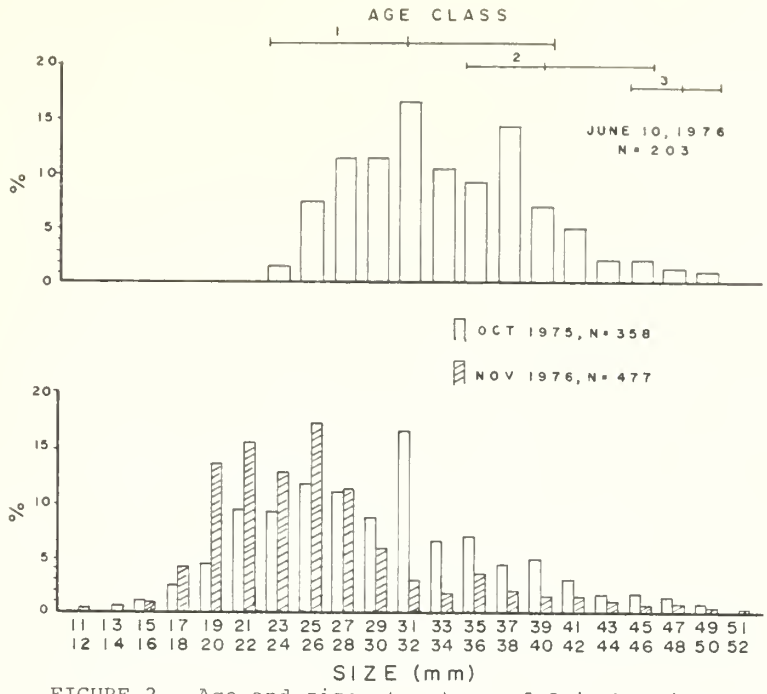
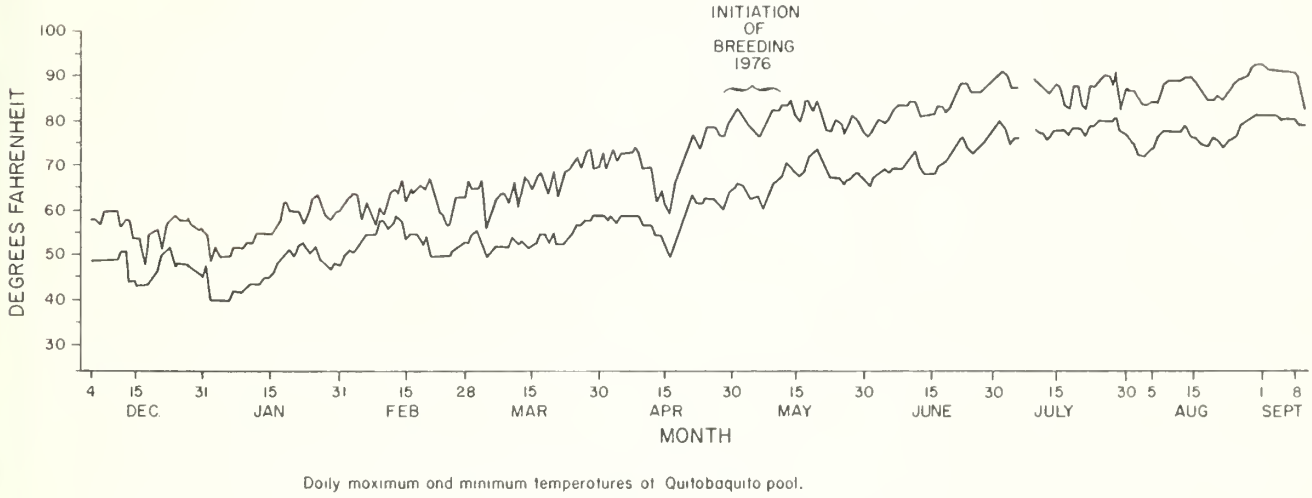



FIGURE 2. Age and size structure of Quitobaquito pupfish.




Daily maximum and minimum temperatures at Quitobaquito pool.

FIGURE 3. Daily temperature maximums and minimums from December 1975 to September 1976.

The number of territorial males in the index area was highest early in the breeding season (May and June) and decreased drastically after June (Fig. 4). This indicates that most of the population's breeding effort was early. The selective advantages associated with breeding early are not known at this time.

Habitat utilization of males changed during the breeding season. In May and June, blue, territorial males were observed in two habitats, i.e., along the pool edge and off-shore in deeper water above the vegetation. Once these off-shore males attracted a female in the open water above the vegetation mats, they would disappear beneath the vegetation so it is not known where they spawned. In July, few males held territories off-shore although many were present along the pool edge (Fig. 5). The edge habitat was characterized by a (1) sloping or vertical solid substrate of plant roots and earth, and (2) an open-water zone along the bank. The off-shore habitat had (1) a muck bottom of precipitated $CaCO_3$ and decayed plant debris (2) dense aquatic vegetation that often extended to the surface, and (3) lower nighttime dissolved oxygen levels than the edge habitat. Water quality data indicated that temperature or D. O. levels were not responsible for the change in habitat utilization by males (Fig. 6). Temperature/depth relationships were similar for both habitats and the early morning D. O. level in the off-shore area was slightly better in July than May. This may have been due to vegetation senescence.

Habitat preference experiments indicated that males preferred to establish territories in shallow areas with solid substrate (Fig. 7). A preference for solid substrate over soft substrate was indicated by a chi-square value of 3.76 which is significant at the .10 level of probability. A preference to breed away from the pool wall in the open was also indicated as only 4 out of 13 males held territories that bordered the wall. It was also interesting that no females were seen spawning with males in the soft substrate area although repeated spawnings were seen with other males. There was a strong preference to breed in shallow water since all 14 males chose habitat less than 15 cm deep.

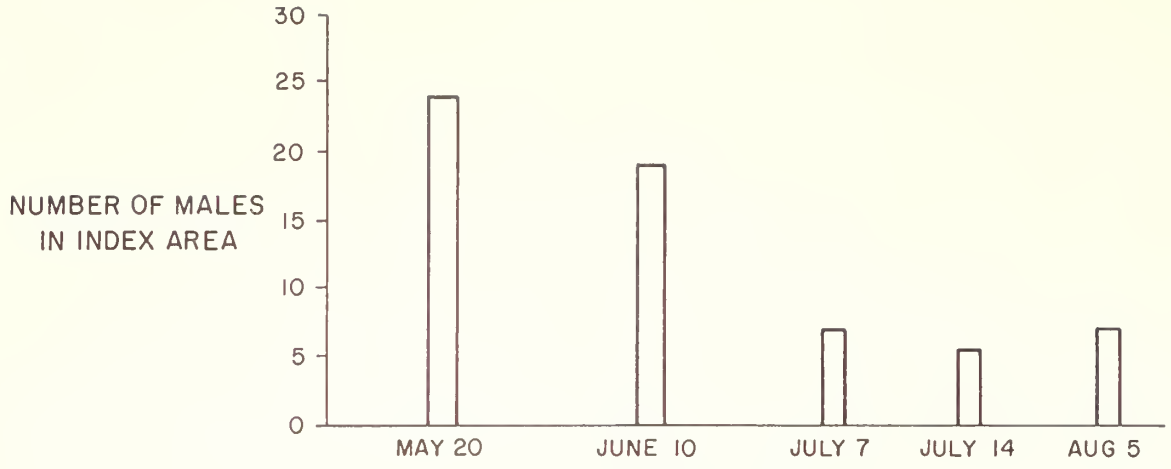
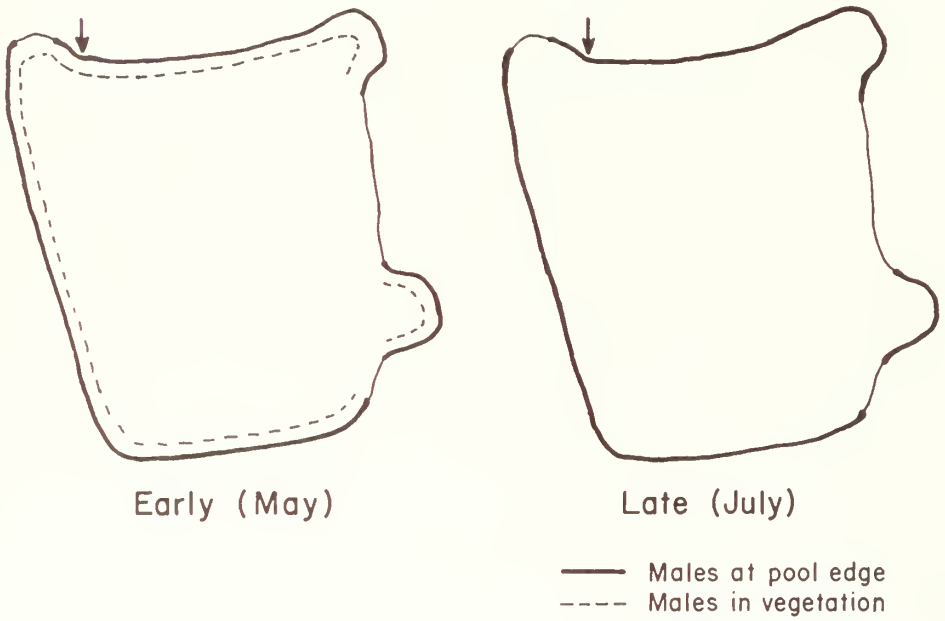
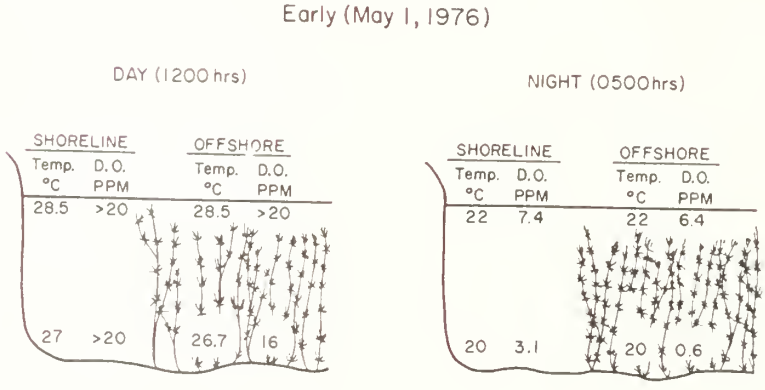



FIGURE 4. Timing of breeding by males.




LOCATION OF BREEDING MALES

FIGURE 5. Geographic location of breeding males in May and July.



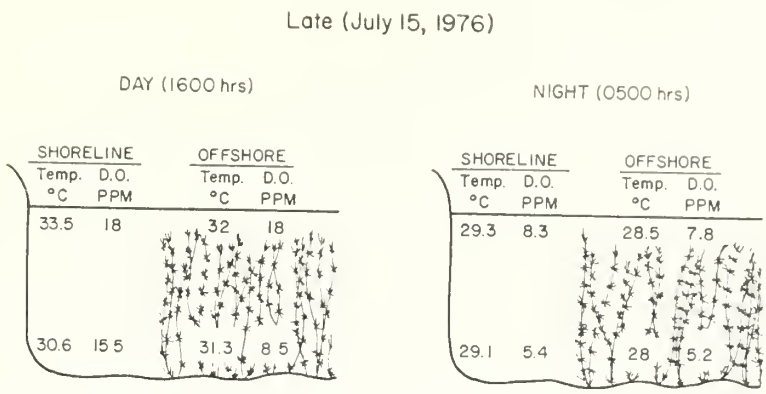
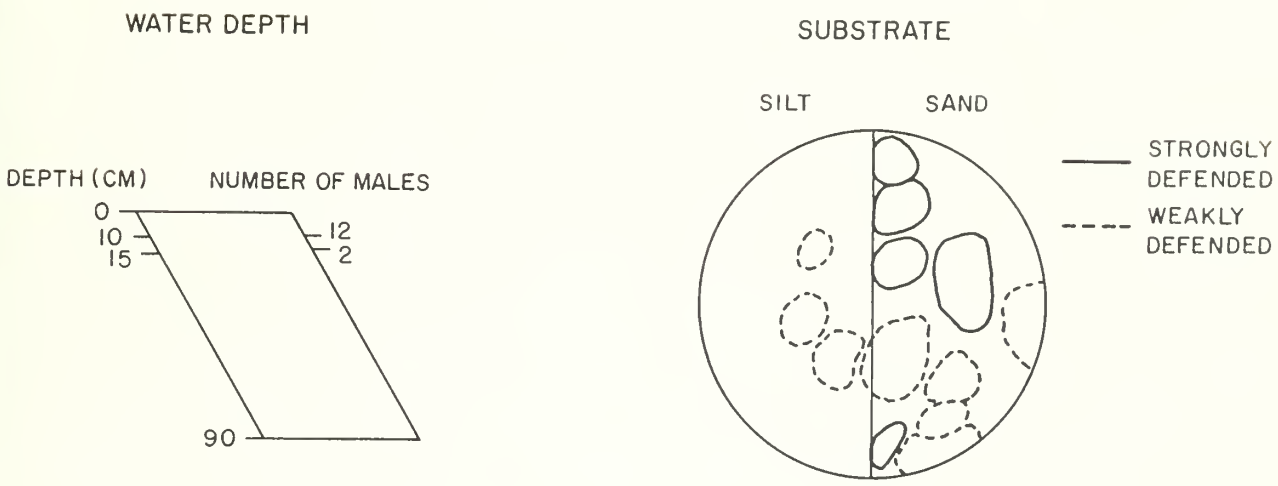



FIGURE 6. Water quality of pool in May and July.




## MALE SELECTION OF TERRITORY

FIGURE 7. Experimental selection of territories by males.

Although the experimental data are limited, the results suggest that the edge habitat offered breeding males the preferred habitat with a more solid substrate, more open habitat (for better visibility of females?) and, probably a better chance to nest in shallow, warmer water than the off-shore habitat. Using an empirically derived density of males along the edge of 3/m, an estimated 233 to 266 m of edge habitat, and approximately 1000 to 1300 breeding size males in June, there may not have been sufficient area to accommodate all these males at one time. If all these males preferred to nest along the edge when peak numbers of males were breeding, then the presence of males off-shore in May but not later in July can be explained by the fact that the edge habitat was limited in abundance. Thus males breed off-shore early because preferred breeding habitat along the edge is occupied; later in July there are less males breeding (Fig. 4) and all males can find a territory in the edge habitat.

Thus, the data indicate that while the deepening of Quitobaquito in 1962, may have afforded a more secure water level, a certain amount of preferred breeding habitat may have been forfeited.

### LITERATURE CITED

COLE, G. A. and M. C. WHITESIDE. 1965. An ecological reconnaissance of Quitobaquito Spring, Arizona. Jour. Ariz. Acad. Sci. 3:159-163.

COX, T. J. 1966. A behavioral and ecological study of the desert pupfish (*C. macularius*) in Quitobaquito Springs, Organ Pipe Cactus Nat. Mon. Arizona. Ph.D. dissertation, Univ. of Arizona, Tucson.

CLOPPER, C. J. and E. S. PEARSON. 1934. The use of confidential or fiducial limits illustrated in the case of the binomial. Biometrika 27: 404-413.

DEACON, J. E. 1967. The ecology of Saratoga Springs, Death Valley Nat. Mon., Rept. to Nat. Park Ser., Mimeo, p. 104.

EVERHART, W. H., A. W. EIPPER and W. D. YOUNGS. 1975. Principles of Fisheries Science, Cornell Univ. Press, Ithaca, N.Y.

JESTER, D. B. and B. G. TERRY. 1976. Aspects of the life history of the White Sands Pupfish. *Cyprinodon tularosa*, in Salt Creek, New Mexico. Unpublished Manuscript.

KYNARD, B. E. 1976. Preliminary study of the desert pupfish and their habitat at Quitobaquito Springs, Arizona. Final Rept. to U.S. Nat. Park Ser., Mimeo, p. 43.

LUMHOLTZ, C. 1912. New Trails in Mexico, Charles Scribner's & Sons, New York, N.Y.

MILLER, R. R. 1943. Man and the changing fish fauna of the American Southwest. Pap. Mich. Acad. Sci., Arts, Letters. XXVI:365-404.

SOLTZ, D. L. 1974. Variation in life history and social organization of some populations of Nevada pupfish, *C. navadensis*. Ph.D. dissertation, Univ. of Calif. at Los Angeles.

# A REVIEW OF CIRCUMSTANCES AFFECTING THE ABUNDANCE OF *GAMBUSIA GAIGEI*, AN ENDANGERED FISH ENDEMIC TO BIG BEND NATIONAL PARK

Clark Hubbs and John G. Williams[1]

Extinction of our endemic biota is receiving increasing attention. Many of the endangered organisms have complex threats that may involve substantial economic factors and complex land ownership problems. We discuss below the problems associated with one endangered fish that lives entirely within one national park. Despite the apparent simplicity, the efforts required to perpetuate the species may illustrate the types of difficulties that may ensue when other taxa are threatened.

*Relationships.* *Gambusia gaigei* was considered as related to *G. senilis* and *G. nobilis* by Hubbs (1929) who placed the species in the *Gambusia nobilis* species group. Subsequent authors have placed *G. gaigei* in either the *G. nobilis* or *G. senilis* group (depending upon whether *G. senilis* and its relatives are considered as in a distinct group from *G. nobilis*). All authors consider *G. gaigei* closely related to *G. senilis*.

The sole controversy on the distinction of *G. gaigei* are based on the relationships with the subsequently named *G. hurtadoi* and *G. alvarezi*. Rosen and Bailey (1963) considered the two Chihuahuan species as junior synonyms of *G. gaigei* an action presumably endorsed by Alvarez (1970) who did not list the two species among the fishes of Mexico. In contrast, Rivas (1963) considered the three to represent distinct species as did Peden (1973, 1975) who studied behavioral differences. Their action was endorsed by Miller (1977) who listed all three species as components of the Chihuahuan Desert fish fauna. Despite the minor controversy of species level distinctions, there is no question that distinct races are involved and each would fall under the provisions of the Endangered Species Act of 1973.

*Historical Status.* - *Gambusia gaigei* was first recognized by Carl L. Hubbs (1929) who described the species based on specimens collected by Frederick M. Gaige on 3 August 1928 "from a marshy cattail slough fed by springs located close to the Rio Grande at Boquillas, Brewster County, Texas, opposite the Mexican village of the same name." No further specimens were collected until 11 June 1954 but these were obtained from Spring (= Graham Ranch Warm Spring) (Figure 1). It is highly likely that the type locality is not Spring 4 as Frederick M. Gaige wrote (to Clark Hubbs) in 1956, Hubbs and Springer (1957), that the "Boquillas Spring is a different one at which a bathhouse was built". In 1937 and 1938 the Boquillas area was visited by J.T. Van Tyne and W.F. Blair and by Leo T. Murray. Dr. Van Tyne reports (Hubbs 1940) that "this cattail slough was being eroded rapidly by side cutting of the Rio Grande in flood when I visited Boquillas in Aug., 1938. If the process went on long after I was there, this type locality is gone. The fish, however, will persist in the spring above the flood plain". Both the Van Tyne and Murray reports better fit Spring 4 (or even Spring 1) than the springs near the Old Ranger Station (now the Research Station). Spring 4 is substantially larger (Van Tyne) than the others and distinctly above the flood plain (Murray). It seems likely, therefore, that Van Tyne and Murray may have thought Spring 4 was the type locality. In contrast, however, Gaige specifically disagreed and stated that he collected the fish at a different spring and one at which a bathhouse had been built. His memory is substantiated by observations by Carl L. Hubbs that fish collected by Gaige in 1928 differ morphologically from those obtained at Spring 4 in 1954. There is a spring near the present road leading to the ford across the Rio Grande to Boquillas Village. That spring has concrete walls and fits the Gaige description very well. Furthermore, Ranger John Palmer felt that it was the Boquillas Spring but that it had ceased flowing for a while in the early 1950's. This spring now has populations of *Gambusia affinis* and extensive searches have not resulted in discoveries of any resident *G. gaigei*. Parenthetically, *G. gaigei* were placed in that spring in 1956 but no survivors were noted.

Although the Van Tyne and Murray observations do not substantially detract from the probability that *G. gaigei* originally were collected from Boquillas Spring they do suggest that *Gambusia* occurred in Spring 4 during their visits – the status of field biological research in the 1930's was that type localities were seldom so precisely located that a sample from 2 km distant would not be construed to be a different location. I have checked with W.F. Blair who accompanied Dr. Van Tyne and he cannot recall the details of the itinerary of their visit to the Boquillas area. The evidence available supports a hypothesis that in 1930 *G. gaigei* lived in at least 2 springs (and perhaps also Spring 1) on the north shore of the Rio Grande 2-4 km west of Boquillas Canyon.

Subsequent efforts to discover additional populations of *G. gaigei* in the Boquillas area have been unsuccessful. The various outflows at Hot Springs, "Bathtub" springs, small outflows very close to the river bank, and even Glenn Springs have been examined but no *G. affinis* obtained. At present *G. gaigei* abounds in the outflow of Boquillas Spring and Spring 4.

Regardless of the probability that *G. gaigei* once lived in Boquillas Spring the entire known population is descended from Spring 4 stocks. Boquillas Spring was examined in 1956 and no fish were seen in that pool. The district ranger, John Palmer, reported that the spring had gone dry "a few years ago", presumably during the drought years. Water was in the spring pool that fall but no fish. Later *G. affinis* were seen there, presumably invaders from the adjacent Rio Grande.

There is little firm information on the conditions at Spring 4 prior to June 1954 when it was visited by V.G. Springer and Clark Hubbs. At that time the spring was enclosed in a rock and concrete circular wall ca. 2 m high--this wall still stands but is now covered by a concrete roof. The waters from this pool overflowed through a hole (still existing) on the west side and emptied into a dredged ditch flowing at a right angle to the south. That dredged ditch was "1 to 10 foot wide and 2 feet deep." Traces of a retaining earth dike can be noted on the west side of photographs of that ditch taken in 1956 by Jerome Dorf (Figure 2). The dredged ditch extended south "about 40 feet from the spring to form a pool about 20 feet wide, 40 feet long, and 4 feet deep". That was the total range of *G. gaigei* in 1954 and 1956. In 1956 Clark Hubbs examined the region west of

[1]Department of Zoology, University of Texas, Austin.

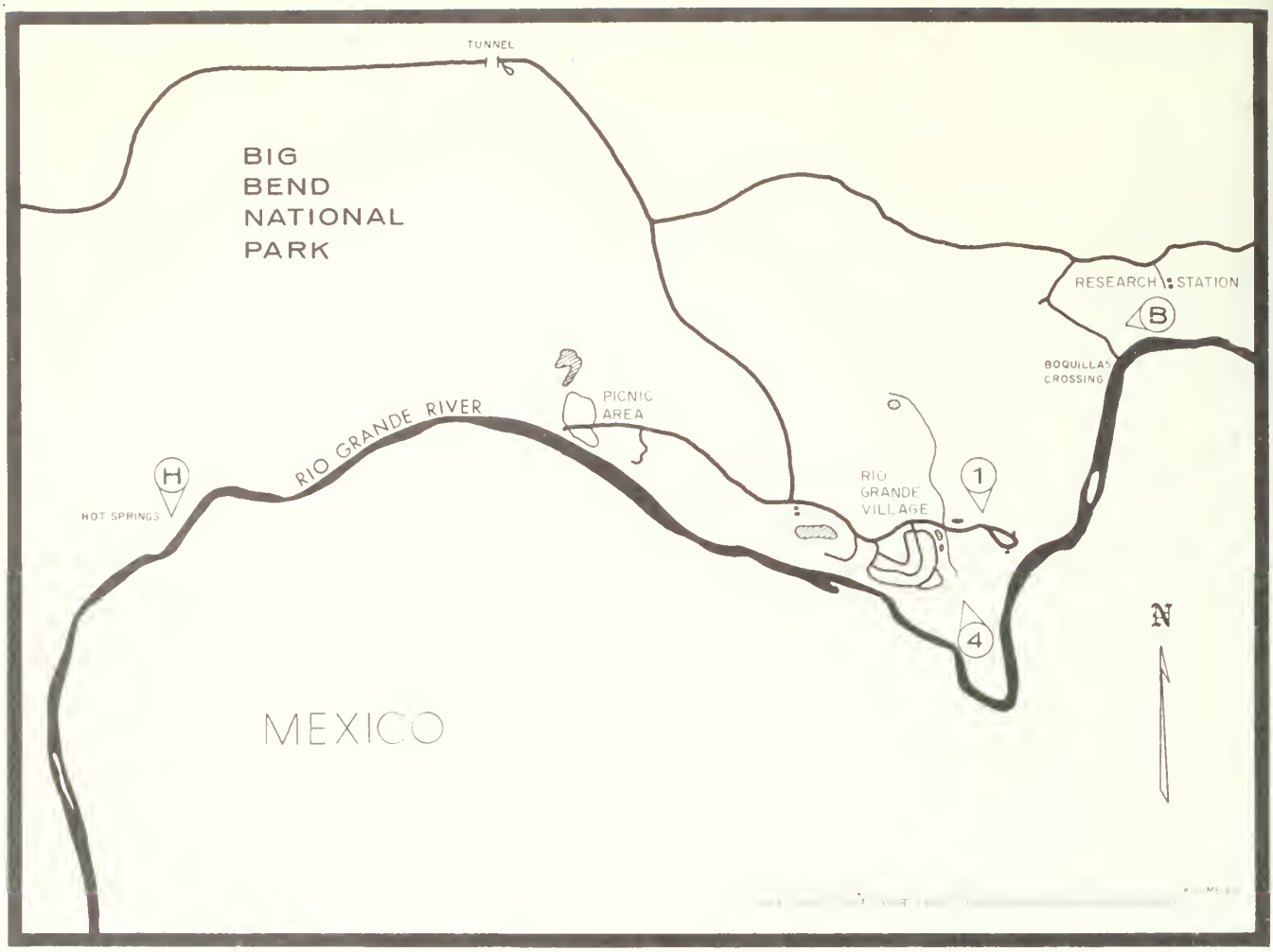



FIGURE 1. Map of the Rio Grande Village Region showing locations associated with *Gambusia gaigei*. Springs 1 and 4 are located as are Boquillas Spring (B) and Hot Springs (S). The two refugia are NE of Rio Grande Village, SW (old) adnd NE (new) of the intersection on the road leading each toward spring 1.

the dredged ditch and noted what appeared to be a natural stream course that extended to a row of trees among which remnants of an obvious spring run could be observed. This water course can still be noted 20 m ± east of Rio Grande Village Camp Ground at the start of the Nature Trail.

It was apparent in 1954 that the dredging and pool construction was relatively recent, presumably the previous summer. By 1956 the surrounding emergent vegetation had drastically increased (Figure 3), so much that it had to be cut and removed to facilitate remedial work that fall. Presently, the vegetation has so overgrown the area that it is not possible to determine the precise location of the dikes and water courses unless the "reeds" are cut again. In 1954 and 1956 (drought years) little or no water left the "40 x 20 foot" pool. Now (normal rainfall year) a stream leaves and crosses the nature trail ca. 20 m east of the "natural" stream course. That water soon drops precipitously into the Rio Grande.

The dikes were built in conjunction with planned development at Rio Grande Village. The objective seems to have been the construction of a children's fishing pool. Apparently, catchable fish did not naturally populate the pool so they were supplemented with fish ("catfish" and "perch") seined from the Rio Grande. Presumably, that action also resulted in the release of *G. affinis* (as well as *Notropis lutrensis* and *braytoni*) also. As there are no pre-1954 samples available, it is unknown whether the mosquitofish previously lived in the Spring 4 outflow above the steep north bank of the Rio Grande; presumably, that bank served as a barrier to the upstream dispersal of *G. affinis*. Under any circumstances most fish sampled in 1954 were *G. gaigei*, but conditions were vastly different on 27 and 28 April 1956 when *G. affinis* were much more abundant than *G. gaigei*. Following that observation recommendations for remedial action were made (Hubbs and Broderick 1963). The serious nature of the statu of *G. gaigei* is underscored by Matthiessen's (1959) premature report of its extinction.

The first remedial program was on 9 October 1956 when 25 *G. gaigei* were seined from the dredged ditch and placed in live tanks. Then the pool area was treated with rotenone in a futile effort to eradicate *G. affinis* from the ditch and pool. Fewer than 25 additional *G. gaigei* were found after the treatment, suggesting that a delay would have caused Matthiessen's pessimistic report to have been valid. No other *G. gaigei* have been found in the Spring 4 outflow, but *G. affinis* was soon seen to have repopulated that region. Fifteen of the 25 fish were placed (5 in each) in Boquillas Spring, Glenn Springs, and a stock tank along the Glenn Springs Road. None was seen again and presumably died. The other 10 fish were divided into two units, 6 to a tank adjacent to Panther Junction and 4 (2♀ + 2♂) transferred to Austin. Two of the 6 fish at Panther



FIGURE 2. Dike forming west side of the Rio Grande Village Fishing Pool. Spring 4 is adjacent to the base of the power pole in the middle of the figure. The northern extent of the dike can be seen extending along the left margin of the photograph which was taken during rotenone application.

Junction died, the others survived and reproduced but all succumbed during the following winter (presumably due to cold weather). One of the two females taken to Austin died but the other female and the 2 males survived the winter in a laboratory aquarium room (including one time when a part of the building was treated with an insecticide and the fish in 1/4 of the aquaria perished). The following spring the three survivors (and only living representatives of the species) were returned to Big Bend National Park and placed in one of two adjacent pools maintained for this species. These two pools are adjacent to and south of the asphalt road connecting the Rio Grande Village and the group campground by the Berkeley Cabin. The descendants flourished and commonly exceeded 1000 individuals and for a time all was well.

The campground in the Chisos Basin commonly was filled and the campground and associated facilities at Rio Grande Village were needed to accommodate the overflow as well as visitors desiring a river bank camp site. A number of native shade trees were planted around the campgrounds. These trees were irrigated with Rio Grande water which accumulated in a pond on the immediate north bank of the asphalt road. Overflow water from that pond supplemented the water in the *G. gaigei* refuge. Presumably *G. affinis* were pumped from the Rio Grande with the irrigation water. Apparently, green sunfish *(Lepomis cyanallus)* entered the refugium by the same provenance. Some of the *Gambusia* entered the uppermost (northern) pond, thrived and spread to the middle pond (the lowermost = southern, commonly dried so often that it contained no living fish). When this situation was discovered on 16 April 1960 it was obvious that the processes of 1954-1956 were again under way and it was expected that it would be an even more rapid decline in *G. gaigei* abundance as the contaminated pond had somewhat different environmental conditions than those that occurred in the Spring 4 area. Consequently, 15 *G. gaigei* were collected and transported to Austin (2 died) but 40 young were born. Sixteen of the 50-60 fish were transferred to the University of Michigan for insurance against a catastrophe. During the 1960 summer the present refugium pool was dug and filled with water pumped from Spring 4 (also Spring 1.) Twenty of the 38 surviving in Austin were taken to the park on 7 August and placed in the new pool (Figure 4). The old refugium pool was seined at that time and the 8 *G. gaigei* that were collected were transferred to the new refugium. Subsequently, no *G. gaigei* have been found in the old refugium. As soon as it had been recorded that the new refugium had a viable population, the Michigan stocks were discontinued. The remaining 18 fish in Austin were transferred to the Brackenridge Field Laboratory at which location they have been continuously cultured.

During 1968 Ranger Naturalist Roland Wauer noticed that green sunfish were in the new refugium. Presumably they had been placed there by "sport" fishermen who had caught them in the old refugium. Regardless of their source, they were



FIGURE 3. Stock rescue efforts prior to rotenone application in 1956. Note the heavy growths of emergent vegetation left after the majority had been removed and stacked in left background.




FIGURE 4. Present refugium pool, 13 X 31 m prior to establishment of a flow through system and raising of pool level to the base of the trees.

there and presented a problem. The water level in the pool was lowered, *G. gaigei* set aside, and all remaining fish eliminated. Then the *G. gaigei* were returned and the population was reestablished and flourished. Pool maintenance involved periodic checks of water level and if low it was filled with water pumped from Spring 1. As that spring had no surface flow there was little potential for fish introduction along with the water. At periodic intervals the emergent vegetation, that grew near the banks and often extended well across the shallow refugium pond, was cut or pulled up. Some was removed but much was left as a source for nutrient recycling. This action undoubtedly resulted in an accumulation of muck on the bottom, and a gradual decrease in depth of a pond that had its depth "regulated" by control of surface level. Refugium pond security was primarily by isolation. There is no extensive publicity concerning the pond which is located in a brushy wooded grove at the end of an earth trail. The pond is surrounded by 3 strands of barb wire on top of a woven wire fence with a locked gate. A N.P.S. sign briefly explains the purpose of the pool to persons who happen onto the spot.

The *G. gaigei* population cultured in Austin similarly underwent developments. The stock was transferred to a 6 m diameter x 2 m deep plastic lined swimming pool in 1965. Periodically, subsets from that population are taken into the laboratories on the main campus to ensure overwinter survival. Other subsets have been placed in smaller plastic lined pools but those have now been discontinued. In 1971 a subset was taken to a concrete-lined 10 $m^2$ pool x 4 m deep. An adjacent identical pool was used to house another backup population of the related and critically endangered *Gambusia amistadensis*. Both concrete-lined ponds were supplied with well water from a single outlet between the ponds. Flow to both went through a T which unfortunately had no valve structure. The water went from the T to the bank of each pond. When dead *G. gaigei* were found following a cold night in 1972, it was noted that the hose to that pond had been moved; apparently, at some time in the past someone had taken a drink from the hose and carelessly dropped it so that it no longer flowed into the pool. Some *G. gaigei* survived this disaster. The hose was returned to the pond but placed beneath the surface as was the hose to the *G. amistadensis* pool. Direct water connection between the pools made it possible that both backup populations were contaminated by individuals of the other species entering by swimming up one hose and passing down current in the other to the second pool. Thus, the stocks in the concrete-lined ponds may have been contaminated. In 1973 the U.S. Fish and Wildlife Service was considering options for future use of the National Fish Hatchery at Dexter, New Mexico. One of the proposals was to have it used as a center for research on rare and endangered species. The preparatory studies included an evaluation as to whether various endangered species would survive there. Fishes chosen for this test were those housed in the concrete-lined ponds as they were

less valuable than those known to have been kept separate. After the Dexter stocks were known to survive and flourish, they were replaced by pure stocks on 9 August 1976.

Following the 1968 problems with green sunfish, the *G. gaigei* in the refugium near Rio Grande Village again flourished. The status was periodically examined by a variety of visitors and Park Service personnel. The next notable observation of difficulties was in December 1975 when Harry Steed observed dead *Gambusia* and others swimming erratically so that they beached themselves among the leaves that had fallen onto the bank. This behavior is suggestive of lethal cold shock: 1) the weather on the preceding night had been cold; 2) the water surface was low; and 3) the accumulation of organic debris had raised the bottom. As no source of inflow water was available to mitigate against the climate, it seems likely that the 1972 problems at the concrete-lined pond in Austin had been repeated in 1975 at Big Bend. The absence of previous occurrences was undoubtedly due to the larger volume of water that depressed thermal oscillations caused by sudden cold weather. A major contributant to the new problem was undoubtedly the unexpected shallowing of the pond due to accumulation on its bottom. No special attention was paid to Ranger Steed's observations but on 16 March 1976 John G. Williams and Thomas Lucier observed the refugium and found no fish. Following that disturbing report, Roland Wauer, Clark Hubbs, and John Williams visited the park on 6 May and together with local park service personnel, Frank Deckert, Hugh Crenshaw, and Harry Steed examined the pond and found no fish. On 7 August Roland Wauer, Clark Hubbs, Lemule Garrison, and numerous park service personnel visited the area and noted live *Gambusia*, presumably descendants of rare surviving females, young, fertilized eggs aborted by dying females, or stocks maintained indoors in the park at the time the outdoor stocks died. At that time the stock was supplemented by stocks transported to Big Bend from Austin.

*Future Status.* - The National Park Service has established a flow through system based on water from Spring 1 to insure survival until plans for a more permanent and natural system can be activated. The plans envision use of water from Spring 1 or 4 to establish a natural spring run similar to that that preceded development at Rio Grande Village. Spring 4 has merit as it is a known locality inhabited by *G. gaigei* but its proximity to the existing campground may cause problems. Spring 1 has merit as it can have access regulated, is likely to have once held *G. gaigei*, has similar physico-chemical factors to Spring 4 as it is based on the same aquifer, and is in the vicinity of several historical sites and can serve as the basis of a historic and environmental information exercise through a guided tour. Either alternative could reestablish a natural stream system that should redirect selection toward the natural *G. gaigei* genome.

## LITERATURE CITED


ALVAREZ DEL VILLAR, JOSE. 1970. Peces Mexicanos (claves). Serie investigacion pesquera, estudia No. 1. 166 pp.

HUBBS, CARL L. 1929. Studies of the Fishes of the Order Cyprinodontes VIII. *Gambusia gaigei*, a new species from the Rio Grande. Occ. Pap. Mus. Zool. Univ. Mich. 198:1-11.

HUBBS, CARL L. 1940. Fishes from the Big Bend Region of Texas. Trans. Texas Acad. Sci. 23: 3-12.

HUBBS, CLARK. 1971. Competition and isolation mechanisms in the *Gambusia affinis* X *G. heterochir* hybrid swarm. Bull. Tex. Mem. Mus. 19: 1-47.

HUBBS, CLARK and HAROLD J. BRODERICK. 1963. Current abundance of *Gambusia gaigei*, an endangered fish species. Southwestern Naturalist 8: 46-48.

HUBBS, CLARK and VICTOR G. SPRINGER. 1957. A revision of the *Gambusia nobilis* species group, with descriptions of three new species, and notes on their variation, ecology, and evolution. Texas J. Sci. 9:279-327.

MATTHIESSON, H. 1959. Wildlife in America. 304 pp.

MILLER, R.R. 1977. Composition and derivation of the native fish fauna of the Chihuahuan desert region. *In*: Transactions of the Symposium on the Biological Resources of the Chihuahuan Desert Region, U.S.-Mexico. R. H. Wauer and David Riskind (eds.), National Park Service, GPO, Washington, D.C.

PEDEN, A.E. 1973. Variation in anal spot expression of gambusiin females and its effect on male courtship. Copeia 1973:250-263.

PEDEN, A.E.. 1975. Differences in copulatory behavior as partial isolating mechanisms in the poeciliid fish *Gambusia*. Canadian J. Zool. 53:1290-1296.

RIVAS, L.R. 1963. Subgenera and species groups in the poeciliid fish genus *Gambusia* Poey. Copeia 1963:331-347.

ROSEN, D.E. and R.M. BAILEY. 1963. The poeciliid fishes (Cyprinodontiformes). Their structure, zoogeography, and systematics. Bull. Amer. Mus. Nat. Hist. 126:1-176.

# POSTGLACIAL DISPERSION AND PRESENT DISTRIBUTION OF SALMONID FISHES IN THE NORTHERN CASCADES RANGE

Robert Wasem[1]

North Cascades National Park and Ross Lake and Lake Chelan National Recreation Areas occupy 2,770 $km^2$ in the northeastern portion of the Northern Cascades Physiographic Province. This province, one of eight in Washington, covers about 26,300 $km^2$ or roughly 15 percent of the state. The province extends north from Snoqualmie Pass to the Fraser River valley in southern British Columbia, and is bounded on the east by the Okanogan Highlands and on the west by the lowlands of the Puget Trough Province.

The Northern Cascades Province has been described by Franklin and Dyrness (1973), Fenneman (1931), and Livingston (1969). Generally, the northern Cascades Range consists of extremely rugged, deeply dissected topography of great relief which is topographically mature. Peaks and ridges maintain somewhat uniform elevations ranging between 1,800 m and 2,600 m, and are bisected by deep U-shaped valleys with minimum elevations of 50 m or less.

By far the most important fishes to the economy and recreation of the Pacific Northwest are the nine native and four introduced species of salmon, trout, charr, whitefish and grayling of family Salmonidae. Modern fish fauna of the province has been at least seven million years in development. According to Miller (1965), fossil evidence of fish evolution in North America is lacking but about 60 percent of the existing fauna probably does not predate the early Pliocene or late Miocene. Evidence of Salmonidae in Europe dates to the Eocene Epoch, but in North America fossil remains of genera *Oncorhynchus* and *Prosopium* can be traced only to the early and mid-Wisconsin period of Pleistocene glaciation. Remains of genus *Salvelinus* have been discovered in deposits of the Yarmouth post-Kansan interglacial period, while genus *Salmo* made an early fossil appearance during late Miocene with no further record until early Wisconsin Glaciation (Miller 1965).

Existing salmonid fauna of the province probably evolved from common *Salmo*-like ancestors beginning in mid- to late-Tertiary times. Salmonid evolution may have started during temperate climates of the Miocene in shallow saline seas and extensive lava-dammed lakes and their tributary streams. Ichthyfauna development continued through the Pliocene as temperate conditions and mild mountain building disturbances, which began in the late Miocene, continued.

Uplift of the present Cascade Range did not begin until mid- to late Pliocene (Livingston 1969), the process requiring about six million years. Compared with post-Pleistocene landscapes, these late Pliocene mountains were lower in elevation and of rounded, more gentle relief because the mountain mass had yet to reach its maximum uplift and be further modified by glaciation. Also, few, if any, high mountain lakes existed, and the numerous stream courses were probably similar to those of present day unglaciated mountainous regions, i.e., with more uniform though frequently steep gradients. As the Tertiary Period drew to a close, ancestral salmonids occupied coastal lowland waters in addition to the slowly diminishing stream environments of the uplifting Cascade Range.

The Pleistocene Epoch, spanning 1.5 million years, was the age of ice in the Cascades as in other parts of the world. Uplifting of the Cascade Range continued and several great stratovolcanic cones were formed, including Mount Baker and Glacier Peak in the northern portion of the range. The Quaternary history of the Northern Cascades Province and adjacent areas is described by Crandell (1965) and Richmond et al. (1965). Glacial activity was highlighted by repeated advances and retreats of alpine glaciers, four major and several minor invasions from the north of large continental glaciers, ice sculpting of the mountain topography, temporary alteration of drainage patterns, and formation of temporary ice-dammed lakes along ice margins. Also, extensive areas of the Columbia River drainage basin were periodically flooded following rapid release of water from several large glacial lakes in the intermountain region.

The northern Cascade Range was extensively modified by local alpine glaciers and the Puget and Okanogan Lobes of the Cordilleran Ice Sheet. This ice mass invaded the Cascade Range from more northern regions of abundant precipitation. Changes in mountain topography included formation of: (1) deep, straight, U-shaped, main drainages; (2) hanging tributary valleys with truncated spurs; (3) matterhorns, aretes and cirque basins; and (4) fluvioglacial depostion on lower valley floors.

The Columbia River east of the province was pushed south into new channels while its south-flowing tributaries were periodically covered by the Okanogan Lobe or by long valley glaciers extending from the lobe. Valley glaciers of this type occupied the Yakima, Clelan-Stehekin, Entiat, and Wenatchee river valleys during late Pleistocene.

During the most recent or Fraser Glaciation, the Puget Lobe extended further south on the west slope of the Cascade Range than did the Okanogan Lobe on the east. This ice mass periodically blocked and diverted tributary streams of the Puget Sound into ice-dammed lakes and new channels. Depending on the extent of the ice advance, westward-flowing rivers such as the Fraser, Nooksack, Skagit, Stillaguamish, Skykomish and Snoqualmie, were diverted into temporary lakes along the eastern margin of the ice flow, and eventually drained through the Chehalis River flowing to the ocean around the southern edge of the ice. During the several mild interglacial periods, these drainage systems renewed their normal preglacial patterns and the Puget Sound was again connected to the ocean by Admiralty Inlet and the Strait of Juan de Fuca.

Salmon Springs Glaciation, corresponding with early to middle Wisconsin time, was followed by 15,000 years of Olympia Interglaciation during which time the Puget Lobe retreated into what is now Canada. This was followed by the Fraser

[1]North Cascades National Park, Sedro Woolley, Washington 98284.

Glaciation which began about 25,000 years ago, progressed through the Evans Creek and Vashon stades, and made one last advance before completely melting away from the Fraser lowlands about 9,000 years ago. Associated alpine glaciers began melting about 15,000 years ago.

According to Miller (1965), ichthyfaunas of the late Pleistocene were probably similar to those of today as the few known salmonid fossils of this period cannot be distinguished from living species. Miller postulates that severe climatic changes accompanied by frequent ice invasion and retreat may have provided impetus for salmonid evolution and speciation during these unsettled times.

McPhail and Lindsey (1970) describe fish refuge and reinvasion during and following recent Pleistocene glaciation. Major areas of ice refuge in western North America during maximum Fraser and Pinedale Glaciation periods were: (1) Yukon River valley of Alaska, (2) streams and shallow lakes of the exposed Bering land bridge, (3) Columbia River basin of the Pacific slope, and (4) headwaters of the Missouri River of the Atlantic slope. Native salmonids of the Pacific Northwest found asylum only in the Columbia River basin both in the ocean and in freshwater habitats along the everchanging ice margins. All but the mountain whitefish (*Prosopium williamsoni*) and the cutthroat trout (*Salmo clarki*) also took refuge in the Bering land bridge but did not repopulate southern areas by range extensions from this far northern sanctuary. The introduced Arctic grayling (*Thymallus arcticus*) and lake trout (*Salvelinus namaycush*) reestablished native ranges from both the Bering and Mississippi refuges. Another introduced form, the brook trout (*Salvelinus fontinalis*), survived glaciation in a southern portion of the Mississippi refuge (McPhail and Lindsey 1970).

According to Crandell (1965) radiocarbon dating indicated the Puget ice lobe at one point near present Olympia moved forward 100-160 m/year. Assuming similar rates of ice advance and retreat throughout the Pleistocene, individual fish would have had little difficulty in safely retreating before the advancing ice masses. However, some may have been isolated in glacier-dammed lakes where they might have survived glaciation. By and large, however, most fish slowly retreated before the ice occupying all suitable habitat around the perimeter of the ice masses. No suitable aquatic refuge existed on the nunatak islands projecting above glacial ice fields. These high peaks and ridges did not support fish life prior to glaciation.

Some fishes may have been forced to coastal areas of the lower Columbia and Chehalis river systems during retreat before the Puget Lobe of Cordilleran ice. By the fact that all native species of trout, charr, and salmon are, to some degree euryhaline, is evidence of their ability to survive in estuaries and other coastal waters with wide ranges in salinity. Diadromous or sea-run strains of coastal cutthroat trout (*S. c. clarki*), Dolly Varden charr (*Salvelinus malma*), and rainbow trout or steelhead (*Salmo gairdneri*) are native to all western slope drainage systems.

As fishes retreated before the ice advance, they likewise reoccupied habitats left ice-free as glaciers melted back during the several lengthy interglacial periods. Extent of reinvasion depended upon barriers to upstream migration such as glacial deposits, high falls, and steep cascades. Fishes followed the retreating ice up the aquatic pathways of main-stem rivers, and penetrated deeply into the heart of the northern Cascades Range before encountering these migration blocks. Only low-gradient floodplain portions of smaller tributary streams were populated, because of their intermittent or interrupted flow characteristics and steep gradients over the U-shaped valley walls. Some fish may have migrated to near headwater areas of larger streams only to become isolated as lower valleys were blocked by rock avalanche, or as waterfalls formed because of continual erosion over bedrock outcrops in deep fluvioglacial drift deposits of the valley floors. There is evidence to suggest this may be the case with several Dolly Varden populations such as those in the Marble Creek and Newhalem Creek drainages.

There may be another explanation for the presence of native unstocked species, particularly Dolly Varden, above existing waterfall barriers. A species isolated in a glacier-dammed lake along the ice flow margin during Fraser Glaciation might have survived and then entered tributary streams to that temporary lake above inundated stream barriers.

With the demise of Fraser Glaciation, fish repopulated the province by way of eight primary avenues: (1) the Fraser-Chilliwack river system from the north and west; (2) the Nooksack, Skagit, Stillaguamish, Snohomish-Skykomish-Snoqualmie systems from the west; and (3) the Chelan-Stehekin Wenatchee and Entiat river systems via the Columbia River from the south and west. Fish migrated from the Puget Sound for a distance of about 170 km before reaching the first impassable barrier in the upper Chilliwack River. In the Nooksack river system these distances were 88 km in the north fork, 67 km in the middle fork, and 89 km in the south fork. In the Skagit river system fish moved about 194 km along the main-stem of the Skagit, 143 km on the Sauk River, 135 km up the Suiattle River, 143 km up the Baker River, and 143 km on the Cascade River--all major tributaries of the Skagit. In the Stillaguamish system, fish migrated 64 km up the north fork and 63 km up the south fork before encountering barriers, while in the Snohomish-Skykomish river system the distance was approximately 105 km. Salmonids managed to repopulate the Snohomish-Snoqualmie drainage system for a distance of 79 km before being stopped at the formidable barrier of Snoqualmie Falls.

On the eastern slope of the northern Cascade Range three important river systems provided fish access into southern portions of the province. Higher elevations of all three drainages were covered by Cordilleran ice of unknown age, while mid-valley portions were filled with large alpine glaciers of Salmon Springs Glaciation and the Evans Creek Stade of more recent Fraser Glaciation (Crandall 1965, Richmond et al. 1965). Lower valley portions near their confluence with the Columbia River were free of ice at all times with the exception of the Chelan-Stehekin drainage which was covered by a spur from the toe of the Okanogan Lobe during the Vashon Stade of Fraser Glaciation. Fishes in the Wenatchee and Entiat river drainages could take refuge in lower unglaciated stream areas and in the adjacent Columbia River, and then repopluate about 94 km of the Wenatchee River main-stem and 46 km of the Entiat River main-stem following glacial retreat.

Fish life may have survived Fraser Glaciation in a small portion of Lake Chelan sandwiched between the Okanogan Lobe and the large, alpine Chelan Glacier invading the drainage from the north during the Evans Creek Stade of 20,000 years

ago, and the Vashon Stade of 15,000 years ago. Apparently some of the lower Chelan-Stehekin River drainage was always unglaciated during late Pleistocene (Waters 1933) thereby providing sanctuary for fishes that had entered prior to its migrational isolation from the Columbia River. Dr. Robert Behnke[2] has advanced the hypothesis that the westslope cutthroat trout (*S. c. lewisi*) of Lake Chelan may have been carried to that vicinity by the waters of Glacial Lake Missoula during massive flooding on at least three occasions, the most recent during an interstade following the early stade of Pinedale Glaciation some 21,000 years ago. Similarity of Lake Chelan fauna with that of the Rocky Mountain and intermountain regions supports this hypothesis. Apparently the endemic cutthroat trout of the Lake Chelan-Stehekin River drainage are unique in that their native geographic position was the furthest west of any of the larger-spotted interior cutthroat.

With recession of the Chelan Glacier, which began as much as 20,000 years ago, Dolly Varden and cutthroat trout followed the melting ice for approximately 106 km to the first major barrier encountered in the Stehekin River just above Agnes Creek. If it can be assumed that the ice front retreated at a mean rate of as much as 200 m/year, about 530 years would have been required for many generations of salmonids to inhabit all accessible portions of the drainage. Comparable time periods were probably required for fishes to initially colonize or recolonize other glaciated drainage basins of the northern Cascade Range.

Fraser Glaciation ceased with the demise of the Sumas Stade about 9,000 years ago. A period of Mount Mazama ash deposition occurred between 7,000 and 6,000 years ago followed by 1,000 years of hypsithermal activity of unusually mild temperatures. There is some evidence to suggest considerable fish mortality resulting from these extensive ash deposits. During the Hypsithermal interval lacustrine sedimentation, fluvial deposition, and frequent mudflows aggraded many stream channels resulting in a constant change in extent and character of fish habitat. During the past 4,000 years of Neoglaciation ichthyfaunas probably retained their early postglacial geographic range with only minor variation as stream habitats were drastically altered by periodic mudflow, flood, rock and snow avalanche, forest fire and log jamming. Remnant alpine cirque glaciers continued to fluctuate in size depending upon short-term climatic changes. New alpine and subalpine lakes sometimes formed as the glaciers shrank leaving water-filled bedrock basins. But additional fish habitat did not materialize because virtually all subalpine and alpine lakes and tarns were formed on drainage divides at headwaters of steep-gradient streams whose waters plunge over many waterfall barriers to upstream fish movement. These numerous high mountain cirque lakes were, therefore, naturally barren of fish life because of this physical isolation.

Beginning about 1814 Caucasian man began exploration of the region. Several military and International Boundary survey expeditions were carried out (Baker 1900, Pierce 1883), but expedition journals made little mention of aquatic life encountered. However, two significant journal entries served to establish the presence of indigenous trout far up two major drainages. Henry Custer of the U.S. International Boundary Commission Survey noted dining on "black spekled trout" captured by his Indian companions in the Skagit River a few kilometers north of the 49th parallel on 21 August 1859. Lt. Henry Pierce, leader of a military expedition from Fort Colville reported "lusty trout" in the lower Stehekin River in late August 1882. Smith and Anderson (1921) provide limited information of fish distribution in several large coastal stream systems probably prior to significant fish introductions. McPhail (1967) gives a more recent review of freshwater fish distribution in the western portion of the province.

The following discussion of recent fish distribution will be mainly confined to the northeastern portion of the Northern Cascades Province. Before 1900 mountain whitefish were believed to inhabit most coastal streams including the mainstem and floodplain tributaries of the Chilliwack, Nooksack, Skagit and Baker rivers. This situation has apparently not changed to the present as this species has not been widely dispersed by man into other favorable habitats. Surprisingly the mountain whitefish has not been reported from the Lake Chelan-Stehekin River drainage, although native to the Columbia River and such tributaries as the Entiat and Wenatchee rivers.

The Dolly Varden also has not benefited from man's fish cultural practices during the past 100 years. One known exception involved the 1966 release of 14,600 fingerlings of the Alaskan strain by the Washington Game Department in the lower Stehekin River[3]. Their survival and influence upon the gene pool of the southern strain is not known. The creation of Ross, Diablo and Gorge Lakes for hydroelectric power and flood control isolated upriver populations from the ocean and enabled them to gain access to several formerly inaccessible tributaries to the upper Skagit River. At present sea-run and resident stream populations of Dolly Varden essentially occupy the same main-stem river habitat as prior to 1900, but must now compete with a variety of introduced salmonids in many of these areas. Dolly Varden are now extremely scarce in the Lake Chelan drainage and none have been introduced to the high mountain lakes of the northern Cascades Range.

Five anadromous species of Pacific salmon of genus *Oncorhynchus* occupied all major western slope drainages below migration blocks prior to 1900 and essentially are found in this same range today, except for some minor range extension due to circumvention of natural barriers by fish ladder construction. Also some stream habitat has been lost because of dam construction. French and Wahle (1965) and Fulton (1968) provide information regarding salmon distribution in the Columbia River basin. Chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) do not migrate through the Columbia River system to the Wenatchee, Entiat, Methow, and other eastern slope streams. However, significant spring and summer runs of Chinook salmon (*O. tshawytscha*) with smaller numbers of coho salmon (*O. kisutch*) and sockeye salmon (*O. nerka*) travel great distances from the Pacific Ocean to spawn in these drainages. Lake Chelan now supports a landlocked population of Chinook salmon as a result of annual plants initiated in 1974 by the Washington Department of Fisheries.

Kokanee salmon, a landlocked dwarfed form of sockeye, may have been native in the Chilliwack

[2]Letter dated 4 August 1975, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins.

[3]Undated letter of October 1976 from Clair Sackenreuter, manager of the Clelan Fish Hatchery.

River and Baker River drainages as a result of evolution from residual sockeye salmon stocks in lacustrine environments of Chilliwack Lake and the original or natural Baker Lake. Presently they spawn in these two river systems within the national park. Kokanee were introduced into Lake Chelan in 1917 and are now well-established in the drainage. Kokanee provide about 90-95 percent of the current sport harvest. In autumn months kokanee spawn in several smaller tributaries and in the Stehekin River above Lake Chelan. Several proglacial lakes outside the immediate study area also support kokanee salmon populations. These are the Whatcom, Samish, and Stevens Lakes on the western slope and the Wenatchee, Cle Elum, Kachess, and Keechelus Lakes on the east side of the Cascades.

Before 1900 rainbow trout populated virtually all major river systems on the west side of the Cascades but were absent in the Lake Chelan-Stehekin River system until introduced in 1917. Construction of five hydroelectric dams in the Skagit and Baker Rivers between 1919 and 1959 contributed to range extensions up previously inaccessible tributary streams, particularly in the upper Skagit system. Steelhead, the anadromous form of rainbow, occupied all major western slope rivers below migration barriers. Their present range, essentially unchanged, includes the Fraser-Chilliwack, Nooksack, Skagit, and Wenatchee Rivers and their larger tributaries.

Presently rainbow trout inhabit virtually all lower-gradient streams on the west side of the Cascade Range, as well as eight high elevation lakes in the northeastern portion of the province. Three high lakes, Lake Chelan, and the lower Stekekin River support eastern-slope rainbow populations. This species is a favorite of both anglers and fish culturists and, therefore, has received widespread dispersal by massive stocking programs beginning in the early 20th century.

Prior to 1900 rainbow trout were apparently more widespread in coastal waters than were the fine-spotted coastal cutthroat trout (*S. c. clarki*), which confined itself to lower elevation streams of the Puget Sound. Both sea-run and resident cutthroat populations developed in the Chilliwack, Nooksack, Skagit and other river systems. As previously mentioned, a large-spotted interior subspecies of cutthroat may have invaded the Lake Chelan drainage system following the flooding of Glacial Lake Missoula during Pinedale Glaciation of the late Pleistocene. As with rainbow trout, cutthroat have also been widely dispersed to naturally inaccessible high elevation lakes and streams by individuals, fish stocking and other outdoor clubs, and agencies of the State and Federal government. All high mountain lake introductions have utilized either the Yellowstone subspecies (*S. c. bouvieri*)[4] or the westslope cutthroat. The latter is currently propagated by the Washington Game Department as their Twin Lakes strain, which reportedly was originally derived from the native Lake Chelan cutthroat (*S. c. lewisi*). Interbreeding with the coastal cutthroat subspecies may take place if westslope and Yellowstone subspecies, introduced and perpetuated in the numerous high lakes west of the Cascade crest, move downstream to main-stem river habitat. Only one natural lake in the immediate study area has been stocked with the Washington Game Department's Tokul Creek cutthroat, a strain of coastal cutthroat reserved for management of lower elevation waters.

Fortunately, introductions of exotic salmonids have not been widespread in the northeastern portion of the province. Brook trout maintain significant populations only in several small streams and ponds and in four high elevation lakes. Other than these lakes, brook trout in the Lake Chelan-Stehekin River and upper Skagit River systems generally are sparse with only an occasional specimen being seen. Additional brook trout populations occur in at least 40 high lakes in the western portion of the northern Cascades Range. Brook trout high lakes are rare on the eastern slope of the Cascades.

Golden trout (*Salmo aguabonita*) were first stocked in 1959 and are known to be surviving in small numbers in only two high lakes of the northeastern portion of the province. Their status in five other remote alpine lakes is not known at this time. The present status of golden trout is not known in six other western slope high lakes outside the study area. Golden trout populations are not known to exist in high lakes along the eastern slope of the Cascades Range.

Arctic grayling are presently found only in Upper Granite Lake of the Cascade River drainage. This is the only population of grayling in Washington. Apparently brown trout (*Salmo trutta*) maintain a small population in Baker Lake and Lake Shannon (both reservoirs), as occasionally several are reported captured by anglers.

Lake trout have been introduced to at least 10 lakes and reservoirs in the province, but not to any waters in the immediate study area in the northeastern portion. Most of these introductions are not successful. However, lake trout are reportedly established in two high elevation lakes --Isabel on the western slope and Eightmile on the eastern slope of Cascade Range. This nonnative species is also established in Cle Elum Lake, a lower elevation reservoir on the east slope.

Since 1900 the native ranges of all salmonids have, to some degree, been modified by activities of man. Such activities include hydroelectric dam construction, development of irrigation and flood control impoundments, commercial and sport fish harvest, road construction, river channel modification, agricultural practices, timber harvest, and industrial water pollution. Release of exotic salmonids and large numbers of hatchery-reared salmon and trout have been made to maintain commercial stocks and enhance recreational opportunity for an increasing human population. Understanding native fish distribution is further complicated by the release of large numbers of both native and exotic salmonids in high mountain waters naturally barren of fish life.

One research effort at North Cascades National Park is to determine past and present ichthyfauna distribution by field survey and collection and analysis of historical data. This is prerequisite to the identification and preservation of pristine waters and endemic populations of salmonids, cottids, and others.

[4]Behnke, R. J. 1975. The native cutthroat trouts of Wyoming, I: Evaluation of collections from the Green River and Bear River drainages. 12 pp. typewritten.

REFERENCES CITED

BAKER, MARCUS. 1900. Survey of the northwestern boundary of the United States, 1857-1861. U.S. Geol. Surv. Bulletin No. 174. Washington D.C.

CRANDELL, D. R. 1965. The glacial history of western Washington. Pages 341-353 *in* H. E.

Wright, Jr. and D. G. Frey, eds. The Quaternary of the United States. Princeton University Press, Princeton, N.J.

FENNEMAN, N. M. 1931. Physiography of western United States. McGraw Hill Book Co., New York.

FRANKLIN, J. F. and C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington, USDA Forest Service General Technical Report PNW-8. U.S. Government Printing Office, Washington, D.C.

FRENCH, R. R. and R. J. WAHLE. 1965. Salmon escapements above Rock Island Dam, 1954-60. U.S. Fish and Wildlife Service Special Scientific Report - Fisheries No. 493. U.S. Government Printing Office, Washington, D.C.

FULTON, L.A. 1968. Spawning areas and abundance of Chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River basin--past and present. U. S. Fish and Wildlife Service Special Scientific Report - Fisheries No. 571. U.S. Government Printing Office, Washington, D.C.

LIVINGSTON, V. E., JR. 1969. Geologic history and rocks and minerals of Washington. Washington Department of Natural Resources, Division of Mines and Geology. Information Circular No. 45. State Printing Plant, Olympia, Wash.

McPHAIL, J. D. 1967. Distribution of freshwater fishes in western Washington. Northwest Sci. 4(1):1-11.

McPHAIL, J. D. and C. C. LINDSEY. 1970. Freshwater fishes of northwestern Canada and Alaska. Fish Res. Board Canada Bull. 173. Ottawa.

MILLER, R. R. 1965. Quaternary freshwater fishes of North America. Pages 569-581 *in* H. E. Wright, Jr. and D. G. Frey, eds. The Quaternary of the United States. Princeton University Press, Princeton, N.J.

PIERCE, H. H. 1883. Report of an expedition from Fort Colville to Puget Sound, Washington Territory, by way of Lake Chelan and Skagit River . . . . August and September, 1882 (Washington, 1882) *in* Alfred Downing, Sketch Book, Washington State Historical Society, Tacoma, Washington.

RICHMOND, G. M., R. FRYXELL, G. E. NEFF, and P. L. WEIS. 1965. The Cordilleran Ice Sheet of the northern Rocky Mountains and related Quaternary history of the Columbia Plateau. Pages 231-242 *in* H. E. Wright, Jr. and D. G. Grey, eds. The Quaternary of the United States. Princeton University Press, Princeton, N.J.

SMITH, VICTOR and M. G. ANDERSON. 1921. A preliminary biological survey of the Skagit and Stillaquamish rivers. School of Fisheries, University of Washington, Seattle. Unpublished.

WATERS, A.C. 1933. Terraces and coulees along the Columbia River near Lake Chelan, Washington. Bull. Geol. Soc. Am. 44:783-820.

# MAN INDUCED ACID DRAINAGE IMPACT ON BENTHIC MACROINVERTEBRATE COMMUNITIES IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK[1]

William F. Trumpf[2], Eric L. Morgan[3] and Ray Herrmann[4]

## INTRODUCTION

In 1967 U. S. Highway 441 was relocated to accommodate increasing visitor use of the Great Smoky Mountains National Park. This management strategy temporarily alleviated the "log-jam" effect caused by the influx of tourists although reconstruction created new environmental problems for the Park.

Following the construction program in which new road fill was used, a native brook trout (*Salvelinus fontinalis*) kill occurred for approximately 8km downstream from the construction activity in a small stream valley, Beach Flats Prong. Concomitant with this observation were dense white-yellow precipitates coating the stream substrate for nearly 2km downstream from the road fill. It was assumed that the fish kill was related to the construction activity, more specifically to a toxic substance produced during construction operations, and possibly over a period of time the toxic material would be washed away and ecological stability re-established. The U. S. Fish and Wildlife Service, six months later, attempted to reintroduce brook trout; however, the trial failed as did a second attempt six months later. This enigma was not re-examined until 1972 when the U. S. Fish and Wildlife Service conducted an extensive electrofishing survey and revealed the continued absence of fish in Beech Flats Prong. Initial chemical analysis at this time showed extreme acidic conditions (pH: 4.5) immediately below the road fill while upstream from Highway 441, the pH of the stream approached neutrality. The investigations of Herrmann, et al.(1975) and Espenshade (1963) showed that the road fill was primarily composed of the Anakeesta formation, a pyritic carbonaceous phyllite. This ore-bearing rock occurs primarily as sulfide deposits of copper and iron although other mineral components, such as aluminum and zinc, are present. Through weathering processes, oxidation and hydrolysis of the metal-sulfide rich Anakeesta rock occurs, resulting in acid and heavy metal leachates. The detrimental impact of the Anakeesta leachates on the aquatic biota of Beech Flats Prong has been discussed by Morgan and Jones (1974), Huckabee et al.(1975) and Green (1975).

The goal of this one year study, initiated July 1975 was to further evaluate the extent of ecological degradation on the "stream ecological system" of Beach Flats Prong. Specific objectives included: 1) physical-chemical water quality analyses; and 2) benthic macroinvertebrate community structure assessments.

## STUDY SITE DESCRIPTION

The study stream, Beech Flats Prong, originates near Luftee Gap in North Carolina (Figure 1), flowing southeastward where it converges with numerous streams to the main stem of the Oconoluftee River. Three study sections were selected: a reference (site 1), stressed (site 2) and recovery (site 3). The reference section was located within 100m above the road fill at an elevation of 1500 MSL. Stream width ranged from 0.3 to 0.8m with an average riffle depth of 2 to 6cm. The stressed site, located within 100m below the Anakeesta fill had similar geophysical and flow characteristics and was approximately 25m lower in elevation than the reference site. A third site, located 6km downstream of the Anakeesta fill, at an elevation of 900 MSL was established to evaluate stream accommodation to the man-induced impact. Stream size increased considerably at this downstream locality; stream width ranged from 3-6m and riffle areas varied 15 to 60cm in depth. Sampling sites 1 and 2 were considered first order while site 3 was classified as a second order stream. Interpolation of stream kilometers was determined using U.S. Geological Survey quadrangle maps AMS 4355 III SW-Series V842 and AMS 4355 III SE-Series V842.

## MATERIALS AND METHODS

Water samples were collected monthly at each sampling section and analyzed for total alkalinity (mg/l as $CaCO_3$), phenolphthalein acidity (mg/l as $CaCO_3$), total hardness (mg/l as $CaCO_3$), specific conductance (micromhos/cm), pH and sulfate (mg/l). All sample measurements were performed following established procedures (American Public Health Association, 1971). Stream discharge ($m^3$/sec) was obtained utilizing a pygmy Gurley meter at 0.6 depth along an established transect. Substrate samples were taken and maintained on ice until analyzed for particle size (Inman, 1952) and organic content (EPA 1973).

Biological assessment consisted of monthly quantitative and qualitative collections at the reference, stressed and recovery sites. Quantitative collections were taken in triplicate at each site using a Surber square foot sampler (.093 square meter) with a net pore size of 1024 microns. During December, due to high water, no quantitative samples were taken at site 3. Benthic samples were preserved with 10% formalin in the field. In the laboratory, the samples were washed in a U.S. Standard No. 40 sieve (420 micron), transferred to a white sorting tray and macroinvertebrates separated from debris via hand picking and placed in a final preservative of 70% ethanol. Wet weights of individual taxa were obtained by transferring organisms from the final preservative to a paper towel and waiting approximately 1 minute and taking weights to the nearest 0.1mg.

[1]Support for this project was provided by the U. S. Department of the Interior, N. P. S., Southeast Regional Office, Atlanta, Georgia, Contract No. CX500050206 and in part by the Aquatic Ecology Fund, Environmental Biology Research Center, Tennessee Technological University, Cookeville, Tennessee. Special thanks are extended to the many specialists who assisted in benthic macroinvertebrate verification and identification.

[2]Normandeau Associates, Environmental Consultants, Bedford, New Hampshire.

[3]Environmental Biology Research Center, Tennessee Technological University, Cookeville, Tennessee.

[4]Southeast Regional Office, National Park Service, Atlanta, Georgia.

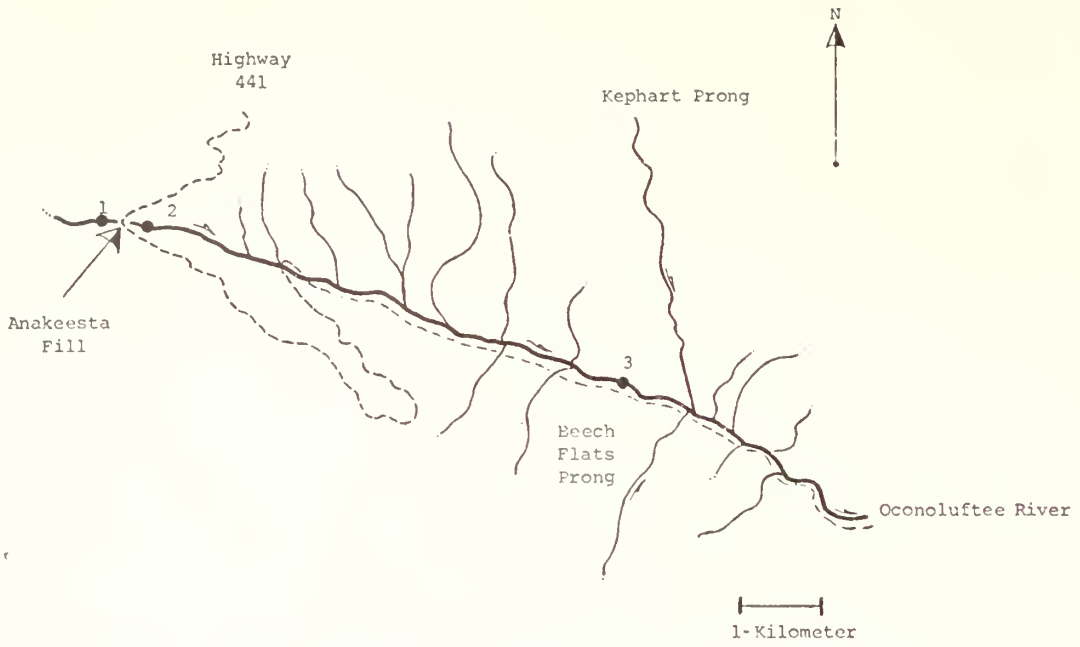



FIGURE 1. Map of Beech Flats Prong showing sampling locations.

Community structure analyses of benthic macroinvertebrates from the study areas included standing crop (numbers and wet weight per square meter), number of taxa (S), Index of Similarity (SI), Important Values (IV), Diversity ($\bar{H}$) and Evenness (J'). Similarities between benthic communities were evaluated on an annual basis by using the index of similarity (SI), and were calculated as follows:

$$SI = \frac{2C}{A + B}$$

where : A = # of species occurring at sampling sites X
B = # of species occurring at sampling sites Y
C = # of species common to both sampling sites X and Y

The closer the value is to one, the greater the similarity of faunas for the two sites. Importance values (IV), modified from Cottam and Curtis (1956), were calculated for each individual genus and each major taxon occurring in the quantitative samples. These importance values indicate the relative contribution made by each taxon to the community with greater contributions occurring when values are high (maximum 200). The species diversity index used, $\bar{H}$ (Brilloiun 1962), is derived from information theory and was calculated from pool quantiative samples at each site. Generally, values around 3 indicatd clean water systems with decreasing values occurring concomitantly with deterioration of water quality. The dominance diversity index used, J' (Pielou, 1966), indicates the distribution of individuals among the species in a community. The higher the J' value (maximum of one), the more uniform the distribution of individuals among the species.

Statistical comparisons of all chemical and biological parameters between sites were accomplished using the student's t-test, (Steel and Torrie, 1960). Confidence intervals of .05 (significant), .01 (highly significant) and .001 (very highly significant) were used to reject the null hypothesis that all sample means of pooled values were from the same populations.

## RESULTS AND DISCUSSION

A summary of the chemical-physical analyses made of samples collected from Beech Flats Prong throughout the one year study are presented in Table 1. At site 1, above the Anakeesta fill, monthly analyses showed that the stream water was acidic with an annual mean pH value of 6.4 and total acidity ranging from 4.5 to 2.0 mg/l. Prior to receiving acid and mineral leachates, Beech Flats Prong is poorly buffered (total alkalinity not exceeding 6.5 mg/l) and of low specific conductance (mean conductivity 23.5 micromhos/cm). Analysis of sulfate concentrations for the year consistently showed a very low anion concentration. The addition of leachate components from the Anakeesta rock at site 2 caused a significant reduction in the pH value ($P > .01$), and total alkalinity ($P > .001$) paralleled by significant increases in total acidity ($P > .001$), sulfates (.001), conductivity ($P > .01$) and total hardness values ($P > .001$). Statistical computations between the stressed site and recovery site revealed that all measured parameters, pH, acidity, alkalinity, hardness, sulfate and conductance were significantly different at the $P > .001$ level of confidence.

The chemical characteristics of Beech Flats at the recovery site, located 6.6 kilometers downstream from the acid source showed no significant variation from those found at the reference site above the source; therefore, the chemical values of these two sites are considered similar to other non-leachate receiving streams in the Great Smoky Mountains National Park. This is in contrast to site 2 where the water quality is atypical of most streams in the Park. Instead, the chemical parameters measured fit descriptions of streams receiving acid wastes (Vandenberg 1974; Dills and Rogers 1972; Koryak et al. 1972; Warner 1971; Roback and Richardson 1969; Parsons 1968; Bick et al. 1953). An excellent literature review of acid mine waste and its effect on the chemistry and biota of streams is given by Parsons (1957).

The dissolved oxygen and temperature values (Table 1) from Beech Flats Prong showed little variation from site to site. The mean annual

TABLE 1. Summary of monthly physical-chemical data collected from sampling sites on Beech Flats Prong, July 1975 through June 1976.

| Sampling Site | Temp-erature | D.O. | pH | Phenol-phthalein Acidity (mg/l as $CaCO_3$) | Total Alkalinity (mg/l as $CaCO_3$) | Total Hardness (mg/l as $CaCO_3$) | Sulfates (mg/l) | Conductivity (micromhos/cm) |
|---|---|---|---|---|---|---|---|---|
| Beech Flats Prong | | | | | | | | |
| 1 | 8 (4-11)* | 9.4 (7.6-10.8) | 6.4 (5.9-6.7) | 3.3 (2.0-4.5) | 3.7 (ND-6.5) | 18.2 (12.0-26.0) | 1.3 (ND-3.7) | 24 (15-51) |
| 2 | 9 (4-15) | 8.8 (5.1-10.3) | 4.7 (4.5-4.9) | 20.7 (17.5-25.5) | 0.4 (ND-2.5) | 57.8 (34.0-84.0) | 67.9 (19.2-97.3) | 89 (59-109) |
| 3 | 10 (4-15) | 9.4 (7.4-11.4) | 6.4 (6.1-6.9) | 3.0 (1.5-4.5) | 2.4 (ND-5.0) | 15.3 (8.0-28.0) | 2.0 (ND-3.7) | 18 (10-42) |

ND = Non-detectable
* = Ranges in parenthesis

TABLE 2. Summary of monthly benthic macroinvertebrate indices and computations from sampling sites on Beech Flats Prong, July 1975 through June 1976.

| Sampling Site | Mean Number/$m^2$ | Mean Wet Weight ($mg/m^2$) | Number of Taxa | Diversity ($\bar{H}$) | Evenness (J') |
|---|---|---|---|---|---|
| Beech Flats Prong | | | | | |
| 1 | 1323 (588-2257)* | 4974 (1106-15512) | 28 (20-35) | 3.62 (3.10-3.83) | .76 (.72-.78) |
| 2 | 241 (68-592) | 328 (142-929) | 12 (6-17) | 2.04 (1.40-2.82) | .59 (.44-.74) |
| 3 | 854 (226-2171) | 3226 (512-6483) | 28 (22-40) | 3.58 (3.03-4.46) | .75 (.65-.84) |

stream discharge values from site 1 (.02 $m^3$/sec) and stie 2 (.03 $m^3$/sec) revealed no observable change. However, contrasting the recovery site with sites 1 and 2 the difference was considerable (mean = 1.15 $m^3$/sec) due to a number of entering tributaries. It was noted by the authors that during periods of intense rainfall the water level of Beech Flats Prong at site 3 rose substantially and in one case (December) rendered sampling of macroinvertebrates unreasonable. Freshets occur commonly in many streams in the Great Smokies and spates have been documented to reduce the faunal assemblages present (Maitland and Penney 1967; Hynes 1968). The resultant "scouring action" as it relates to macroinvertebrate community stability will be discussed later.

Substrate analysis in November revealed that mean phi diameters were quite similar, being predominately composed of pebbles for the control, stressed and recovery sites (diameters 64 - 32mm; -4.85, -4.75 and -4.90, respectively). The phi deviation measure for all sites showed similarities in the dispersion of phi units. The percent organic content of the substrates from site 1 (4.30) and site 2 (4.88) was considerably higher than at site 3 (1.58). This could be attributed to the variation in discharge from low flow at sites 1 and 2 contrasted with high flow at site 3. Due to the similarities in particle size from all sites, comparisons of benthic communities should not be limited by this factor.

Above the Anakeesta fill (site 1) the mean annual density (number/square meter), Table 2, was 1323; (588 to 2257). A significant reduction ($P > .001$) in density (241; 68 to 592) occurred below the acid pollutant source (site 2). At the recovery site, 6 kilometers downstream from the acid source the density of organisms increases significantly ($P > .01$) above that observed at site 2. However, there was a significant decline ($P > .05$) in density when contrasted with the reference site. It was noted that extended

periods of rainfall caused considerable increases in discharge of Beech Flats Prong at site 3. During the September and January collections the riffle areas used for sampling had to be changed to areas of lower velocity while still remaining in the general study section. The authors propose two possible explanations for the exceptionally low density values. First, it is reasonable to assume that sampling occurred on previously exposed substrata and second, the "scouring" action resulting from increased discharge may have reduced the faunal densities (Patrick 1972; Lehmkuhl and Anderson 1972). If it is recognized that one or both of these mechanisms are operating, the significant reduction in density from site 1 to site 3 was not the result of Anakeesta leachates (indicated by other biological and chemical assessments) but instead by the torrential character of Beech Flats Prong 6.6 kilometers downstream from the acid source.

The biomass (milligrams per square meter) of benthos (Table 2) reflected a similar trend attaining a maximum site 1 of 15,512, in June (mean = 4974). Immediately below the Ankeesta Leachate at site 2, biomass was suppressed significantly ($P > .001$) to a mean value of 328 (142 to 929). Biomass estimates at site 3 reached a maximum of 6483.2 in April (mean = 3226) indicating considerable ($P > .001$) recovery from the acid site and approximating those values found at site 1. In general, the biomass from all sites gradually increased from November through June and decreased from July through October. This may be explained through the broad statement that most stream insects mature, emerge as adults, mate and oviposit during the months of May through September (Welch 1952). Thus during periods when biomass estimates were highest the macroinvertebrates were attaining weight through development, culminating at maturity with a subsequent emergence period during the months of May through September.

Importance values for major taxa and dominant genera were calculated on a monthly basis. At site 1, the order Plecoptera (stoneflies) were of major importance to the community (mean I.V. = 80.63; 52.32 to 117.83) with the genera *Alloperla* and *Peltoperla* contributing greatest. *Alloperla* was within the four most important genera for all 12 months. *Peltoperla* also occupied a dominant position in the macroinvertebrate community at site 1, reflecting a trend of greatest importance during September through March and having minimum importance from April through July. Exuvia (larval remains) of *Peltoperla* were first noted attached to streamside vegetation by the authors during collections taken in May and June. Thus, it is reasonable to assume that during periods of low community contribution this organism (probably *Peltoperla maria*) passed through the egg-adult stage becoming less susceptible to detection in community analyses. The order Ephemeroptera (mayflies) contributed considerably to the macroinvertebrate assemblages, with the family Heptageniidae having the majority of genera. Again, the months where ephemeropterans contributed the least (June and July) probably were the periods of peak emergence for heptageniids (Flowers and Hilsenhoff 1975), thereby decreasing the importance of mayflies. Importance values for site 2 reflected the deleterious effects of road fill leachates on community structure. Several mayfly (Ephemeroptera) genera were absent, i.e., *Baetis, Epeorus, Ephemerella, Paraleotophlebia, Pseudocoleon* and *Stenonema*. This is in agreement with the works of Herricks and Cairns (1972) and Koryak et al. (1972). The stonefly (Plecoptera) genera eliminated from site 2 included *Allocapnia, Acroneuria, Brachyptera, Isogenus, Isoperla* and *Paracapnia* while the families Chloroperlidae and Peltoperlidae increased slightly above that observed at the upstream reference site. The genera *Leuctra* (Leuctridae) comprised 15% of the annual biomass at site 2 with greatest contributions occurring from May through September. Harper and Hynes (1970) found that species of Leuctra "emerge during late spring, early summer, throughout the summer or during late summer periods." Thus, this may explain the high importance values measured for these warmer months, i.e., maximum size attainment of larvae, and low importance found in the remaining cooler months of the year. Associated with the Anakeesta leachates was an increase in importance of Diptera (I.V. = 98.99; 44.32 to 132.33) with the midges (Chironomidae) maintaining the dominant position (I.V. = 54.68; 0 to 105.37). Increases in tolerant taxa (Chironomidae) at the stressed site has apparently been associated with the reduction in competition for food and space requirements (Herricks and Cairns 1972 and Koryak et al. 1972). The authors feel this concept helps explain the increase in chironomid importance at the receiving site. Definite trends for Trichoptera (caddisflies) importance were difficult to ascertain. Periods when high importance values were found, i.e., November and December, may possibly be explained by an increase in aquatic invertebrate drift from upstream areas, although no documentations were made. Other trends included: elimination of crayfish (Decapoda), a drastic reduction in segmented worms (Annelida), and an apparent increase in the flatworms (Turbellaria).

Annual analysis of importance values from the recovery site revealed no detectable seasonal trends for the taxonomic groups of Ephmeroptera (mayflies), Plecoptera (stoneflies), Trichoptera (caddisflies) or Diptera (flies and midges). The mean number of taxa collected throughout the year showed no significant variation from site 1 (28; 20 to 30) and site 3, (28; 22 to 40) in contrast to a significant ($P > .001$) reduction at site 2 (Table 2).

Faunal comparisons based on the index of similarity showed sites 1 and 3 were most similar (SI = .83), sites 2 and 3 least similar (SI = .57) and sites 1 and 2 intermediate with a similarity index of 0.64. These relationships were expected due to the elimination at the acid site of taxa common to both the control and recovery sites.

The annual diversity ($\bar{H}$) and evenness (J') values (Table 2) revealed that the macroinvertebrate communities were comparable at sites 1 and 3 with a significant ($P > .001$) reduction in diversity at the acid receiving site. Although statistical analyses showed a decrease ($P > .001$) in evenness values at site 2 when compared to the site 1 no statistical differences were noted between the stressed and recovery site. Again, this may be a result of the torrential character of site 3. Possibly at high flow intervals the species uncapable of compensating are washed out causing a community dominated by adapted species. A similar observation has been shown by Ryck (1975) who stated "The reductions in invertebrate densities were attributable to substantial losses in a few taxa." Diversity ($\bar{H}$) and evenness (J') values for the control and recovery sections were equivalent to those values found by Mathis (1973; 1968b). He showed the bottom fauna in his study area (Little Stony Creek) was more equitably distributed among the species, thus redundancy was low (equated inversely with our measures of J') and diversity high. The atypical diversity and evenness values found at the acid receiving site is also paralleled by the findings of Mathis and Dorris (1968a). They showed that maximum redundancy and minimum diversity occurred at stations where brine concentrations were highest.

Thus, the benthic macroinvertebrate biota from the reference and recovery sites may be described as supporting diverse and evenly distributed assemblages of macroinvertebrates, in contrast to the acid site which supported benthic communities of low diversity and high faunal repititions.

## LITERATURE CITED


AMERICAN PUBLIC HEALTH ASSOCIATION. 1971. Standard methods for the examination of water and wastewater, 13th ed. Am. Public Health Assoc., New York, NY. 874 p.

BRILLOUIN, L. 1976. Science and information theory, 2nd ed. Academic Press New York, NY 351 p.

COTTAM, G., and J. T. CURTIS. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451-460.

DILLS, G. C., and D. T. ROGERS, JR. 1972. Aquatic-biotic community structure as an indicator of pollution. Geol. Surv. Ala. Circ. 80:25 p.

ESPENSHADE, GILBERT H. 1963. Geology of some copper deposits in North Carolina, Virginia and Alabama. U.S. Geol. Surv. Bull. 1142-I iv +50 pp.

FLOWERS, R. W., and W. L. HILSENHOFF. 1975. Heptageniidae (Ephemeroptera) of Wisconsin. Great Lakes Entomol. 8(4):201-218.

GREEN, R. L. 1975. Benthic macroinvertebrate communities in Great Smoky Mountains National Park streams influenced by acid drainage. M.S. Thesis. Tenn. Tech. Univ., Cookeville, Tennessee.

HARPER, P. P., and H. B. N. HYNES. 1970. The Leuctridae of Eastern Canada (Insecta: Plecoptera). Can. J. Zool. 49:915-920.

HERRICKS, E. E. and J. CAIRNS, JR. 1972. The recovery of stream macrobenthic communities from the effects of acid mine drainage. Fourth symp. Coal Mine Drainage Res. Inst. 370-398 p.

HERRMANN, R., J. W. HUCKABEE, R. L. GREEN, E. L. MORGAN and R. D. JONES. 1975. The nature of acid pollution in a small mountain stream, Great Smoky Mountains. Geol. Soc. Am., SE Sect. 24th Annu. Meet., Boulder, Co. 7(4):499.

HUCKABEE, J. W., C. P. GOODYEAR and R. D. JONES. 1975. Acid rock in the Great Smokies: Unanticipated impact on aquatic biota of road construction in regions of sulfide mineralization. Trans. Am. Fish. Soc. 104(4), 677-684.

HYNES, H. B. N. 1968. Further studies on the invertebrate fauna of a Welch mountain stream. Arch Hydrobiol. 65-360.

INMAN, P. L. 1952. Measures for describing the size distribution of sediments. J. Sed. Petrol. 22:125-145.

KORYAK, M., M. A. SHAPIRO, and J. L. SYKORA. 1972. Riffle zoobenthos in streams receiving acid mine drainage. Wat. Res. 6:1239-1247.

LEHMKUHL, D. M. and N. H. ANDERSON. 1972. Microdistribution and density as factors affecting the downstream drift of mayflies. Ecology, 53(4):661-667.

MAITLAND, P. S. and M. M. PENNY. 1967. The ecology of the Simuliidae in a Scottish river. J. Anim. Ecol. 36:179-206.

MATHIS, B. J. 1973. Species diversity of benthic macroinvertebrates and limnological conditions in a 1st order mountain stream. Trans. Ill. Acad. Sci. 66(3):29-32 p.

MATHIS, B. J. 1968a. Community structure of benthic macroinvertebrates in an intermittent stream receiving oil field brines. Am. Midl. Nat. 80(2):428-439.

MATHIS, B. J. 1968b. Species diversity of benthic macroinvertebrate in three mountain streams. Trans. Ill. Acad. Sci. 61(2):171-176.

MORGAN, E. L. and R. D. JONES. 1974. Acid pollution in wilderness streams. J. Tn. Acad. Sci. XLIX(2):57.

PARSONS, J. D. 1968. The effects of acid strip-mine effluents on the ecology of a stream. Arch. Hydrobiol., 65:25-50.

PARSONS, J. D. 1957. Literature pertaining to formation of acid-mine wastes and their effects on the chemistry and fauna of streams. Trans. Ill. State Acad. Sci. 50:49-59.

PATRICK, RUTH. 1972. Benthic communities in streams. Conn. Acad. Arts Sci. 44:271-284.

ROBOCK, S. S., and J. W. RICHARDSON. 1969. The effects of acid mine drainage on aquatic insects. Proc. Acad. Nat. Sci. Phila. 121:81-99.

STEEL, R. G. D., and J. H. TORRIE. 1960. Principles and procedures of statistics with special reference to Biological sciences. McGraw-Hill, New York. 481 pp.

VANDENBERG, R. J. 1974. The effects of acid mine pollution on the benthic macroinvertebrates of the Dry Fork of Belt Creek Drainage. M.S. Thesis Montana State Univ., Bozeman.

WARNER, R. W. 1971. Distribution of biota in a stream polluted by acid=mine drainage. Ohio J. Sci. 71(4):202-215.

WEBER, C. I., ed. 1973. Biological field and laboratory methods for measuring the quality of surface waters and effluents. U.S. Environmental Protection Agency, Cincinnati, OH.

WELCH, PAUL S. 1952. Limnology, McGraw-Hill Co., New York, NY 538 p.

# AGE STRUCTURE, AS DETERMINED BY VERTEBRAL SECTIONING, AND SEX RATIO OF BROOK TROUT (*SALVELINUS FONTINALIS*) FROM COSBY CREEK, GREAT SMOKY MOUNTAINS NATIONAL PARK[1]

Michael H. Hoff and Eric L. Morgan[2]

## INTRODUCTION

Presently there is a paucity of life history information on brook trout (*Salvelinus fontinalis*) in the Great Smoky Mountains National Park. Without accurate age information correlated with length and weight measurement, sex ratios, fecundity, and other data which characterize the life history of the brook trout, the fisheries biologist cannot make educated decisions to properly manage the remaining populations of this important species. King (1937) listed several possible reasons for the original retrogression of the brook trout in the Smokies including: logging activities with their associated destruction of habitat, harmful fishing practices, and the introduction of exotic salmonid species. More recently, Jones (1975 personal communication) has estimated that the brook trout population is still declining in the Smokies at a rate which will lead to their extinction in this area within 20 years.

Brook trout are characteristically very difficult to age using scales since the scales are very small and do not exhibit annuli as distinct as most centrarchid and percid fishes. Lennon (1967) found that brook trout from the Smokies were exceptionally difficult to age since their scales were extremely thin and fragile, along with having relatively indistinct annuli and circuli. Other biologists (Jones 1975 personal communication; Griffith 1976 personal communication) have attempted to age the brook trout by the scale method, but were unsuccessful probably because they did not have access to a high quality microprojector comparable to the one Lennon (1967) used in his study. Even though Lennon's study will be used as a benchmark for the age-growth information contained in this paper, his results are not necessarily valid since he did not prove the suspected year-marks to be true scale annuli. Hatch (1961) discovered that spawning checks on brook trout scales can leave features quite similar to those of true annuli. However, previous studies have shown that vertebrae could be used for aging the channel catfish (Appelget and Smith 1951) and the tadpole madtom (Hooper 1949).

The purpose of this study was to determine whether vertebral sections from brook trout collected from the Smokies appear to display annular markings. Furthermore, since markings were found that were similar in description to known vertebral annuli, tentative conclusions based on these data were made.

## DESCRIPTION OF STUDY AREA

Cosby Creek is a softwater, steeply sloped stream originating at an altitude of approximately 1219 meters above sea level (MSL) in the vicinity of Rocky Face Mountain, Cocke County, Tennessee, Great Smoky Mountains National Park. From its headwaters Cosby Creek flows in a southwestern direction for 0.5km, it then changes to a northwestern heading on which it continues for the remainder of its 7km drainage through the Park. Cosby Creek is unique in that it is one of the lowest elevations in the Park which contains brook trout. Many named and unnamed tributaries empty into Cosby Creek, and several of these (Toms Creek, Crying Creek, and Rock Creek) also contain populations of brook trout. In addition to brook trout, rainbow trout also inhabit a substantial portion of lower Cosby Creek and its tributaries.

Since Cosby Campground is located in close proximity to Cosby Creek, the lower areas of this stream receive heavy fishing pressure from tourists during the camping season. However, with the initiation of 22.5 cm size limit on brook trout during the 1975 fishing season, followed by the 1976 regulation which closed fishing on brook trout waters, angling mortalities should have been quite low for two seasons.

All trout used in this study were collected between 690 and 790 MSL (this was determined from Tennessee Valley Authority quadrangle maps AMS 4355 II NW-Series V842 and AMS 4355 I SW-Series V841). This stream section ranged in width from 1.6 to 6.7 meters. Riffle depth ranged from 5 to 15cm while mean pool depth ranged from 0.2 to 1.0m. Instream cover for the trout inhabitants in this area was relatively scarce because undercut banks, overhanging vegetation, and aquatic macrophytes were found to be almost nonexistent. Trout shelter mainly took the form of crevices between and under boulders in the stream channel. The remainder of the stream substrate consisted of cobble, pebble, gravel and sand. From a 12 month survey of the benthic macroinvertebrate community of this area, trout food resources were dominated by crayfish, mayflies, caddisflies and stoneflies.

## MATERIALS AND METHODS

All brook trout were sexed by direct observation of the gonads. All trout were collected using a 700 volt, ½ amp A.C. backpack electrofishing unit (O & R Equipment Co., Los Angeles, California). The trout were then measured to the nearest millimeter (total length) and weighed to the nearest hundredth of a gram using a Sartorius Model 1100 balance (Brinkman Instruments Inc., Westbury, New York). Each fish was then numbered and preserved in a 10% neutralized formalin (1 teaspon Borax per 1 liter 10% formalin) solution. Neutralized formalin was used so that

[1]The authors are indebted to the National Park Service for the brook trout specimens collected from Cosby Creek, and to the Tennessee Valley Authority-Forestry, Fisheries, and Wildlife Division for use of the jeweler's saw used to section the trout vertebrae. Acknowledgment is also due to Ron Jones and Allen Kelly from the Gatlinburg Field Station of the U. S. Fish and Wildlife Service for assistance in both this phase and the remainder of the study on brook trout in the Smokies. This study was funded by the Southeastern Regional Office of the National Park Service and, in part, by Aquatic Ecology Funds from the Environmental Biology Research Center, Tennessee Technological University.

[2]Environmental Biology Research Center. Tennessee Technological University, Cookeville, Tennessee 38501.

the vertebrae would not be rendered useless for aging by decalcification (Tesch 1968).

In the laboratory the anterior half of the spinal column was removed from each fish, desiccated, and then manually cleaned of the tissue remaining on the vertebrae. Each spinal column was sectioned from five to fifteen times using a Moto Tool Model No. 1 (Dremel Manufacturing Co., Racine, WI). Sections were viewed by a compound microscope equipped with a transmitting light source.

## RESULTS AND DISCUSSION

Since the vertebrae of the 40 to 80mm brook trout were too thin and fragile to cut by the methods outlined in this study, the age of these fish was determined using a length-frequency distribution (Figure 1). These age 0 trout were distinguishable from the other age classes since no overlap occurred in the length distribution of trout over 110mm with those under 80mm.

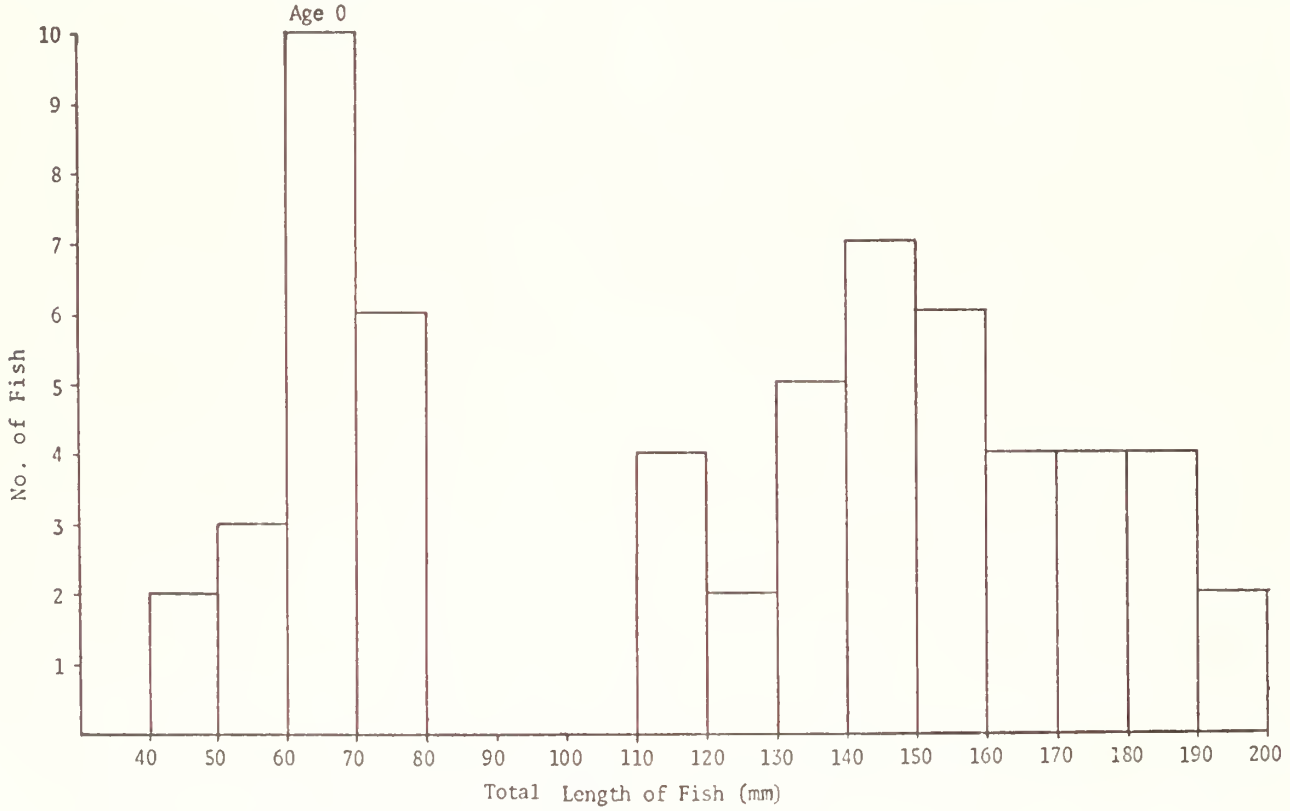



FIGURE 1. Length-frequency distribution of 62 brook trout collected from Cosby Creek on June 20, 1976.

After cutting each vertebral section of the trout over 110mm in total length, that section was viewed under the microscope to assure that at least one section from each fish was thin enough for the light to clearly transmit through the section, but not so thin that the circuli became indistinguishable. The author found that sections made in the areas of the prezygapophasis and the postzygapophasis from any vertebra of the same fish contained similar sets of alternating light and dark circuli. However, sections cut near the middle of each vertebrae were either uniformly dark and rather opaque or contained rudiments of the neural and hemal arches of the vertebrae. Tesch (1968) believed that summer zones of the vertebrae should appear black, and the winter zones white, when viewed with transmitted light. Therefore, the annulus was considered to be the inner edge of the dark bands. On that basis the trout collected in Cosby Creek were aged, and the results are listed in Table 1. The corresponding total length, weight and sex for each specimen are also listed in Table 1.

Even though the design of this experiment did not include procedures for verfication of the age determinations, for the purposes of this paper the results are assumed correct so that some conclusions can be drawn. The reader, however, is advised that one or more of the annuli appearing on the vertebral sections may be spawning checks similar to those found on brook trout scales by Hatch (1961).

Of all the brook trout collected in Cosby Creek, no fish was older than age class 3, longer than 200mm, or heavier than 76gm. This small size and slow growth rate could be a result of the low fertility of this montane stream, the small stream size, or a combination of these and other factors. Ricker (1932) found that the maximum size which a brook trout attained was apparently correlated with the size of the water body in which it lived. In the small brooks of Ontario a half pound (227gm) trout was unusually large, while in large lakes and rivers of the same area specimens of 4 (1.81kg) or 5 (2.27kg) pounds were not infrequently reported.

Lennon (1967) published the only known age-growth data of the brook trout in the Smokies. He found that one-year-old brook trout ranged in total length from 102 to 226mm, two-year-olds from 203 to 226mm, three-year-olds from 127 to 226mm, and four-year-olds from 203 to 226mm. Of the 217 brook trout he aged, 49% were in age group 1, 41% in group 2, 9% in group 3, and only 1% in group 4. The data computed in the course of this study appears to correlate quite well with that of Lennon's study even though Lennon grouped his fish in inch classes, while the fish in this study were measured to the nearest millimeter. One-year-old brook trout captured in Cosby Creek

TABLE 1. Suspected age, total length, weight, and sex of brook trout collected from Cosby Creek on June 20, 1976.

| Suspected Age (years) | Total Length (mm) | Weight (grams) | Sex |
|---|---|---|---|
| 3 | 192 | 75.10 | M |
| 3 | 191 | 66.48 | F |
| 3 | 180 | 62.24 | M |
| 3 | 175 | 56.09 | M |
| 3 | 172 | 51.07 | M |
| 3 | 165 | 56.02 | M |
| 2 | 182 | 53.66 | M |
| 2 | 181 | 64.88 | F |
| 2 | 180 | 63.31 | M |
| 2 | 179 | 58.50 | M |
| 2 | 174 | 49.65 | F |
| 2 | 165 | 49.76 | F |
| 2 | 164 | 52.09 | F |
| 2 | 162 | 53.21 | M |
| 2 | 155 | 48.57 | M |
| 2 | 155 | 40.69 | M |
| 2 | 153 | 37.40 | F |
| 2 | 152 | 34.56 | M |
| 2 | 151 | 32.45 | M |
| 2 | 151 | 33.75 | M |
| 2 | 146 | 33.86 | F |
| 2 | 145 | 37.59 | M |
| 2 | 145 | 31.32 | F |
| 2 | 144 | 30.87 | M |
| 2 | 142 | 22.96 | F |
| 2 | 138 | 27.33 | F |
| 2 | 129 | 21.22 | M |
| 1 | 140 | 26.08 | M |
| 1 | 140 | 28.04 | M |
| 1 | 139 | 28.91 | M |
| 1 | 137 | 24.92 | F |
| 1 | 136 | 24.40 | F |
| 1 | 134 | 28.54 | F |
| 1 | 134 | 21.99 | F |
| 1 | 126 | 22.25 | F |
| 1 | 126 | 19.21 | F |
| 1 | 122 | 20.95 | M |
| 1 | 119 | 15.00 | F |
| 1 | 117 | 14.21 | M |
| 1 | 115 | 15.72 | M |
| 1 | 110 | 10.60 | F |
| 0 | 75 | 4.88 | * |
| 0 | 74 | 4.92 | * |
| 0 | 74 | 4.96 | * |
| 0 | 72 | 4.68 | * |
| 0 | 71 | 4.05 | * |
| 0 | 70 | 3.77 | * |
| 0 | 69 | 3.57 | * |
| 0 | 69 | 3.54 | * |
| 0 | 68 | 3.80 | * |
| 0 | 67 | 3.15 | * |
| 0 | 66 | 3.28 | * |
| 0 | 66 | 3.48 | * |
| 0 | 65 | 3.62 | * |
| 0 | 64 | 3.12 | * |
| 0 | 64 | 2.97 | * |
| 0 | 62 | 2.89 | * |
| 0 | 59 | 2.41 | * |
| 0 | 56 | 2.33 | * |
| 0 | 50 | 1.77 | * |
| 0 | 45 | 1.05 | * |
| 0 | 41 | 0.81 | * |

*Immature specimen.

ranged in total length from 110 to 120mm, two-year-olds from 129 to 182mm, and three-year-olds from 165 to 192mm. This inconsistency of growth apparently renders the length-frequency distribution useless for brook trout older than age class 0. Age group 0 composed 34% of the 62 brook trout collected in Cosby Creek while 23% were in age group 1, 34% in group 2, and 10% in age group 3.

When the growth rate of the brook trout in Cosby Creek was compared with that of McFadden's (1961) study, it was apparent that the brook trout captured in the Wisconsin stream grew much more rapidly than those collected in the Smokies. In his study of Lawrence Creek, Wisconsin, McFadden found that the average lengths of brook trout in age classes 0, 1, 2, and 3 and 4 during September were approximately 102, 241, 305 and 356mm respectively. Even though some three-year-olds and several four-year olds were collected by Lennon (1967) and by the author, no fish from the Smokies was longer than 254mm. This was 60mm less than the average length of 3 year olds and 100mm less than the average length of 4 year olds in Lawrence Creek, Wisconsin.

Another interesting phenomena noted by Lennon (1967) was that brook trout populations in streams of the Smokies seemed to be numerically dominated by males. He calculated a ratio of 68% males and 32% females in a sample of 311 trout collected from 8 streams. Lennon also found that the sex ratio became more unbalanced favoring males, with increasing age. In the author's sample of brook trout, 56% of the mature fish were males and 44% were females. However, when the sex ratio for only age classes 2 and 3 was calculated, 63% of the sample were males and only 37% were females. In contrast, McFadden (1961) determined that females numerically dominated the upper age classes of Lawrence Creek. Lennon (1967) postulated that a certain ovarian disease discovered in both the brook and rainbow trout of the Smokies was responsible for the mortality of the mature females. However, the author found no mature female brook trout specimens to contain ovaries in the diseased condition described by Lennon. The male dominated adult brook trout population may, instead, be the result of some other sex-specific mortality. For instance, the stress of spawning activities may tax the females so greatly that they cannot survive the conditions of winter which are attributed to cause a great percentage of trout mortality in streams (Maciolek and Needham 1952; Reimers 1963; Needham et al. 1945).

## CONCLUSIONS

The method of aging brook trout in the Smokies by vertebral sectioning should be investigated further and either verified or refuted.

Based on the unverified results of this study, the brook trout is very slow growing in Cosby Creek as compared to fish from Lawrence Creek, Wisconsin.

The brook trout in Cosby Creek exhibited an unbalanced sex ratio favoring the males. This was especially apparent in the older age classes of this species.

## LITERATURE CITED

APPELGET, J., and L. L. SMITH. 1951. The determination of age and rate of growth from vertebrae of channel catfish, *Ictalurus lacustris punctatus*. Trans. Am. Fish. Soc. 80:119-139.

HATCH, R. W. 1961. Regular occurrence of false annuli in four brook trout populations. Trans. Am. Fish. Soc. 90:6-12.

HOOPER, F. F. 1949. Age analysis of a population Ameiurid fish *Schilbeodes mollis* (Herrmann). Copeia 1949, No. 1 34-38.

LENNON, R. E. 1967. Brook trout of the Great Smoky Mountains National Park. U. S. Fish and Wildl. Serv. Tech. Pap. 15:18.

MACIOLEK, J. A., and P. R. NEEDHAM. 1952. Ecological effects of winter conditions on trout and trout foods in Convict Creek, California 1951. Trans. Am. Fish. Soc. 81:202-217.

MCFADDEN, J. T. 1961. A population study of the brook trout, *Salvelinus fontinalis*. Wildl. Soc., Wildl. Mon. No. 7:73.

NEEDHAM, P. R., J. W. MOFFETT, and D. W. SLATER. 1945. Fluctuations in wild brown trout populations in Convict Creek, California. J. Wildl. Manage. 9:9-25.

REIMERS, N. 1963. Body condition, water temperature, and over-winter survival of hatchery reared trout in Convict Creek, California. Trans. Am. Fish Soc. 92:39-46.

TESCH, F. W. 1968. Age and growth. In Ricker, W. E. ed. Methods for assessment of fish production in fresh waters. IBP Handbook No. 3 Blackwell Scientific Publications, Oxford, England: 348.

# THE ENVIRONMENT OF SOUTH FLORIDA, A SUMMARY REPORT[1]

B. F. McPherson,[2] G. Y. Hendrix,[3]
Howard Klein[2], and H. M. Tyus[4]

## INTRODUCTION

In 1968 the planned construction of an international jetport in the Big Cypress Swamp of south Florida by the Dade County Port Authority triggered a controversy and a series of events that involved private and public interest. Local conservation groups and concerned citizens questioned the potential effects of such a jetport and the attendant urban growth in the Big Cypress Swamp both on the nearby Everglades National Park and on the south Florida environment. The Federal Government initiated, through the U.S. Department of the Interior, a preliminary study to evaluate the environmental impact of the proposed jetport. That study (Leopold and others, 1969) indicated that the proposed jetport would adversely affect not only the ecosystem of Everglades National Park, but that of the remainder of south Florida as well. For that reason the Federal Government opposed the construction of the jetport at the proposed location.

In the pact with Dade County and the State of Florida, the Federal Government agreed, however, to aid in the location and purchase of a new and acceptable site for the jetport. An obligation of the Federal Government under this pact was to implement an ecological study of south Florida. Five bureaus of the Department of the Interior--National Park Service, Geological Survey, Bureau of Sport Fisheries and Wildlife (now Fish and Wildlife Service), Bureau of Outdoor Recreation, and the Bureau of Indian Affairs--and two former Interior agencies--Federal Water Quality Administration (now Environmental Protection Agency) and Bureau of Commercial Fisheries (now National Marine Fisheries)--were asked to particpate. These bureaus and agencies completed 51 separate reports (available through the U.S. Department of Commerce, National Technical Information Service). This summary report, which is an overview of the south Florida environment, is based on and covers the highlights of the 51 reports.

The South Florida Environmental Study identified and described the natural ecosystems of south Florida as they functioned before man began to have major impact on these systems. Where remnants of natural systems still function as before, they were measured and described.

The study also encompassed the agricultural and urban developments of south Florida and their impact on the ecosystems. Man is a natural component of the system and, like all living components, seeks to attain some degree of balance or equilibrium with the rest of the system.

This report concludes phase one of the South Florida Environmental Study and fulfills in part the Department of the Interior's obligation to Dade County and the State of Florida to study and report upon the south Florida environment.

## SYNOPSIS

After 1900, men came in increasing numbers to south Florida and began extensive modification of the vast wilderness of swamps, forests, marshes, prairies, and bays. The original south Florida ecosystem that evolved over thousands of years gave way to a new three-part ecosystem which incorporated an agricultural component, an urban component, and a component of the original ecosystem that is largely undeveloped but still has been affected by man. These components are interrelated through the flow of energy and resources.

The remaining natural component of the south Florida ecosystem includes freshwater and terrestrial systems such as ponds and sloughs, sawgrass marshes, wet prairies, hammock forests, bay heads, cypress forests, pine forests, mixed swamp forests, and dry prairies; and coastal systems such as bays, coral reefs, mangroves and saline marshes, and beaches and dunes.

The freshwater and terrestrial systems are controlled, in part, by the moisture in the soil, or by the duration and the depth of inundation; these in turn are determined by the amounts and frequency of rainfall, the infiltration capacity of the soil and underlying bedrock, and by land altitude. High areas that are seldom flooded usually support pine forests, hardwood hammock forests, or grassland systems. Low areas that are flooded part of the year are wetlands, which include prairies, marshes, or swamp systems. The hydrologic environment, however, is not the sole control on a system. Fire, tropical storms, frost and cold weather, saltwater intrusion, and man also affect it.

Freshwater is a key environmental factor in that it not only affects a system directly, but it also affects other controlling environmental factors such as fire, soil, temperature, and saltwater intrusion. Freshwater is also a key factor manipulated by man.

Many of the plants and animals of south Florida are adapted to and dependent on the seasonal fluctuations of freshwater levels. During wet seasons aquatic plant production abounds; small crustaceans and fish feed on the growing plants or plant remains. With abundant food and space, aquatic animal populations increase. As water levels decline during the dry season, the small aquatic animals are forced to concentrate in scattered ponds, tributary creeks, and sloughs. The concentrated biomass then becomes a rich source of food for larger fish, alligators, snakes, birds, and mammals.

---

[1]Complete paper published as a U.S. Geological Survey Professional Paper 1011, 1976, 81 p.

[2]U.S. Geological Survey, Miami, Florida.

[3]U.S. National Park Service, Everglades National Park, Homestead, Florida.

[4]U.S. Fish and Wildlife Service, Raleigh, North Carolina.

The coastal systems of south Florida are dependent on currents, tides, waves, and in most cases freshwater runoff, to circulate and transport salts, nutrients, and other essential products. Freshwater runoff also dilutes seawater. Mangrove forests usually grow where freshwater runoff is greatest and salinity is seasonally reduced, whereas coral reefs occur in areas of little or no runoff and normal seawater salinity. In estuaries and bays, salinity varies during the year depending on the amount of runoff and evaporation. Within these systems, salinity is a major controlling factor on the distribution of organisms.

The coastal systems are also affected by other environmental factors such as cold weather, water turbidity, and tropical storms. Coral reefs, for example, flourish only in shallow, clear, warm seas and cannot endure temperatures below about 18°C (64°F). Bays and estuaries also benefit from clear water and are adversely affected by turbidity, which reduces sunlight penetration to sea grass and algal beds and thus reduces productivity. Tropical storms often alter coastal systems and are the major natural force that changes the distribution of mangrove forests.

Mangrove forests serve several important functions in the regional system of south Florida. They provide the nutrients and the shelter essential for maintenance of estuarine productivity and coastal fisheries. Tidal flushing carries mangrove leaf litter and seeds into coastal water where they are broken down by microorganisms and are made available as food to estuarine and marine species. The tangled mangrove roots and submerged trunks provide small animals with shelter from predators. Mangroves help to keep the water clear by trapping debris and sediment, and they also provide some protection to upland environments during tropical storms.

Shallow bays and estuaries are feeding and nursery grounds for many marine and estuarine species. Food is not only flushed into the bays and estuaries from mangrove forests and marshes but it also is produced in the bay by sea grass and algal communities. Juveniles of many marine species derive food and protection in estuaries and bays and thus require these habitats to complete their life cycles. More than 75 percent of marine commercial and sport fish of south Florida utilize and depend on bays and estuaries. The importance of these fish is stressed by the fact that marine commercial and sport fishing in the state generates more than $600 million annually.

Man has been altering the ecosystem of south Florida extensively for 70 years. About 35 percent (7,700 $km^2$ or 3,000 $mi^2$) of the natural habitat of the ecosystem has been destroyed by agriculture or urbanization. The remaining natural habitat is now threatened by exotic plants and animals, altered water levels and flows, severe fires, pollution, loss of animal and plant populations, and by further growth and development.

Man's most dramatic and long-term effects on the ecosystem have resulted from drainage. Wetlands originally occupied about 75 percent of south Florida, but through the years much of this land has been drained. In southeast Florida, drainage has lowered water levels as much as 1.5 to 1.8 m (5 to 6 ft) below the 1900 level and has disrupted the natural systems. In southwest Florida, drainage has lowered water levels as much as 0.6 to 1.2 m (2 to 4 ft) over a 195-$km^2$ (75-$mi^2$) area near Naples and has lowered them an undetermined amount over the remaining western Big Cypress Swamp. Drainage reduces productive wetlands, promotes organic soil oxidation and damaging fires, and has permitted seawater intrusion in some areas of excessive water-table lowering. Drained lands usually become farms and urban areas that themselves further alter the environment.

The introduction by man of exotic plants and animals has also altered parts of the natural systems of south Florida and threatens to alter much more. Exotic species often compete with and utlimately replace native ones and thus drastically change systems. Drainage and land clearing have increased the opportunity for exotic species to become established by stressing native species and reducing their ability to compete. Perhaps the most dramatic invasion is the rapid spread of cajeput, Australian pine, and Brazilian pepper

The populations of many of south Florida's wildlife species have declined. Eleven species of birds and three species of mammals are endangered. Perhaps the most dramatic is the decline of wading birds from about 2.5 million in 1870 to 150,000 in 1973.

The introduction of toxic chemicals, nutrients, and pathogenic organisms in increasing amounts threatens to further alter the ecosystem of south Florida. Most are transported to and accumulate in the aquatic environment where they degrade the quality of the water and alter or destroy life. Water quality has deteriorated over much of the region, and the deterioration is greatest in the east coast urban area. Most canals that drain urban or agricultural land contain toxic chemicals and high concentrations of nutrients. High nutrient concentrations favor the growth of dense stands of nuisance aquatic plants that clog canals and further degrade water quality. Canals also can serve as pathways to the estuaries for pollutants.

Dredge and fill and bulkheading are major threats to estuaries and marine fishery resources of south Florida. These activities not only reduce the vital litoral zone that serves as a nursery and feeding area but they also alter freshwater and nutrient inflow. Moreover, dredging increases the amount of sediment suspended in bay water; this sediment blocks out light necessary for photosynthesis. Tides transport the suspended sediment to other parts of the estuary where it may settle and suffocate plants and animals far removed from the dredging operation.

Agricultural and urban systems require freshwater to sustain them, and thus they compete with the remaining natural systems. Urban water shortages were indicated by the need to impose water-use restrictions in southeast Florida during the 1970-71 drought, and by progressive lowering of water levels each dry season in coastal parts of southwest Florida. The present difficulty in water supply is linked to urban demands that require increasing diversions of water from the natural and agricultural systems. Altered flow patterns of freshwater in the natural system adversely affect wetland and estuarine systems. The agricultural systems also depend on an adequate water supply, without which productivity drops.

Water-management methods have been proposed to increase the availability of freshwater to satisfy the future urban and agricultural demands during prolonged drought. In southwest Florida a water-management method to increase availability of water would require, at this time, only reducing the discharge of water from canals. In southeast Florida, however, saving more water would require management techniques such as backpumping excess storm water and increasing the

storage of Lake Okeechobee. Reducing canal flow by backpumping storm water into the conservation areas could save possibly 50 percent of the total canal runoff, which ranges from 28 to 193 $m^3/s$ (1,000 to 6,800 $ft^3/s$) in southeast Florida. Backpumping, however, may have some adverse environmental effects on the natural system. For example, in parts of the Everglades it would raise water levels, prolong inundation, probably alter water quality, and thereby cause vegetative changes. Backpumping would also decrease the flow to the estuaries and thus alter salinity and nutrient input there. In addition, backpumping would provide some degree of flood protection for land now unsuitable for residential development and thereby enhance land values in formerly undevelopable tracts.

Agricultural and urban systems rely on the remaining natural systems not only for such commodities as land, but also for the benefits or "free services" provided by the natural systems. These services include maintaining a stable quality environment through oxygen production, recycling nutrients, dispersing and detoxifying pollutants, retaining biological diversity, and producing fish and wildlife. If the natural systems are destroyed or greatly reduced, the services they once provided free must be provided by the agricultural or urban systems, usually at a high cost.

Agricultural and urban systems require an input of energy in addition to that supplied by the sun, wind, and rain. Most of this energy is imported as fossil fuel or as a fossil-fuel product. Urban societies, in particular, require a large input of outside energy to build and maintain their complicated structure of transportation, schools, laws, communication networks, buildings, and public services. Continued growth or even maintenance depends on the availability of energy. As cities grow, so do energy requirements; if these are not met, stress occurs and the quality of life deteriorates.

In recent years, urban growth in south Florida has been rapid. The population increased from slightly less than 0.5 million in 1940 to 2.5 million in 1970. If present trends continue, by 2000 south Florida would have more than 4.4 million residents, or about an 80-percent increase from 1970.

## LITERATURE CITED

LEOPOLD, L. B., and others. 1969. Environmental Impact of the Big Cypress Jetport: U.S. Dept. of the Interior, 155 p.

# ESTUARINE AND COASTAL MARINE FISHERY MANAGEMENT IN EVERGLADES NATIONAL PARK

Gary E. Davis[1]

## INTRODUCTION

Fishing is the only consumptive use of natural resources considered acceptable within national parks in the United States of America. In Everglades National Park, at the southern tip of Florida, it is practically the raison d'etre for Florida Bay, Whitewater Bay, and the Gulf of Mexico's coastal waters that constitute nearly half of the 6,000 $km^2$ Park. The fishery policy of the National Park Service encourages recreational exploitation and permits commercial harvest of fishery resources in Everglades National Park on a sustained yield basis (National Park Service 1975a). Sustained fishery yields must be dynamically balanced with natural ecosystem requirements if the overriding congressional mandate to the Park Service to maintain the nation's park resources unimpaired for use and enjoyment of future generations is to be faithfully executed. As long as there was a low level of fishery exploitation, relatively undeveloped watershed, and low demand for water resources in south Florida, a laissez-faire approach to fishery management was successful. However, in response to increased demands for water resources and flood control, the entire hydrological system in southeastern Florida was modified by an extensive canal and levee system (Fig. 1). This system is intensively managed to meet agricultural and urban needs. Demands for fishery products and recreation opportunities have also increased dramatically in recent years. The effects of this watershed management and increased fishing activity on "downstream" estuarine nurseries and coastal fisheries require active management to ensure their perpetuation. Management of these fisheries implies control of the population dynamics of the species involved, but control of recruitment, migration, growth, and mortality of these populations is clearly not possible. To some extent, protection of unimpaired habitat and unaltered environmental conditions assures limited control of recruitment, growth and natural mortality. General national park regulations and special fishing regulations for Everglades National Park (C.F.R. 36) protect the marine and estuarine habitat in Everglades National Park from overt destruction by human development, and in that general manner afford a measure of indirect control of the fisheries. Watershed management, such as controlled water releases into the upper everglades system or prescribed burning of sawgrass strands and pine forests, also offers an additional mode of indirect fisheries management, but the relationships between watersheds and fisheries are unknown, except in the broadest of terms.

Currently the only means of direct management of Park fisheries is through control of man's harvest, or fishing mortality. Fishing mortality plays a special role in national park ecosystems which are managed by policy "to maintain and perpetuate their inherent integrity." (National Park Service 1975a). Within the framework of the ecosystem, man is a predator, but a very special kind of predator for two reasons. First, the biomass harvested by man is removed from park ecosystems, not recycled as it would be by a "natural" predator. Second, the human sport-fishing populations do not exhibit the density dependent relationships with their fish prey populations that are typical of other predator-prey relationships. In these fisheries, man does not suffer the direct consequences of over harvest, and the aesthetic and recreational values of fishing in a wilderness will attract people, even if the possibility of catching fish is very poor. Because man is such a special predator, and control of his harvest offers the only direct control of the Everglades National Park fisheries, efforts have been made to estimate human harvest and its impact on the population dynamics of the fishes.

## OBJECTIVES

The fisheries data acquisition program at Everglades National Park has two major objectives: they are to gather data to estimate total human fishery harvest in the Park; and to monitor population levels of the sport and commercial species comprising the major Park fisheries.

## BACKGROUND

Even though fishery scientists have been using catch per unit of fishing effort techniques to monitor the relative abundance of fish populations since the 1890's (Rounsfell 1975), most large scale fishery statistical systems do not collect or report an effective measure of fishing effort. Furthermore, catch statistics for recreational marine and estuarine fisheries are not conveniently acquired, and until recently, sport harvests have apparently not been considered significant impacts on these resources. For these reasons the routine procedure of reporting only total commercial harvest (Shields and Joyce 1972) does not provide the basic information necessary to effectively understand and manage the mixed recreational and commercial fishery in Everglades National Park on a sustained yield basis. The program described here provides not only accurate estimates of total harvest for the major sport and commercial fisheries, but also yields catch rate estimates of fish availability with sufficient precision to permit evaluation of seasonal fluctuations. It also provides accurate estimates of boating and fishing activity.

The need for fishery data from Everglades National Park was established as early as 1935, when the National Park Service was committed to managing the fishery resources of Florida Bay and the mangrove lined estuaries along the southwestern coast of Florida within the Park by J.B. Cammerer, Director of the National Park Service (Copeland et al. 1936) during early planning discussions with local fishermen. Four years after the Park was established in 1947, the first special regulations concerning fisheries management in the Park were promulgated in the Code of Federal Regulations, but it was not until 1958 that any systematic effort was made to collect the basic data necessary to monitor the fisheries to determine whether or not the management goal of "sustained yield" (Wirth 1959) was being achieved. For ten years, from 1958 to 1969, investigators from the nearby University of Miami, principally James B. Higman, conducted surveys of fishermen at Flamingo,

[1]P.O. Box 279, Homestead, Florida 33030.

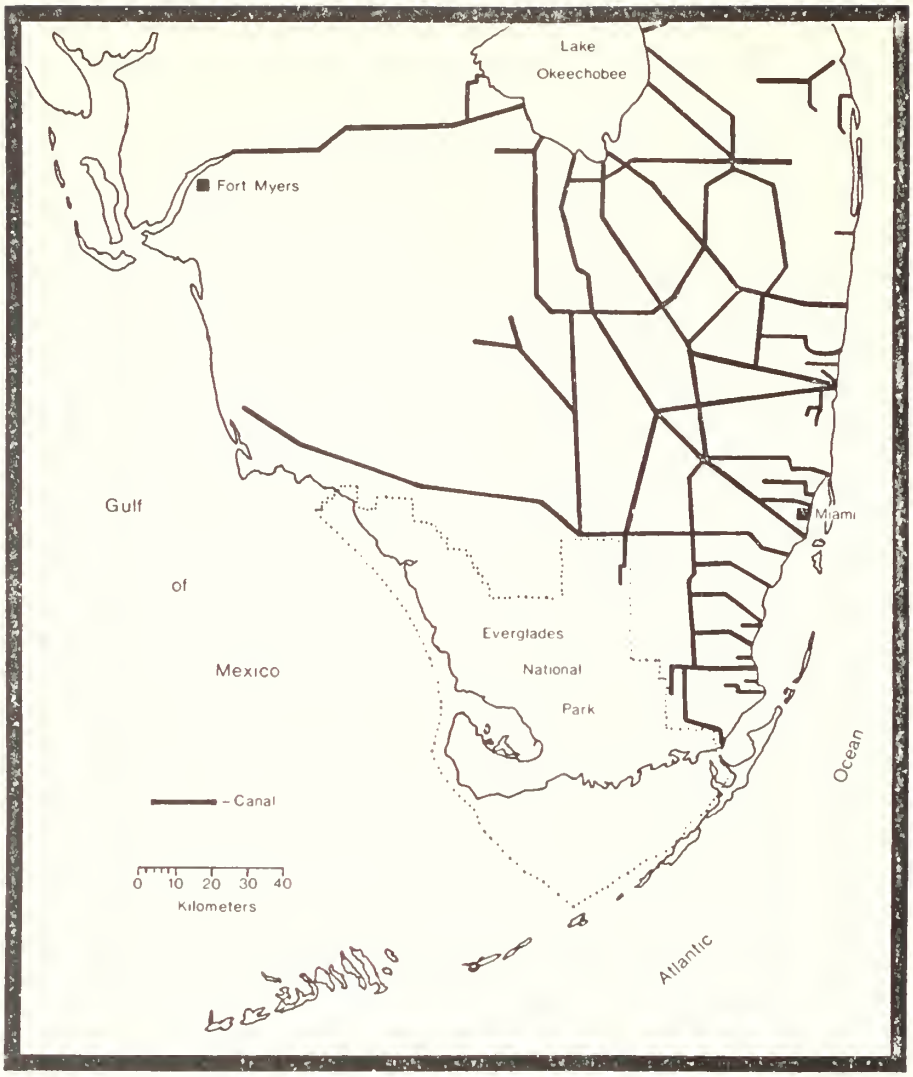



FIGURE 1. Major canals in South Florida.

Florida. These National Park Service supported studies are the foundation of the present fisheries data collection program. Summaries of this work and recommendations for improvements in data collection and analysis have been published previously (Higman 1967; Caillouet and Higman 1973a,b). One of the recommendations was to collect catch data from the more than 200 professional guide and commercial fishermen using Everglades National Park.

Since 1965, all commercial and guide fishermen fishing in the Park have been required to obtain a no-fee fishing permit from the Superintendent of Everglades National Park and report their catches to him as a condition of the permit (36CRF7.45g). These catch data consisted of total monthly catches, by species, for each fisherman. They were summarized in annual aquatic resources reports NPS (M)-3 for Everglades National Park (file N2621). Unfortunately these catch reports did not include any measure of fishing effort, so population monitoring from them must be considered tenuously.

Development of the present data acquisition program began in 1972. Its primary aim was to improve the precision of catch rate estimates and measures of fishing effort for both sport and commercial segments of Park fisheries. It also standardized all fishery data collection and provided real time quarterly reports which included estimates of total harvest and fishing effort in the park. In conducting their early surveys, Caillouet and Higman (1973a) found the variability in sport fishermen's catch rates at Flamingo to be so great they could not collect large enough samples to detect population changes in all but the two most abundant species in the sport fishery, except on an annual basis. A detailed stratification of the fishermen and refined measures of their fishing effort were added to alleviate this problem. Improved precision in calculating the catch rates was achieved by using the regression line fitting technique suggested by Caillouet and Higman (1973a). Fishing effort parameters were added to commercial and guide fisherman catch reports.

The purpose of this presentation is to describe the fishery data acquisition program currently used in Everglades National Park. Data are collected and summarized in five categories: 1) boating activity, 2) sport fishing, 3) guide fishing, 4) commercial fishing, and 5) stone crab trapping. Six standardized reports are produced from these data: 1) weekly sportfishing activity, 2) monthly boating activity, 3) quarterly sportfishing, 4) quarterly commercial fishing, 5) annual sportfishing, and 6) annual commercial fishing. I will briefly describe collection and summary of each of these data categories.

Used in conjunction with the computer programs described here and in a user guide (National Park Service 1975b) developed by the National Park Service Office of Data Systems in Washington, D.C.,

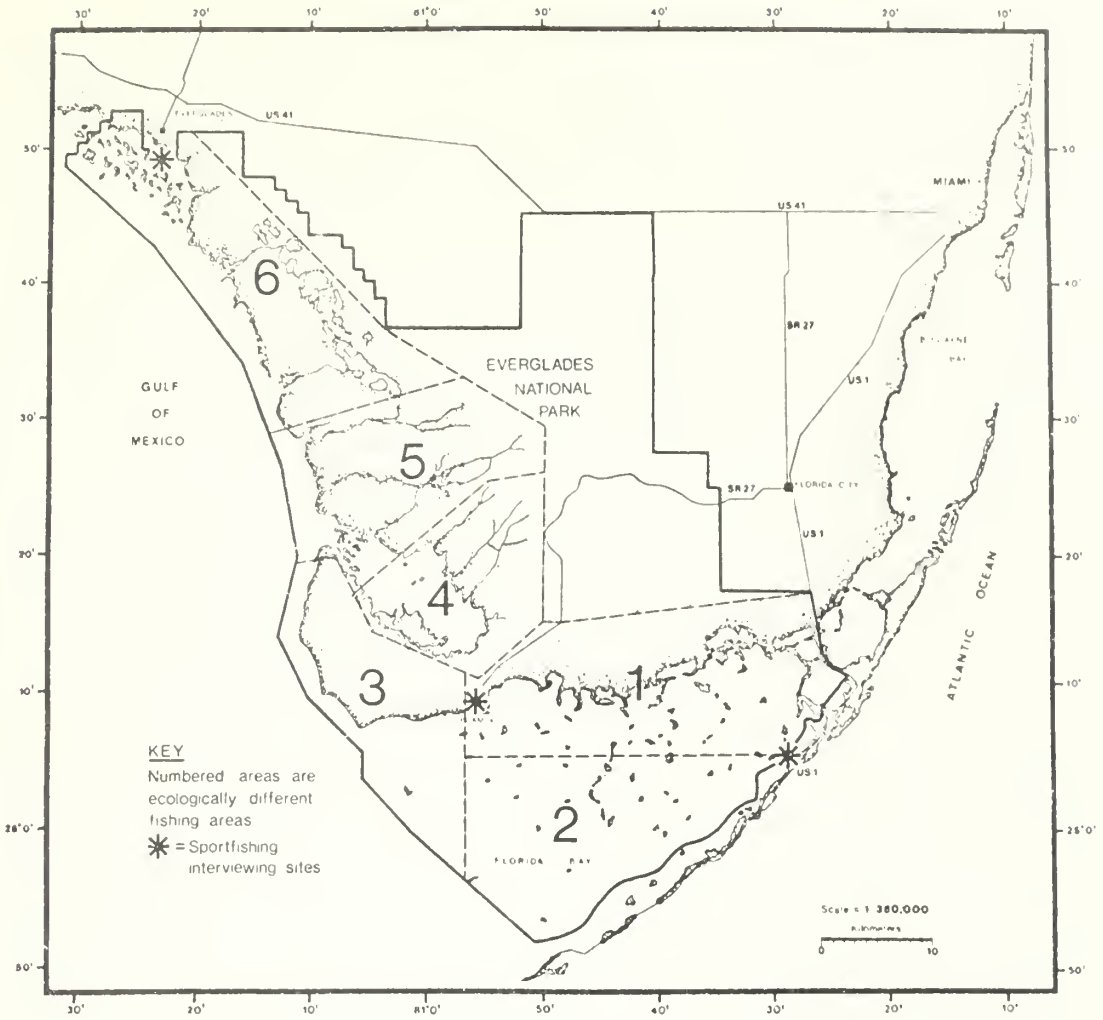



FIGURE 2. Map of Everglades National Park showing six ecologically different fishery zones.

this data acquisition program provides resource managers with the basic information they need to evaluate their management actions and other factors influencing the fishery resources in the Park.

## DATA COLLECTION

*Boating activity* is measured by daily counts of empty boat trailers made every morning before 1100 hours at the launching ramp at Flamingo by Park Rangers.

*Sport fishing* data are collected by dockside interviews with recreational fishermen at launching ramps at Chockoloskee Island, Flamingo, Key Largo, Plantation Key, and Upper Matecumbe Key (Fig. 2). Economic constraints have restricted the interviewing effort to Flamingo since 1973. In 1972, interviews were conducted on both weekdays and weekends. After 1972, only weekend days were sampled. Each interview consists of 13 data elements. Length measurements are made of selected species.

The data elements are:

1. Date

   The date of the interview.

2. Trip hours

   The interval from the time the party left the dock to its return.

3. Party size

   Total number of people in the boating party.

4. Time fished

   The number of hours actually spent fishing.

5. Species preference

   The species most preferred by the party.

6. Area fished

   One of the six ecologically different fishing areas in the park (Fig. 2).

7. Location of Interview

   Location of the interview.

8. Time of Interview

   Time of day of the interview.

9. Party skill

   Party composition, skilled, novice, family or food.

10. Trip origin

    Point of origin of fishing trip.

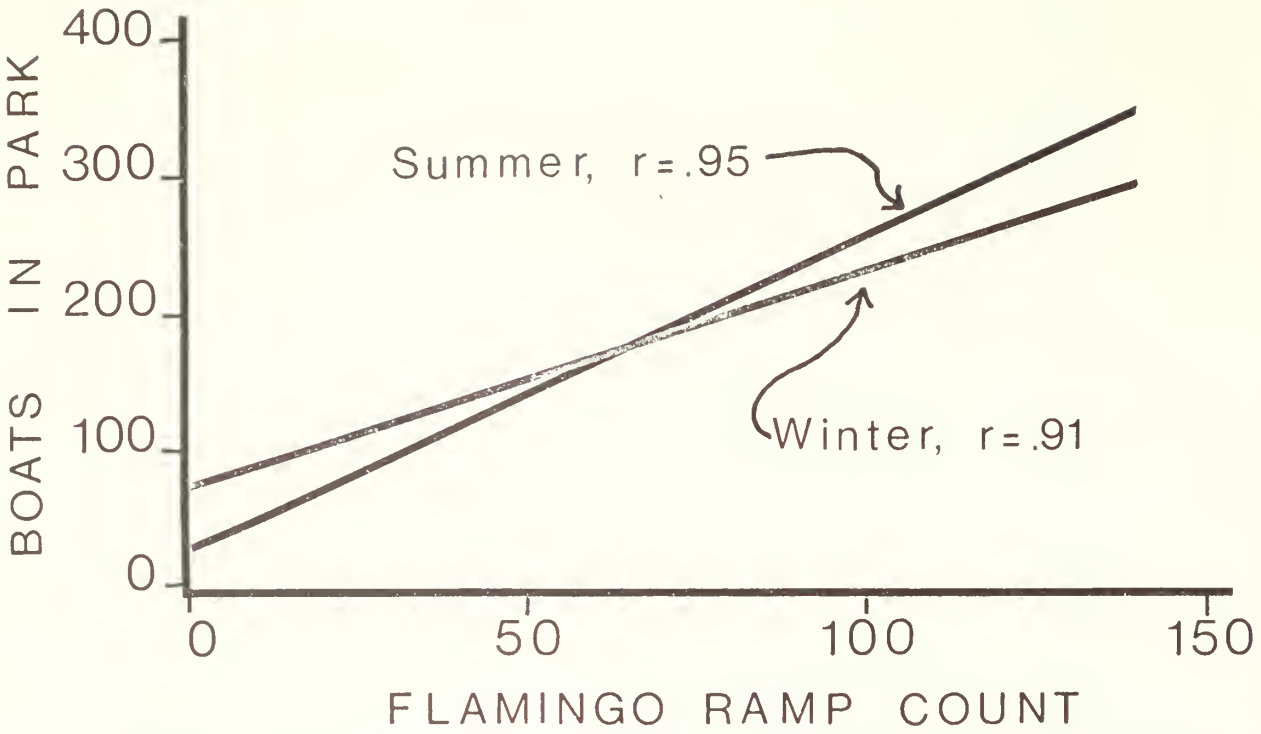



FIGURE 3. Regression of the number of boats observed in Everglades National Park on the number of empty boat trailers at the launching ramp at Flamingo, Florida.

TABLE 1. Age structure of red drum, *Sciaenops ocellata*, in the recreational harvest at Flamingo, Florida (percent frequency).

| Age class | Year | |
|---|---|---|
| | 1960-61 | 1974 |
| 0 | 2 | 4 |
| 1 | 80 | 22 |
| 2 | 14 | 23 |
| 3 | 3 | 36 |
| 4[a] | 1 | 11 |
| 5 | 0 | 3 |
| 6 | 0 | 1 |
| N | 1,000 | 948 |

[a]Indicates age of maturity.

TABLE 2. Age structure of gray snapper, *Lutjanus griseus*, in the recreational harvest at Flamingo, Florida (percent frequency).

| Age class | Year | |
|---|---|---|
| | 1958-59 | 1974 |
| 0 | 1 | 1 |
| 1 | 7 | 11 |
| 2 | 60 | 40 |
| 3 | 26 | 19 |
| 4 | 4 | 19 |
| 5 | 2 | 7 |
| 6[a] | 0 | 2 |
| 7 | 0 | 1 |
| N | 910 | 902 |

[a]Indicates age of maturity.

11. Residence of party

    Residence of party.

12. Fish kept

    The number of fish kept.

13. Fish released

    The number of fish released.

*Guide and Commercial Fishing* data are collected with daily catch reports submitted monthly by fishermen on trip tickets. These catch and fishing effort data are checked for completeness and transcribed to a 76 column format, with 9 data elements, for key punchin g. The data elements are:

1. Permit Number

   A five digit permit number. The first two digits indicate the year the permit was issued, the last three digits identify the permittee.

2. Date

   The date of the fishing activity.

3. Hours Fished

   The number of hours fished.

4. People Fishing

   The number of people fishing.

5. Area Fished

   The area fished.

6. Gear Used

   Type of gear used.

7. Net Sets

   The number of net sets, where applicable.

8. Weight

   The weight of fish caught in pounds.

9. Catch

   The number of fish caught.

*Stone Crab Trapping*

Daily catch reports are submitted monthly by fishermen on trip tickets. These catch and fishing effort data are transcribed to a 23 column format with six data elements for key punching. The data elements are:

1. Permit Number

   A five digit permit number.

2. Date

   Date the traps were pulled.

3. Traps Pulled

   The number of traps pulled.

4. Nights Fished

   The number of nights the traps were fished.

5. Weight

   The weight of claws caught.

6. Area Fished

   The area fished.

## DATA SUMMARIES

*Boating Activity*

Aerial surveys were conducted of the waters of Everglades National Park during which all boats observed in the Park were counted and their locations recorded. Boats were also categorized by type as sport fishing, commercial fishing, sail, canoe, houseboat/cruiser, or National Park Service patrol. Surveys were flown on randomly selected mornings, stratified by month. From July 1972 through June 1973, seven flights were made each month stratified by day of the week. From July 1973 to July 1975, four surveys were flown each month, with two weekend days and two weekdays randomly selected.

Flamingo is situated centrally between Florida Bay, the Gulf of Mexico, and Whitewater Bay, and provides access to all three bodies of water. Since boating activity originating there was representative of all park waters, acting as a "barometer" of total boating activity, the ramp counts at Flamingo were used as an index of boating use in the park. Aerial survey counts of fishing boats were regressed on corresponding trailer ramp counts to produce two seasonal predictive equations. These were applied to the daily ramp counts, yielding daily estimates of the total number of fishing boats in the park. In the summer (June-October), 92% of the botas in the Park were engaged in sport fishing, but during the winter (November-May) only 87% were classified as recreational fishing boats. The accuracy of the aerial boat surveys was evaluated by comparing the known presence of ranger patrol boats in general areas, such as northeast Florida Bay (determined after the flights), and the flight observations of ranger patrols. Of 127 ranger boats available for sighting, 121 (95%) were observed during the flights. In addition, monthly mean counts for area 6, the upper Gulf coast, were compared with monthly mean counts of aerial surveys flown independently by the Deltona Corporation (1975) over the same area from July 1972 to July 1974. There was no significant difference in the two counts ($t = 0.28$, $P > .99$), suggesting little bias in the techniques of either group.

*Sport fishing*

At the end of each quarter (July, October, January, and April) completed interview forms are sent to the National Prak Service Southeast Regional Office, Atlanta, Georgia, for key punching, and input, via terminal, to a computer program stored in the operations library in Washington, D.C. This computer program is described in detail in the Everglades National Park fish catch statistical system data processing user guide.

Seven summary reports are produced by this program each year: four quarterly, one semiannually, one three-quarterly, and one annually. These reports all have the following elements:

*Sport Fishery Report Elements*

1. Date
2. Trip length ($\bar{x}$ & S.D.)
3. Party size ($\bar{x}$ & S.D.)

4. Time fished ($\bar{x}$ & S.D.)

5. Catch per trip ($\bar{x}$ & S.D.)

6. Total interviews

7. Total catch by species

8. Total man·hours fished

9. Total man·hours boating

10. Unsuccessful parties (N & % total)

11. Total interviews by area, skill, residence, and species preference.

12. Catch rates, std. errors, and sample sizes for:

    a. all interviews

    b. skill groups

    c. area fished

    d. weekend/holiday/weekday

    e. species by area

    f. species by skill group and day

    g. species by area by skill group and day

    h. species by species preference

*Guide and Commercial Fishing*

At the end of each quarter (July, October, January, and April) the completed catch report forms are also sent to the National Park Serivce, Southeast Regional Office, in Atlanta for key punching, and input, via terminal to a computer program stored in the operations library in Washington, D.C. The completed summary reports and data cards are mailed back to Everglades National Park for analysis, final report preparation, and storage. The same seven summary reports are produced by this program annually. These reports all have the following format:

*Commercial and Guide Fishing Report Elements*

1. List permit numbers and number of days reported.

2. Number of permittees reporting.

3. Daily hours fished by guides and hook and liners (N,$\bar{x}$,S.D.).

4. Total days fished by guides, hook and liners, and net fishermen (N,$\bar{x}$,S.D.).

5. Total man·hours of guide fishing.

6. Unsuccessful guide trips (N,%).

7. Number of reports by area.

8. Total catch by species (N, weight, and mean weight).

9. Catch rates, standard errors, and sample sizes by species by area and permit type.

*Stone Crab Trapping*

Legal stone crab harvest takes place in Florida, and therefore in Everglades National Park, from October 15th to May 15th (Fl. Stat. 370). Completed stone crab catch report forms are also sent to the National Park Service Southeast Regional Office in Atlanta in January, April, and July for key punching and input, via terminal, to a computer program stored in the operations library, Washington, D.C. The completed summary reports, catch report forms, and data cards are mailed to Everglades National Park for analysis, final report preparation, and storage. Three tri-seasonal and an annual report are produced with this program. They all have the following elements:

1. Range of dates included in report.

2. Total catch in pounds of claws.

3. Total trap nights of fishing effort.

4. Total number of permittees reporting.

5. Catch rates, standard errors, and sample sizes for:

    a. Each permittee

    b. All permittees combined

*Catch rate is expressed as pounds of claws per trap·night.

REPORTS

Six standardized reports are prepared from the boating and fishery data summarized by the computer programs. These reports inform park management, the park staff, and the local community of the immediate conditions in the fisheries by showing what is being caught and whether fishing is good or poor. The reports also describe seasonal trends in fish availability and harvest. They identify guide and commercial fishermen who are complying with the provisions of their permits by reporting their catches. These standardized reports also provide the basis for long term trend identification and detailed analysis of fish population dynamics, boating use patterns, and fishery harvests.

*Weekly Sport Fishing*

A summary of the catch and fishing effort from the sport fishing interviews at the Flamingo ramp is prepared after each weekend. It includes the total catch, by species, observed by the interviewers, the size range (total length) for each species measured, and the number of fishermen interviewed. These data are presented in tabular form, and are accompanied by a short narrative statement. The statement includes an estimate of the total number of fishermen in the park over the weekend derived from the Flamingo ramp counts and the regression equations. It also summarizes the highlights of the data from the table, such as the total number of fish caught, the percentages of the more popular sport fish in the catch, average and maximum sizes of common species, and provides some perspective on general conditions compared with recent past conditions. This report is distributed to:

1. Everglades National Park Management and Staff.

2. The Miami Herald.

3. South Florida Fishing News.

4. Other interested parties, as requested (Miami Beach Rod & Reel Club).

5. Posted on the Flamingo ramp bulletin board.

*Monthly Boating Activity*

The regression equations are applied to the daily ramp counts reported by the Flamingo rangers to yield daily estimates of boating activity in the Park. The monthly total is reported to the Chief Ranger's Office at the end of the month to be used in the monthly public use report, SF-10-157. The monthly totals are also used to estimate total fishing effort for the Quarterly Sportfishing Report.

*Quarterly Sport Fishing Report*

The format of this quarterly report consists of a narrative statement and a table. The elements of this report are:

1. Number of fishermen in the park**[1]
2. Number of boats in the park*
3. Number of fish caught by sport fishermen*
4. Percentage of the fishermen who caught no fish*
5. Mean length of time spent fishing on each trip+[2]
6. Mean number of fish caught by the entire party on each trip+
7. Percentage fishermen living in local, south Florida, or other areas+
8. Percentage of fishermen classified as novice, skilled, family, or "food" fishermen+
9. Percentage of fishermen with no species preference+
10. Species most preferred by fishermen+
11. Percentage of fishermen who preferred species named in item 10+
12. Species and percentage of the three next most preferred species, listed in descending order of preference+

The table lists the total number of fish caught in the park by the four skill categories of fishermen, and the total number of gray snapper, spotted seatrout, red drum, and snook caught by each of the skill groups.

*Quarterly Commercial Fishing Report*

The format of this report consists of a list of the commercial fishermen and their respective park permit numbers who reported their activities and the number of days of fishing each reported. There is also a summary of the total catch reported by these fishermen, and the mean weights of selected species. A measure of total fishing effort (the number of days fished) and the geographical distribution of the fishing effort are also summarized. This report is distributed to the staff of Everglades National Park.

Field checks by Park Rangers are used to evaluate the degree of compliance by commercial fishermen and professional guides in reporting their catches. Rangers on boat patrols report sightings and contacts with permittees. The dates, areas, and catches (when available) reported by the Rangers are compared with the fishing activity reported by the fishermen. Nearly 600 Ranger reported contacts from July 1971 to July 1975 showed that most of the permittees observed fishing in the park reported their catches accurately. Further it was apparent that fishermen who reported their catches, did so all of the time, and fishermen who did not report their catches were also consistent in their non-compliance. Therefore it seems reasonable to estimate the total commercial and guide catch from the reported catch by assuming that the non-reporting fishermen are catching and fishing at the same rates as the reporting fishermen, and adjusting the reported catch by the percentage of the fishermen observed by Rangers in the Park who do not report their catches.

*Annual Sport Fishing Report*

This report has the same format and distribution as the quarterly sport fishing report and is prepared in the same manner, except that the annual computer summary report is used which combines all four quarterly reports.

*Annual Commercial Fishing Report*

This report has the same format and distribution as the quarterly commercial fishing report, except that the annual computer summary report is used which combines all four quarterly reports.

## RESULTS

A brief summary of the results of this program shows that during each of the last three years 12,000 to 15,000 sport fishermen were interviewed and 2,000 to 3,000 catch reports were submitted by professional guides and commercial fishermen. Analyses of these data gave annual harvest estimates of about 1.5 million kilograms by 150,000 recreational and 250 commercial fishermen from a 3,000 $km^2$ area in Everglades National Park. With the notable exception of the stone crab fishery, none of the major species shows signs of overfishing. However the effects of disrupted fresh water flow into park estuaries was apparent. Traditionally hyposaline estuaries showed significantly elevated salinities, and proportionally more mature game fish have been caught in recent years than were caught 15-18 years ago (Tables 1 and 2).

The trap fishery for stone crabs in the park has shown an alarming 80% decline in catch rate beginning in January 1972, when measures of fishing effort were first collected, through the 1975-76 season. Since fishing effort (number of traps) was saturated throughout this period, and many fishermen quit fishing in park waters two thirds of the way through the last two seasons because of economically unsatisfactory yields, the catch rate decline appears to reflect a significant reduction in stone crab stock in the park. An investigation of stone crab ecology and population dynamics is underway to establish and evaluate management alternatives to protect stone crab stocks in the park.

A feasibility study to establish an estuarine and coastal marine water quality monitoring program is also underway. It will review the historical data base and evaluate available technology for long term water quality monitoring of the 3,000 $km^2$ coastal area of the park.

Combining the fishery data collection program I have described here with the forthcoming water quality monitoring program and indicated species specific studies, such as the stone crab project, we will be able to provide park managers with timely descriptions of park fisheries, identify

[1] * calculated
[2] + from computer summary

alternative management actions to optimize fishery yields, and accurately predict the potential results of various environmental conditions and management programs on fishery resources. Already the program has identified specific areas of concern. Stone crab stocks have been severely reduced by fishery harvest, but the problem has been identified and remedial actions are being designed. The remainder of the fishery resources of Everglades National Park show no evidence of harvest induced stress, but detrimental effects on these resources of watershed management practices have been identified, which is the first step in protecting them.

Excluding the aesthetic and recreational values of the Park fisheries, the dock side value of the harvest and the direct expenditures of the recreational fishermen place the annual value of the Park fisheries at about $4.5 million. The annual cost of operating the fisheries data acquisition program I have described is about $20,000, cr 0.4% of the value of the fishery. I think this is a small price to pay for the resource protection afforded.

LITERATURE CITED


CAILLOUET, C.W., JR. and J.B. HIGMAN. 1973a. Accuracy of sampling procedures and catch rates in sport fishing. Sea Grant Coastal Zone Mgmt. Bull. 1, Univ. of Miami, Miami, Florida. 25 p.

CAILLOUET, C.W., JR. and J.B. HIGMAN. 1973b. Sample size in sport fishery surveys. Trans. Amer. Fish. Soc. 102(2):466-468.

COPELAND, D.G., J.W. HOFFMAN, and W.R. PORTER. 1936. A report to Everglades National Park Commission by Committee on lands and boundaries for proposed Everglades National Park. October 19, 1936. Everglades National Park, P.O. Box 279, Homestead, Fl. 22 p.

DELTONA CORPORATION. 1975. Characteristics of the sport fishery in the Ten Thousand Islands area of Florida from June 1, 1971 - June 30, 1974. Marco Island, Florida. mimeo. 62 p.

HIGMAN, J.B. 1967. Relationships between catch rates of sport fish and environmental conditions in Everglades National Park, Florida. Proc. Gulf Carib. Fish. Inst. 19:129-140.

NATIONAL PARK SERVICE. 1975a. Management Policies. U.S. Dept. Interior, National Park Service, Washington, D.C. 110 p.

NATIONAL PARK SERVICE. 1975b. Everglades National Park fish catch statistical system data processing user guide, U.S. Dept. Interior, National Park Service Office Systems Design, Washington, D.C. mimeo. 87 p.

ROUNSEFELL, G.A. 1975. Ecology, utilization and management of marine fisheries. C.V. Mosby, Co. St. Louis. 516 p.

SHIELDS, H.W. and E.A. JOYCE. 1972. Summary of Florida commercial marine landings 1972. Fl. Dept. Nat. Resources, But. Mar. Sci. Tech. in cooperation with National Marine Fisheries Service, U.S. Dept. Commerce, Washington, D.C. 62 p.

WIRTH, C.L. 1959. A letter to Senator Spessard J. Holland, U.S. Senate, Washington, D.C., January 24, 1959. File W42-N, Everglades National Park. 2 p.

# SEASONAL BIOMASS ESTIMATES OF MARINE AND ESTUARINE FISHES WITHIN THE WESTERN FLORIDA BAY PORTION OF EVERGLADES NATIONAL PARK, MAY 1973 TO JULY 1974

Thomas W. Schmidt[1]

## INTRODUCTION

Few estuarine and marine fish inventories have been conducted in the extreme south Florida area. Historically, Lonnberg (1894) and Longley and Hildebrand (1941) provided a descriptive study of the ichthyofauna from the Florida Keys and adjacent coastal areas and Henshall (1981) prepared a list of fishes from the Cape Sable region. Recently in Everglades National Park, Tabb and Manning (1961) prepared an annotated checklist on the fish fauna of Whitewater Bay and northern Florida Bay and Rosseler (1967) in the Buttonwood Canal. Springer and McErlean (1962) described the seasonality of the near shore fishes on the Atlantic Ocean side of the Middle Keys area. Hudson et al. (1970) produced a checklist on the fishes of a "lake" in south central Florida Bay.

However, no information is available concerning the seasonal distribution, relative abundance and biomass of these fishes in the Florida Bay portion of Everglades National Park. In Florida, Carter et al. (1973) provided the first systematic survey of estuarine and marine fishes which described their distribution by all three indices of abundance. The study was conducted in the Ten Thousand Islands area adjacent to Everglades National Park.

The importance of these waters as a sport and commercial fishery resource has been documented on numerous occasions by reports from the Rosenstiel School of Marine and Atmospheric Science of the University of Miami to the National Park Service (from Rosen & Dobkin 1958 to Dooley & Higman 1965). Higman (1966) in establishing the importance of the relationship between sport fish catch rates and environmental conditions in Everglades National Park suggests the creation of additional fishery ecological studies. Recently, Clark (1971) showed that fish catch rate differences among sampling stations in Whitewater Bay, were due primarily to variations in salinity, vegetation density and substrate conditions.

McHugh (1967) discussed some collecting gear limitations and biases and the difficulties involved in estimating the size of estuarine fish populations. McHugh concluded, however, that comprehensive and intensive fish faunal studies can be conducted through the combination of various types of scientific fish sampling methods and gear.

Thus, the ichthyofauna of Florida's southwest Gulf coast has been determined primarily from the combination of trawl and seine collections (Carter et al. 1973; Lindall et al. 1973; and Harmack et al.1974). In the Florida Bay study, a trawl was used to sample the demersal fish inhabitating channels and basins of depth in excess of 1 m while the beach seine sampled the entire water column ( <1 m) over nearshore grass beds and intertidal sand and mudflats. Consequently the objectives of these fishery investigations were established in part to provide data for the first time on the seasonal, relative abundance and biomass of the estuarine and marine fish fauna by habitat and their relationship with various environmental parameters. The results will be used to assist in the evaluation of sport and commercial fisheries resource management programs within the Florida Bay portion of Everglades National Park.

## METHODS

The geologic history and sedimentology of western Florida Bay has been described previously by Taft (1964) and Price (1967). The Florida Bay surface area from East Cape Sable to Key Vaca is 557,528 acres with a diurnal tidal range of 1.6 feet (McNulty, Lindall and Sykes 1972). However, that portion within the Park consists of 234,745 acres (950 $km^2$). For this study, Florida Bay was divided into approximately 3 equal areas of 316 $km^2$ and will henceforth be referred to as western Florida Bay (Area I), central Florida Bay (Area II), and the eastern Florida Bay (Area III) (Fig. 1). Data on areas II and III will be presented in a future publication. 176 fish collections were obtained monthly at 12 regular stations from May 1973 through June 1974. Indices of abundance were determined from the regular monthly collections as a standard unit-of-effort.

The sampling gear at the regular stations consisted of one bag seine and a semi-balloon otter trawl. The bag seine was 15.2 m x 1.2 m long and 1.8 m deep with 0.64 cm-bar mesh in the wings and 0.3 cm-bar mesh in the bag. The otter trawl was 4.2 m wide consisting of 2.54 cm-bar mesh netting with a 0.64 cm-bar mesh liner in the codend.

Beginning in May 1973 a standardized monthly sampling schedule was followed based on Lunar tide tables (±3 days of the new moon). Otter trawls were towed for 5 minutes in a straight line at a mean speed of 3.5 mph covering a distance of 200 meters. Trawling occurred during periods of high water on a flood tide. At the seining sites the seine was spread parallel to the shoreline and pulled perpendicular to the shore over a measured course. Seining was usually conducted during early flood tides.

Monthly otter trawl sampling began during October 1973 through June 1974. The monthly standard unit-of-effort for seines consisted of 8 single haul collections. The trawl schedule was composed of 8 collections representing 4 stations with duplicate tows at each site. During the 14 month sampling period there were 68 otter trawl collections.

Florida Bay benthic physical characteristics and submergent vegetative features were determined through the utilization of aerial (color IR 1973) and ortho photography, National Ocean Survey's Nautical Chart 141-SC and supplemented by ground-truth surveys with the otter trawl, bag seine, 15 $cm^2$ Ekman bottom dredge and underwater observation. A previous study by Tabb and Manning (1961) assisted in the general description of shoreline and intertidal habitats in northern Florida Bay. The biological stations were selectively chosen from each representative benthic habitat, and depth range (Fig. 1). Area measurements of the benthic habitats were determined by the dot grid method. Each seine station's covered area was measured metrically by a graduated polypropylene rope. The effective width of the otter trawl net mouth measured in operation was 2.4 m. The total

[1]Everglades National Park, Homestead, Florida 33030.

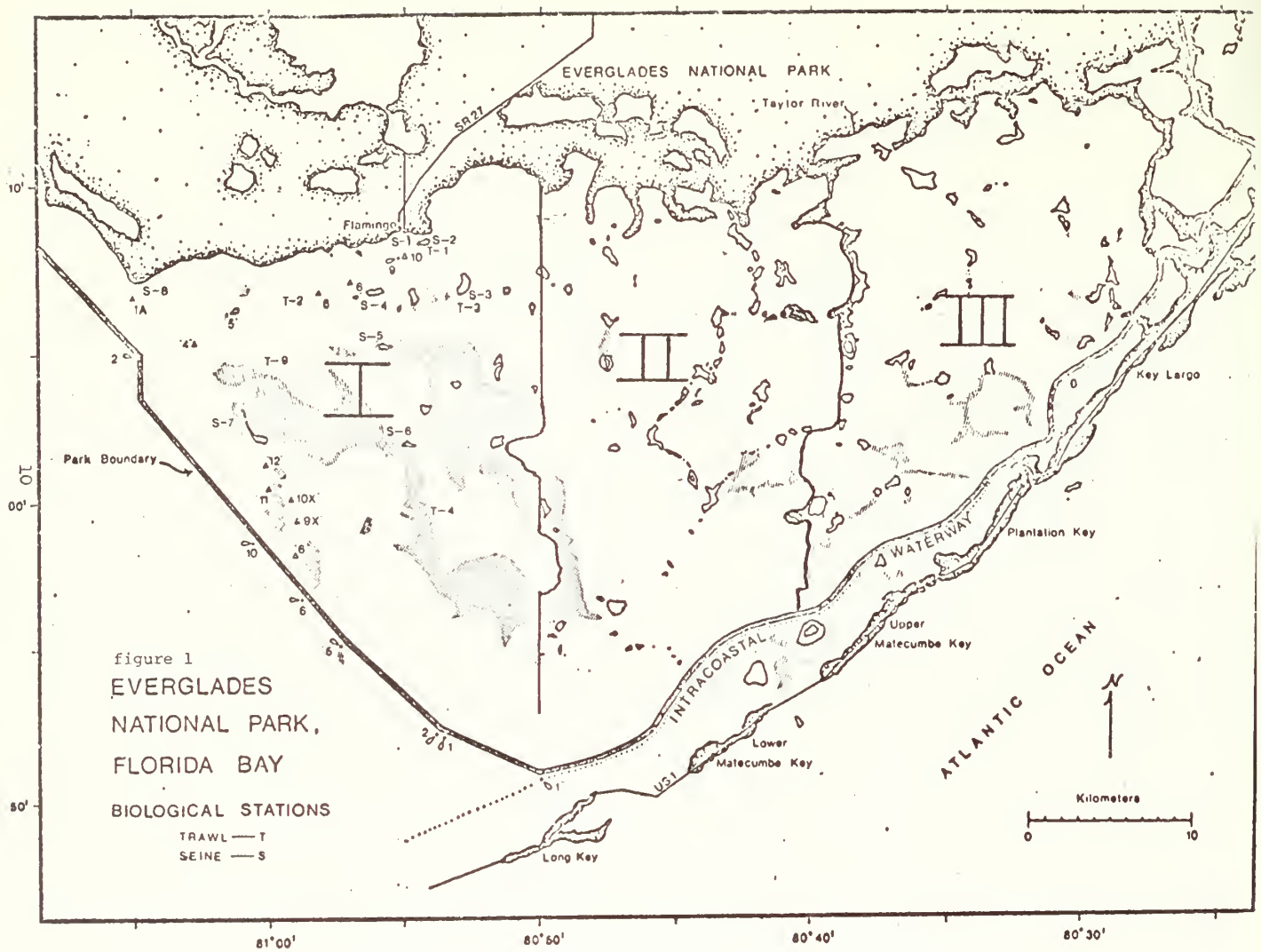



FIGURE 1. Everglades National Park, Florida Bay.

area covered at each trawl station was 960 $m^2$ (2.4 x 400 m). As a result, estimates of fish biomass were defined in terms of $gm/m^2$ and kg/h. Trawl variability was kept manageable by using a small net on short, numerous tows over areas of similar biophysical characteristics.

The catch efficiency of the nets was unknown; thus a constant value of 100% was used. This inference results in minimal estimates of population sizes. Fish samples were preserved in 10 per per cent formalin and returned to the laboratory trailer. Fishes were identified, counted, measured and weighed. Wet weights (biomass) of the fishes were taken with either a beam balance (20 kg capacity) or a trip balance (2 kg capacity) to the nearest 1.0 or 0.1 gm, respectively. Counts were made of the individuals of each species. Their total lengths (anterior extremity with the jaws closed to the tip of the compressed caudal lobes) were recorded to the nearest 1.0 mm.

*Hydrologic and Atmospheric Parameters*

Subsurface salinities (ppt) and water temperatures (C°) were taken with a Beckman salinometer. Dissolved oxygen (ppm) readings were measured with a Yellowsprings Model 54 oxygen meter. pH was determined by a Beckman phistol pH meter. Turbidities were recorded by a Hoch Laboratory Turbidimeter, Model 2100A. The unit of measure was Formazin Turbidity Units (FTU).

Cloud cover was estimated as the proportion of the sky covered by clouds. Wind direction was estimated to the nearest compass point. Wind speed was measured with a hand held Dwyer wind gage and calibrated in m.p.h.

Rainfall data were collected from annual reports of the National Weather Service.

## RESULTS

*Relative Abundance*

A total of 95,344 individuals distributed among 109 species and 45 families was collected by seining and otter trawling from a total 108 monthly collections during May 1973 through June 1974 (Table 1). An additional 17 species were observed or collected in preliminary or supplemental studies such as the Sport fishing survey conducted weekly at the Flamingo boat ramp. Tabe and Manning (1961) during their previous survey reported a total of 106 fish species collected or observed in northwest Florida Bay from July 1957 to September 1960. The number of species shared in common between both studies is 89. However, 16 species were seen only in the Tabb and Manning endeavor while 31 were observed only during the present study.

Station habitat S-1 at the mouth of the Buttonwood Canal accounted for the largest mean no. of

TABLE 1. A list of scientific and common names of fish identified in western Florida Bay from May 1973 to July 1974.

| Family | Species | Common name |
|---|---|---|
| Carcharhinidae | *Negaprion brevirostris* | Lemon shark |
| | *Carcharhinus limbatus* | Blacktip shark |
| Spyrinidae | *Sphyrna tiburo* | Bonnethead shark |
| Pristidae | *Pristis pectinata* | Smalltooth sawfish |
| Dasyatidae | *Dasyatis americana* | Southern stingray |
| Myliobatidae | *Aetobatus narinari* | Spotted eagle ray |
| Elopidae | *Elops saurus* | Ladyfish |
| | *Megalops atlantica* | Tarpon |
| Albulidae | *Albula vulpes* | Bonefish |
| Clupeidae | *Brevoortia smithi* | Yellowfin menhaden |
| | *Harangula juguna* | Scaled sardine |
| | *Opisthonema oglinium* | Atlantic threadherring |
| Engraulidae | *Anchoa cubana* | Cuban anchovy |
| | *Anchoa hepsetus* | Striped anchovy |
| | *Anchoa mitchilli* | Bay anchovy |
| Synodontidae | *Synodus foetens* | Inshore lizardfish |
| Ariidae | *Arius felis* | Sea catfish |
| | *Bagre marinus* | Gafftopsail catfish |
| Batrachoididae | *Opsanus beta* | Gulf toadfish |
| Gobiesocidae | *Gobiesox strumosus* | Skilletfish |
| Ogcocephalidae | *Ogcocephalus radiatus* | Polka-dot batfish |
| Exocoetidae | *Chriodorus atherninoides* | Hardhead halfbeak |
| | *Hyporamphrus unifascistus* | Halfbeak |
| Belonidae | *Strongylura marina* | Atlantic needlefish |
| | *Strongylura notata* | Redfin needlefish |
| | *Strongylura timucu* | Timucu |
| | *Tylosaurus crocidilus* | Houndfish |
| Cyprinodontidae | *Cyprinodont variegatus* | Sheepshead minnow |
| | *Floridichthys carpio* | Goldspotted killifish |
| | *Fundulus chrysotus* | Golden topminnow |
| | *Fundulus confluentus* | Marsh killifish |
| | *Fundulus grandis* | Gulf killifish |
| | *Fundulus similis* | Longnone killifish |
| | *Lucanis parva* | Rainwater killifish |
| Poeciliidae | *Poecilia latipinnia* | Sailfin molly |
| Atherinidae | *Membras martinica* | Rough silversides |
| | *Menidia berylinna* | Tidewater silversides |
| Syngnathidae | *Hippocanpus erectus* | Lined seahorse |
| | *Hippocanpus zosterae* | Dwarf seahorse |
| | *Syngnathus dunckeri* | Pugnose pipefish |
| | *Syngnathus floridae* | Dusky pipefish |
| | *Syngnathus louisanae* | Chain pipefish |
| | *Syngnathus scovelli* | Gulf pipefish |
| | *Corythoichthys albirostris* | Whitenose pipefish |
| Centropomidae | *Centropmus undecimalis* | Snook |
| Serranidae | *Centropristis striatus* | Black seabass |
| | *Diplectrum formosum* | Sand perch |
| | *Epinephelus itajara* | Jewfish |
| | *Epinephelus morio* | Red grouper |
| | *Epinephelus striatus* | Nassau grouper |
| | *Hypoplecterus pyella* | Barred hamlet |
| | *Mycteroperca microlepsis* | Gag grouper |
| Pomatomidae | *Pomatomus salatrix* | Bluefish |
| Rachycentridae | *Rachycentron canadum* | Cobia |
| Echeneidae | *Echeneis neucratoides* | Whitefin sharksucker |
| Carangidae | *CAranx crysos* | Blue runner |
| | *Caranx ruber* | Bar jack |
| | *Caranx hippos* | Crevalle jack |
| | *Chloroscombrus chrysurus* | Atlantic bumper |
| | *Oligoplites saurus* | Leatherjacker |
| | *Selene vomer* | Lookdown |
| | *Trachinotus carolinus* | Florida pompano |
| | *Trachinotus falcatus* | Permit |
| Lutjanidae | *Lutjanus apodus* | Schoolmaster |
| | *Lutjanus griseus* | Grey snapper |
| | *Lutjanus analis* | Mutton snapper |
| | *Lutjanus synagris* | Lane snapper |
| Lobotidae | *Lobotes surinamensis* | Tripletail |
| Gerridae | *Diapterus plumeri* | Striped majarra |
| | *Eucinostromus argenteus* | Spotfin mojarra |
| | *Eucinostromus gula* | Silver jenny |
| | *Gerres cinereus* | Yellowfin mojarra |
| Pomadasyidae | *Anisotremus virginicus* | Porkfish |
| | *Haemulon aurolineatum* | Tomtate |
| | *Haemulon plumeri* | White grunt |
| | *Haemulon sciurus* | Bluestriped grunt |
| | *Orthopristis chrysoptera* | Pigfish |

| Family | Species | Common name |
|---|---|---|
| Sparidae | *Archeosargus probatocepholus* | Sheepshead |
| | *Archeosargus rhomboidalis* | Sea Bream |
| | *Calamus arctifrons* | Grass porgy |
| | *Lagodon rhomboides* | Pinfish |
| Sciaenidae | *Bairdiella batabana* | Blue croaker |
| | *Bariiella chrysura* | Silver perch |
| | *Cynoscion nebulosus* | Spotted seatrout |
| | *Equetus acuminatus* | High hat |
| | *Menticirrhus americanus* | Southern kingfish |
| | *Menticirrhus littoralis* | Gulf kingfish |
| | *Micropogdon undulatus* | Atlantic croaker |
| | *Pogonais cromis* | Black drum |
| | *Scianops ocellatus* | Red drum |
| Ephippidae | *Chaetodipterus faber* | Atlantic spadefish |
| Labridae | *Lachnolaimus maximus* | Hogfish |
| Scaridae | *Nicholsina usta* | Emerald parrotfish |
| | *Sparisoma viridie* | Spotlight parrotfish |
| | *Sparisoma chrysopterum* | Redtail parrotfish |
| Mugilidae | *Mugil cephalus* | Striped mullet |
| | *Mugil curema* | Silver mullet |
| | *Mugil trichodon* | Fantail mullet |
| Sphyraenidae | *Sphyraenida barracuda* | Great barracuda |
| Clinidae | *Paraclinus marmoratus* | Marbled blenny |
| Blennidae | *Chasmodes saburrae* | Florida blenny |
| Callionymidae | *Callionymus pauciradiatus* | Spotted dragonet |
| Gobiidae | *Bathygobius soporator* | Frillfin goby |
| | *Gobionellus smaragdus* | Emerald goby |
| | *Gobiosoma robustum* | Code goby |
| | *Microgobius gulosus* | Clown goby |
| Scombridae | *Scomberomorus cavalla* | King mackerel |
| | *Scomberomorus maculatus* | Spanish mackerel |
| Triglidae | *Prionotus scitulus* | Leopard searobin |
| | *Prionotus tribulus* | Bighead searobin |
| Bothidae | *Bothus ocellatus* | Eyed flounder |
| | *Paralichthys albigutta* | Gulf flounder |
| | *Etropus crossotus* | Fringed flounder |
| Soleidae | *Achirus lineatus* | Lined sole |
| | *Trinectes maculatus* | Hogchoker |
| Cynoglossidae | *Symphueus plagiusa* | Blackcheek tonguefish |
| Balistidae | *Balistes ventual* | Queen triggerfish |
| | *Monocanthus hispidis* | Planehead filefish |
| | *Monocanthus ciliatus* | Fringed filefish |
| | *Aleutra schoepfi* | Orange filefish |
| Ostracidae | *Lactophrys trigonus* | Trunkfish |
| | *Lactophrys quadricornis* | Scrawled cowfish |
| Tetradontidae | *Spheorides nephelus* | Southern puffer |
| | *Spheorides spengleri* | Bandtail puffer |
| Diodontidae | *Chilomycterus antillarum* | Webbed burrfish |
| | *Chilomycterus schoepfi* | Striped burrfish |

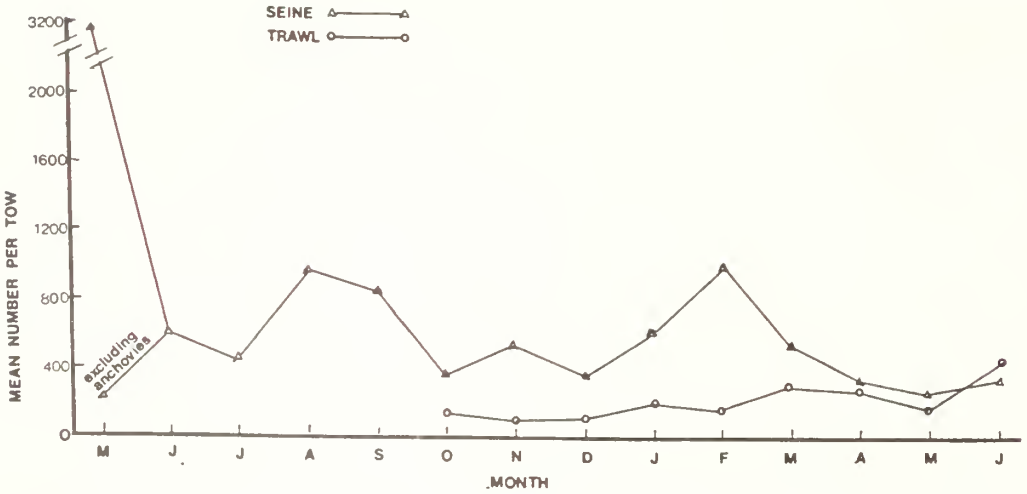



FIGURE 2. Distribution of the mean catches by number at the regular seine and otter trawl stations.

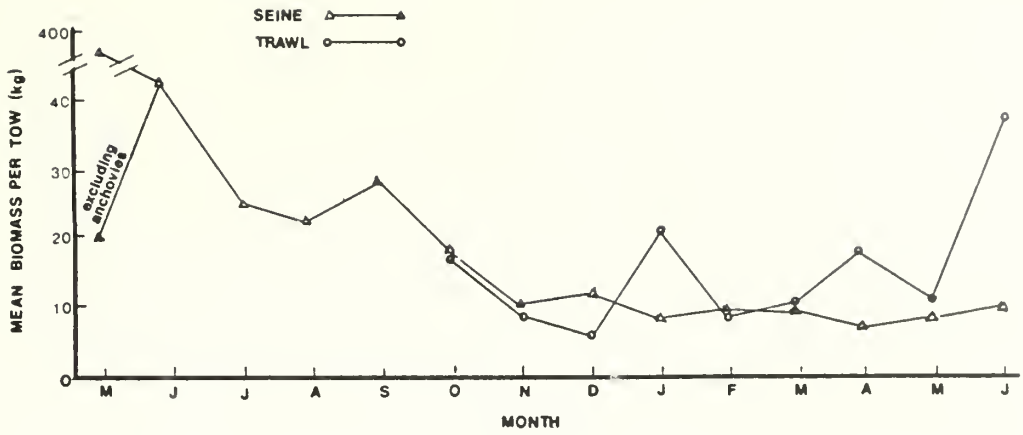



FIGURE 3. Distribution of the mean catches by biomass at the regular seine and otter trawl stations.

TABLE 2. Annual pattern of numbers and biomass of fishes in western Florida Bay (Area I). May 1973-June 1974.

| Station-habitat | Surface area Sampled ($m^2$) | Biomass $gm/m^2$ | Biomass Kg/h | Relative Abundance No. of fish $/m^2$ | Relative Abundance No. of fish /h |
|---|---|---|---|---|---|
| S-1 | 180 | 4.7 ± 4.3 | 47 ± 43 | 4.1 | 41 ± 49 |
| S-2 | 360 | 3.4 ± 3.8 | 34 ± 38 | 0.4 | 4 ± 2 |
| S-3 | 180 | 5.4 ± 4.6 | 54 ± 46 | 4.5 | 45 ± 30 |
| S-4 | 273 | 6.2 ± 5.9 | 62 ± 59 | 0.7 | 7 ± 4 |
| S-5 | 450 | 1.8 ± .9 | 18 ± 9 | 1.9 | 19 ± 15 |
| S-6 | 78 | 14.6±10.7 | 146 ±107 | 8.3 | 83 ± 82 |
| S-7 | 450 | 5.3 ±5.7 | 53± 57 | 0.6 | 6 ± 6 |
| S-8 | 273 | 15.9 ±26.4 | 159±264 | 10.0 | 100 ±241 |

species, maximum number and range during the period of observation. Generally, the mean number of species, and range decreased on a southerly transect toward the open waters of the Gulf of Mexico. By species, the largest total number in the standard monthly collections was recorded in June (45 seines only) and October 1973 (38). Similar increases in the number of species occurred in the same two months with both pieces of sampling gear. The fewest species in the monthly catches occurred between November and January.

Those families which occurred most often in the seine collections were the following: Anchovies (Engraulidae), Killifish (Cyprinodontidae), Mojarras (Gerridae), Porgies (Sparidae), Drums (Sciani-dae), and Grunts (Pomadasyidae). The bay and striped anchovies were the dominant fish species in western Florida Bay from May 1973 to June 1974. Hildebrand (1943) suggested that engraulids are probably the dominant forage item of many of the larger gamefish. Excluding anchovies, numerically the most abundant fish, notably forage species were silver jennies, *Eucinostomus gula*, goldspotted killifish *Floridicythys carpio*, rainwater killifish *Lucania parva*, pinfish *Lagodon rhomboides* and pigfish *Orthopristis chrysoptera*.

*Biomass*

Most fish faunal surveys do not determine the occurrence or abundance of fish by biomass (Springer and Woodburn 1960; Wang and Ramey 1972; Tabb and Manning 1961; Roessler 1970; and Gunter and Hall 1965). However, McFarland (1963) maintained that the biomass of fishes yielded more ecological information than the numerical data. Carter et al. (1973) assessed the relative abundance of fishes by biomass in the Ten Thousand Islands. However, the current study represents the first time in Florida that measures of biomass were used to quantify the standing crop of fishes by estuarine and marine habitat types (Kg/h). The total biomass of fishes collected at the regular stations in Area I was 293.3 kg.

By biomass the most abundant families of fishes in the regular monthly collections were the anchovies (Engraulidae), Stingrays (Dasyatidae), Sharks (Carcharhinidae), Porgies (Sparidae), Mullet (Mugilidae), Mojarras (Gerridae) and the Killifishes (Cyprinodontidae). The most numerous species included the bay anchovy Anchoa mitchilli, striped anchovy *A. hepsetus*, pinfish *Lagodon rhomboides*, southern stingray *Dasyatis americana*, Lemon shark *Negaprion brevioristis*, Silver jenny *Eucinostomus*

TABLE 3. "Wet season" pattern of numbers and biomass of fishes in western Florida Bay. June 1973-November 1973.

| Station - habitat | Biomass gm/m$^2$ | Biomass Kg/h | Relative abundance No. of fish/m$^2$ | Relative abundance No. of fish/h |
|---|---|---|---|---|
| S-1 | 9.0± 3.5 | 90 ± 35 | 6.6 ± 5.1 | 66 ± 51 |
| S-2 | 4.0± 3.3 | 40 ± 33 | 0.4 ± 0.2 | 4 ± 2 |
| S-3 | 3.5± 1.8 | 35 ± 18 | 4.7 ± 2.8 | 47 ± 28 |
| S-4 | 7.2± 7.4 | 72 ± 74 | 0.7 ± 0.3 | 7 ± 3 |
| S-5 | 2.6± 0.7 | 26 ± 7 | 3.2 ± 1.2 | 32 ± 12 |
| S-6 | 24.5± 9.1 | 245 ± 91 | 13.4 ± 9.8 | 134 ± 98 |
| S-7 | 6.4± 4.7 | 64 ± 47 | 0.8 ± 0.7 | 8 ± 7 |
| S-8 | 21.1± 36.7 | 211 ± 367 | 2.3 ± 1.9 | 23 ± 19 |

TABLE 4. "Dry season" pattern of numbers and biomass of fishes in western Florida Bay. December 1973-May 1974.

| Station - habitat | Biomass gm/m$^2$ | Biomass Kg/h | Relative abundance No. of fish/m$^2$ | Relative abundance No. of fish/h |
|---|---|---|---|---|
| S - 1 | 1.7 ± 1.7 | 17 ± 17 | 2.9 ± 5.1 | 29 ± 51 |
| S - 2 | 3.8 ± 4.8 | 38 ± 48 | 0.3 ± 0.3 | 3 ± 3 |
| S - 3 | 8.0 ± 5.8 | 80 ± 58 | 5.3 ± 3.4 | 53 ± 34 |
| S - 4 | 5.9 ± 6.1 | 59 ± 61 | 0.8 ± 0.4 | 8 ± 4 |
| S - 5 | 1.1 ± 0.2 | 11 ± 2 | 1.3 ± 1.0 | 13 ± 10 |
| S - 6 | 8.0 ± 7.2 | 80 ± 72 | 5.8 ± 6.3 | 58 ± 63 |
| S - 7 | 1.8 ± 1.4 | 18 ± 14 | 0.3 ± 0.3 | 3 ± 3 |
| S - 8 | 6.8 ± 5.1 | 68 ± 51 | 4.9 ± 8.5 | 49 ± 85 |
| T - 1 | 1.4 ± 1.2 | 14 ± 12 | 0.05 ± 0.08 | 0.5 ± 0.8 |
| T - 2 | 1.1 ± 1.0 | 11 ± 10 | 0.1 ± 0.1 | 1 ± 1 |
| T - 3 | 7.2 ± 4.2 | 72 ± 42 | 1.0 ± 0.7 | 10 ± 7 |
| T - 4 | 1.6 ± 1.3 | 16 ± 13 | 0.1 ± 0.1 | 1 ± 1 |

*qula* and the gold spotted killifish *Floridichthys carpio*.

The most numerous fish species (anchovy) was found at the nearshore intertidal station habitats primarily S-8 (East Cape) and S-1. Other dominants and their habitat preferences included the pinfish, an important bait and forage of the nearshore Syringodium, habitat at Palm Key Basin (T-3) and Clive Key (S-5); Lemon sharks, offshore at Sandy Key (S-7) and Man-o-War Key (S-6); striped and fantail mullet, *Mugil cephalus, M. Trichodon* at station habitats S-1, Murray Key (S-4) and S-8, silver jenny, one of the most abundant forage fishes in the bay, at all stations except S-8, and seasonally the southern stingray, at station habitat S-8. A summation of the hydrobiological parameters and station habitat descriptions recorded in Area I at each fish sampling station may be obtained upon request from the author.

*Seasonal Patterns of Abundance*

In the extreme south Florida area (Cape Sable region) over 80% of the annual rainfall ($\bar{x}$ 127 cm) occurs from May through October and is known historically as the "rainy season." This prominent rainfall cycle has a pronounced effect on the salinity variations in shallow water tropical ecosystems. Under these conditions nearshore salinity fluctuations in Florida Bay follow behind the onset of the rainy season by nearly one month (Schmidt, in prep.). Consequently, for the purpose of this paper biological data has been presented seasonally as defined by the hydroperiod of June through November (wet season) and December through May (dry season).

Abundance indices varied substantially between the wet and dry seasons. Numerically 60% more individuals occurred during the hydroperiod than during the dry season. However, more importantly over 68% more biomass was taken during the wet season than during the December through May period of observation (Figures 2 and 3).

## DISCUSSION

The local influx of estuarine dependent fish primarily the euryhaline pinfish accounted mostly for the increases in numbers of individuals during the dry season. Although this is normally the period of higher salinities, most aquatic organisms reach their maximum tolerance of higher salinities during the colder months of the year. The preponderance of grunts, silver perch, and anchovies at stations S-1, 4 and 8 attributed to large increases of individuals during the early summer months. Conversely many fish reach their

peak tolerance of low salinities during the warmer months of the year.

By weight, large marine predators and their young-of-the-year (sharks, rays and barracuda) from station habitats 6, 7 and 8 accounted mostly for seasonal biomass increases primarily during the early months of the hydroperiod.

During the course of this study despite individual population fluctuation there was a certain consistency in the various fish communities when viewed on an annual or a seasonal basis. However, a discussion of individual species and degrees of correlation between various species diversity indices, abundance indices and other environmental factors throughout Florida Bay are presently under summation and will be the subject of a future publication.

Thus, the quantitative distribution of marine and estuarine fishes in western Florida Bay undergoes considerable fluctuation, not only in relation to the biological features of each unique habitat but more importantly as they are influenced by the cyclicity of the hydroperiod.

## COMPARISON WITH OTHER SYSTEMS

The fourteen month range in total fish biomass in western Florida Bay was 11 to 159 kg/h with a mean of 57 kg/h (Table 2). There was considerable variation between the seasonal ranges of fish biomass with 26-245 kg/h for the hydroperiod and 11-80 kg/h for the dry season (Tables 3 and 4). These estimates are comparable with values reported from various other offshore and coastal areas. Oviatt and Nixon (1973) in a year long study of the demensel fishes of Narragansett Bay in Rhode Island found a range of 18.6-62.1 kg/h (16.5-56.5 lbs/acre) with a mean of 31.1 kg/h (28.5 lb/acre).

Day et al. (cited in Oviatt and Nixon 1973) found a similar range of 19.8-68.2 kg/h (18-62 lbs/acre) in a shallow Gulf coast estuary while McHugh (1967) reached a higher estimate of 55-310 kg/h (50-282 lbs/acre) from fishery catch data for the Gulf of Mexico. The biomass of these environments is small when compared to specialized marine ecosystems. Bardach (1959) estimated the summer standing crop over a Bermuda coral reef to be 587 kg/h (529 lbs/acre). Quast (1968) determined that the range of fish biomass in a California kelp bed was between 328-371 kg/h (296-335 lbs/acre).

Although the selectivity and limitation of fish sampling gear is well known (Carter et al. 1973; McHugh 1967) these studies together as discussed by Oviatt and Nixon (1973) represent many of the best estimates available of the standing crops of coastal marine fish populations.

## LITERATURE CITED


BARDACH, J.E. 1959. The summer standing crop of fish on a shallow Bermuda reef. Limnology and Oceanography 4, 77-85.

CARTER, M. and L. BURNS, T. CAVINDER, K. DUGGER, P. FORE, D. HICKS, L. REVELLS and T.W. SCHMIDT. 1973. Ecosystems Analysis of the Big Cypress Swamp and Estuaries. U.S.E.P.S., Reg. IV, Atlanta, Ga.

CLARK, S.H. 1971. Factors affecting the distribution of fishes in Whitewater Bay, Everglades National Park. Univ. of Miami, RSMAS, Sea Grant Tech. Bull. No. 8, 100 p.

DOOLEY, J.K. and J.B. HIGMAN. 1965. Studies of the fish stocks in Everglades National Park. Ann. Rept. to U.S.N.P.S. by Inst. Mar. Sci., Univ. of Miami, 56 pp (mimeo).

GUNTER, G. and G. HALL. 1965. A biological investigation of the Caloosahatchee estuary of Florida. Gulf Res. Rep. 2(1):1-72.

HARMIC, J.L., C. M. COURTNEY, T. EDMOND, J.C. KINCH, W.D. KEY, B.J. APPLEBY, J.M. HATCHER and W.L. O'HARRA. 1974. Annual Report Marco Applied Marine Ecology Station, pp. 1-204.

HENSHALL, J.A. 1891. Report upon a collection of fishes made in southern Florida during 1889. Bull. U.S. Fish Comm., 9:371-389.

HIGMAN, J.B. 1966. Relationship between catch rates of sport fish and environmental conditions in Everglades National Prak, Florida. Proc. Gulf and Car. Fish Inst. Nov. 1966 pp. 129-140.

HILDEBRAND, S. 1943. A review of the American anchovies (Family Engraulidae). Bull. Bingham Oceanogr. Coll. 8(2):1-165.

HUDSON, H.J., T.J. COSTELLO and D. ALLEN. 1970. The flora and fauna of a basin in central Florida Bay. U.S. Dept. of Int., U.S. Fish and Wild. Serv., Bur. of Comm. Fish. Spec. Sci. Rept. Fish No. 604.

LINDALL, W.N. and J.R. HALL, W.A. FABLE, JR., and L.A. COLLINS. 1973. Fishes and commercial invertebrates of the nearshore and estuarine zone between Cape Romano and Cape Sable, Florida in South Florida Ecological Study. App. E. Estuarine Dependent Marine Fishes. NMFS.

LONGLEY, W.H. and S.F. HILDEBRAND. 1941. Systematic catalogue of the fishes of Tortugas, Florida. Carnegie Papers Tortugas Lab., 34: 1-331.

LONNBERG, A.J.E. 1894. List of fishes observed and collected in South Florida. Ofvers. Kougl. Akad. Forh. 3:109-131.

MCFARLAND, W.N. 1963. Seasonal change in the number and the biomass of fishes from the surf at Mustang Island, Texas. Publ. Inst. Mar. Sci., Univ. Texas 9:91-105.

MCHUGH, J.L. 1967. Estuarine nekton. In: Estuaries (G.H. Lauff, ed.) Pub. No. 83, AAAS, Washington, D.C. 581-620.

MCNULTY, J.K., W.N. LINDALL, JR., and J.E. SYKES. 1972. Cooperative Gulf of Mexico estuarine inventory and study, Florida: Phase 1, area description. U.S. Dept. Comm. NOAA Tech. Rept. NMFS Circ-368. 125 pp.

OVIATT, C.A. and S.W. NIXON. 1973. The demersal fish of Narragansett Bay: an analysis of community structure, distribution and abundance. Estuarine and Coastal Marine Science I, 361-378.

PRICE, W.A. 1967. Development of the Basin-in-Basin Honeycomb of Florida Bay and the northeastern Cuban Lagoon, Gulf Coast Ass. of Geo. Soc. Trans. 17, 368-399.

QUAST, T.C. 1968. Estimates of the populations and standing crop of fishes. Fisheries Bulletin 139, 57-79.

ROESSLER, M.A. 1972. A checklist of fishes in Buttonwood Canal, Everglades National Park, Florida and observations on the seasonal occurrence and life histories of selected species. Bull. Mar. Sci. 20:860-893.

ROSEN, A. and S. DOBKIN. 1958. The biology of the fish stocks in the Everglades National Park. Prog. Rept. to Supt. Ever. N.P. Homestead, Fl by Mar. Lab. Univ. of Miami 40 pp (mimeo).

SCHMIDT, T.W. in prep. Cyclic hypersaline conditions of Florida Bay, Everglades National Park, Florida.

SPRINGER, V.G. and A.J. MCERLEAN. 1962. Seasonality of fishes on a South Florida shore. Bull. Mar. Sci. Gulf and Caribbean 12(1), 39-60.

SPRINGER, V.G. and KENNETH WOODBURN. 1960. An ecological study of the fishes of the Tampa Bay area. Fla. St. Bd. Consur. Prof. Paper Ser. No. 1, 104 pp.

TABB, D.C. and R.B. MANNING. 1961. A checklist of the flora and fauna of northern Florida Bay and adjacent brackish waters of the Florida

mainland collected through the period July, 1957 through September, 1960. Bull. Mar. Sci. Gulf and Carrib., 11(4):552-649.
TAFT, W.H. 1969. Mineralogy of carbonate sediments along the western margin of Florida Bay. Coastal and Shall. Wat. Res. Conf., pp. 676-677.
WANG, J.C. and E.C. RANEY. 1971. Distribution and fluctuations in the fish fauna of the Charlotte Harbor Estuary, Florida. Mote Mar. Lab., Sarasota, Fl. 56 pp.

# DISTRIBUTION AND ABUNDANCE OF MARINE MAMMALS IN THE WATERS OF THE EVERGLADES NATIONAL PARK

Daniel K. Odell[1]

## INTRODUCTION

Marine mammals are plentiful in the waters of Florida. Based on published accounts (Moore 1963; Layne 1965; and Caldwell & Caldwell 1976) at least 27 species of marine mammals have been sighted and/or found stranded in recent years. The two most commonly seen species in coastal waters (including the Everglades National Park) are the bottlenose dolphin (*Tursiops truncatus*). and the West Indian manatee (*Trichechus manatus*). The bottlenose dolphin is the familiar trained dolphin seen in oceanaria around the world. Its range is world wide in temperate and tropical waters. The taxonomy of the genus is, however, in a state of confusion (Mitchell 1975). The West Indian manatee (sea cow) occurs from the coasts of Central and South America to northeastern Brazil (Husar 1974 ms). It occurs in fresh, brackish, and salt water, and is herbivorous. The manatee is an endangered species (Anonymous 1973). Robertson (1959) considered the bottlenose dolphin and the manatee to be common in the waters of the Everglades National Park. The only studies of marine mammals in Park waters are those of Moore (1951a, b) on the manatee. The purpose of this report is to present the preliminary results of aerial surveys used to assess the distribution and abundance of the bottlenose dolphin and the manatee in the waters of the Everglades National Park.

## METHODS

Aerial surveys to assess the dolphin and manatee populations in Park waters were conducted from September 1973 through June 1976. The primary purpose of the flights through June 1975 was to count the number of boats using Park waters, and marine mammal surveys were secondary. Flights from July 1975 through June 1976 were specifically for marine mammal surveys. The flight path (Figure 1) was approximately the same for each flight and slightly modified in July 1975 to provide better coverage of Whitewater Bay. Each flight had a mean duration of 3.0 hr with a mean survey time of 2.6 hr. Mean linear air survey distance was 286 mi (460 km) per flight. Flights were made approximately every two weeks using a Lake LA-4, 2.5 seat amphibious aircraft. The fact that this aircraft had high wings, lacked wing struts, and had retractable landing gear made conditions excellent for observing. An altitude of 1000 feet (305 m) and an airspeed of 110 mph (117 kph) were stndard flight conditions. At least two observers (pilot included) were on board for each flight. All flights were made between 0800 and 1300 hrs EST. The data recorded for each dolphin or manatee herd sighted included location, number of animals, herd substructure, number of calves, direction of travel, and behavior. Data were collected on a portable cassette tape recorder and transcribed after each flight.

[1]Division of Biology and Living Resources, Rosentiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149.

## RESULTS AND DISCUSSION

Forty-eight (48) survey flights were attempted and 46 completed during the period from September 1973 through June 1976. All statistics given below are based on 46 flights except where noted. The total number of air miles surveyed was 13,156 (21,172 km) with a mean of 286 miles (460 km) per flight. The flight dates and numbers of dolphins and manatees seen are listed in Table 1.

### *Bottlenose Dolphins*

Bottlenose dolphins were observed on all but one of the 48 flights (Table 1). Five hundred seventy-three (573) dolphin herds totaling 1651 animals were sighted. A herd is herein defined as one or more animals in "relatively" close proximity. Mean herd size was 2.88 animals. Figure 2 gives the frequency of sighting of herds of various sizes, which ranged from 1 to 25 animals. Only 56 of the total dolphins seen were calves. The calf:adult ratio was 0.035. This value is probably low because small calves stay very close to their mothers and are difficult to recognize in turbid water.

Fifty percent of the herds sighted were feeding. *Tursiops* appears to be a generalized and opportunistic feeder. Leatherwood (1975) has summarized the scant literature on *Tursiops* food habits and has added some observations on feeding behavior. Both individual and group foraging activities were observed during this study. The only prey species that could be identified with reasonable certainty was mullet (*Mugil* sp). It has been reported (W. Wisby personal communication 1976) that *Tursiops* feeds on spawning snook (*Centropomus* sp.) in the Ten Thousand Islands area (Figure 1).

The distribution of the dolphin sightings within the study area was as follows: Florida Bay, 11%; Whitewater Bay, 33%; Gulf of Mexico, 36%; and inland waters, 20%. The relatively low number of sightings in Florida Bay is probably due to the fact that the water is quite shallow over most of the area surveyed. Food appeared plentiful, if one could judge from the amount of silt stirred up by mullet.

*Tursiops* in South Florida is thought to have two mating/calving seasons each year; one in the fall and another in the spring (see Odell 1975). No good evidence was found to support this. Figure 3 gives the calf:adult ratio by month for all the surveys. Aside from July and September when no calves were seen, the ratio was relatively constant, but tended to increase near the end of the year.

The distribution of herd sightings by month (Figure 4) indicates that dolphin were less abundant in Park waters during the months of September, October, and November. The reason for this is unknown, but it could be related to a fall calving/mating season.

It is difficult to compare the data on *Tursiops* from this study with *Tursiops* in other areas due to the general lack of other data. Overall abundance of dolphins in Park waters can be compared with abundance in Biscayne Bay (Odell 1976) on the basis of herds sighted per survey km. In Biscayne

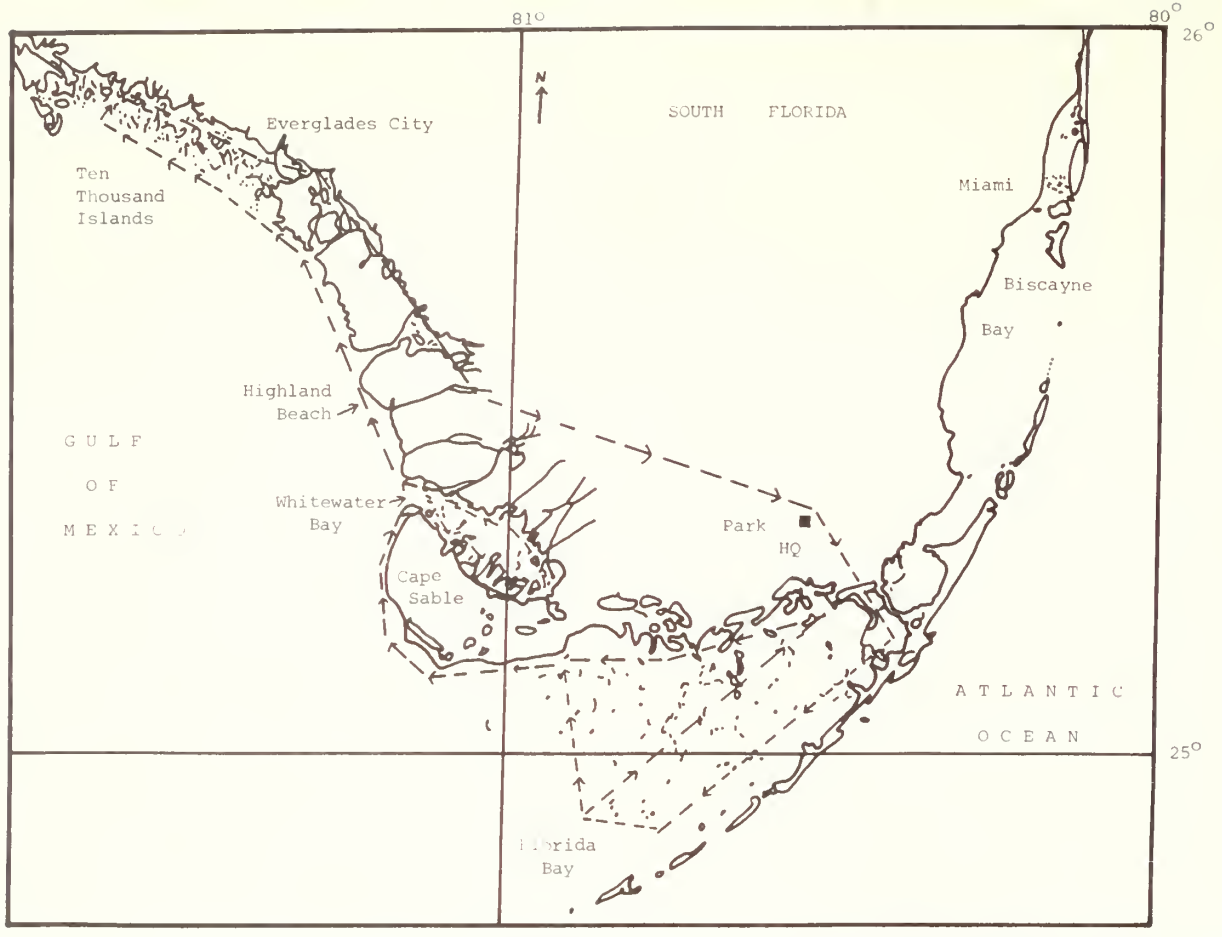



FIGURE 1. Map of south Florida indicating Everglades National Park survey transects (broken lines). Transect line in Ten Thousand Islands, inland waters, and Whitewater Bay is obscured.

Bay sighting rate was 0.009 herds/km, while the rate for the Park was 0.027 herds/km. Obviously, dolphins were considerably more abundant in the Park. The survey distance per flight was approximately the same for both areas (see Odell 1976). Any number of factors including food abundance, pollution, boating intensity, etc., could be responsible for the difference. However, the geographic nature of the two survey areas may be important. The Biscayne Bay survey area was mostly open water, whereas the Park Survey area was generally coastal with the bays being broken up by mangrove islands. It is not possible to make a dolphin population estimate for Park waters for several reasons, including the geographic nature of the area, the variability of environmental conditions during flights (see below), and the fact that there is no basis for considering the dolphins in Park waters as a discrete population.

*West Indian Manatee*

Manatees were not observed as frequently as dolphins (Table 1). The fact that they can remain submerged for up to 20 minutes makes the probability of sighting them less than that of sighting dolphins, which spend a greater amount of time on the surface. In addition, manatees need only to raise the tip of their nose above the surface to breathe.

Three hundred two (302) manatee herds totaling 772 individuals were sighted. Herd size ranged from 1 to 15 with a mean of 2.55. The frequency of occurrence of the various herd sizes is given in Figure 5. The distribution of manatee sightings in Park waters was as follows: Florida Bay, 1%; Whitewater Bay, 46%; Gulf of Mexico, 20%; inland waters, 23%. The reason for low abundance in Florida Bay may be due to shallow water, or, according to Hartman (1974 ms), lack of fresh water for drinking. Food was abundant. While manatees have been observed drinking fresh water, there is no physiological evidence to confirm or deny that they require it.

The overall calf to adult ratio was 0.055. Calving is thought to be aseasonal, and the calf: adult ratios by month (Figure 3) are inconclusive in this respect.

The seasonable abundance of manatees in Park waters is also difficult to assess because of problems in seeing the animals and because little is known about their local movements. They were most easily seen in relatively open water. Figure 6 shows the distribution of manatee herd sightings by month. The abundance appears to be somewhat bimodal, but the significance of this data must partially await information on diurnal and seasonal movements.

Population estimates of marine mammals in coastal waters are difficult to make for several reasons: 1) Lack of information on local and seasonal movements and home range makes it difficult to define a discrete population; 2) Lack of data on the true population density for any area makes population estimates made from surveys difficult to interpret; 3) Environmental conditions (tide, storms, etc.) may not only affect the distribution of marine mammals in an area, but also affect whether or not an animal can be seen from the air.

TABLE 1. Summary of results of Everglades National Park marine mammal survey flights.

| Flight No. | Date | Manatees | | Dolphins | |
|---|---|---|---|---|---|
| | | Adults | Calves | Adults | Calves |
| 1 | 28 Sept 73 | 3 | 0 | 11 | 0 |
| 2 | 16 Oct 73 | 8 | 0 | 5 | 0 |
| 3 | 18 Dec 73 | 1 | 0 | 19 | 1 |
| 4 | 16 Jan 74 | 0 | 0 | 8 | 0 |
| 5 | 15 Feb 74 | 27 | 0 | 39 | 1 |
| 6 | 12 Mar 74 | 0 | 0 | 68 | 0 |
| 7 | 5 May 74 | 0 | 0 | 13 | 0 |
| 8 | 23 May 74 | 0 | 0 | 7 | 0 |
| 9 | 19 June 74 | 1 | 0 | 18 | 0 |
| 10 | 14 Aug 74 | 16 | 4 | 30 | 2 |
| 11 | 13 Sept 74 | 7 | 0 | 15 | 0 |
| 12 | 28 Sept 74 | 3 | 1 | 12 | 0 |
| 13 | 8 Oct 74 | 2 | 0 | 10 | 0 |
| 14 | 31 Oct 74 | 15 | 1 | 5 | 1 |
| 15 | 30 Nov 74 | 0 | 0 | 0 | 0 |
| 16 | 7 Dec 74 | 11 | 0 | 28 | 0 |
| 17 | 6 Jan 75 | 72 | 1 | 54 | 3 |
| 18 | 26 Jan 75 | 28 | 2 | 26 | 2 |
| 19 | 3 Feb 75 | 23 | 1 | 50 | 0 |
| 20 | 5 Mar 75 | 2 | 0 | 17 | 1 |
| 21 | 20 Mar 75 | 3 | 0 | 8 | 2 |
| 22 | 1 Apr 75 | 0 | 0 | 22 | 1 |
| 23 | 12 Apr 75 | 0 | 0 | 30 | 3 |
| 24 | 27 Apr 75 | 0 | 0 | 30 | 1 |
| 25 | 5 May 75 | 23 | 2 | 93 | 6 |
| 26 | 25 May 75 | 16 | 1 | 56 | 0 |
| 27 | 27 June 75 | 6 | 0 | 26 | 0 |
| 28 | 7 July 75 | 46 | 0 | 39 | 0 |
| 29 | 22 July 75 | 11 | 2 | 29 | 0 |
| 30 | 5 Aug 75 | 21 | 1 | 51 | 2 |
| 31 | 18 Aug 75 | 54 | 1 | 27 | 1 |
| 32 | 3 Sept 75 | 0 | 0 | 12 | 0 |
| 33 | 23 Sept 75 | 2 | 0 | 13 | 0 |
| 34 | 2 Oct 75 | 27 | 4 | 34 | 1 |
| 35 | 14 Oct 75 | 17 | 1 | 23 | 2 |
| 36 | 22 Oct 75 | 1 | 0 | 5 | 0 |
| 37 | 11 Nov 75 | 0 | 0 | 40 | 2 |
| 38 | 25 Nov 75 | 5 | 0 | 18 | 1 |
| 39 | 9 Dec 75 | 67 | 4 | 72 | 6 |
| 40 | 23 Dec 75 | 18 | 0 | 43 | 0 |
| 41 | 5 Jan 76 | 49 | 5 | 44 | 0 |
| 42 | 19 Jan 76 | 17 | 2 | 17 | 1 |
| 43 | 17 Feb 76 | 58 | 5 | 88 | 5 |
| 44 | 15 Mar 76 | 8 | 0 | 6 | 0 |
| 45 | 29 Mar 76 | 12 | 0 | 111 | 3 |
| 46 | 12 Apr 76 | 6 | 0 | 109 | 3 |
| 47 | 10 May 76 | 34 | 1 | 61 | 2 |
| 48 | 7 June 76 | 12 | 1 | 52 | 4 |

Factors such as turbidity, sea surface condition, sea surface reflection, substrate color, and water depth can greatly affect the outcome of a survey. In addition, the experience of the observers in sighting the dolphins or manatees, as well as observer fatigue, can affect the results. It is probably that most of these effects can be handled statistically through appropriate testing, but some information on the true density of marine mammals in the study area and randomness of herd distribution are required for the final analysis.

### *Other Marine Mammals*

Three other species of marine mammals were observed in Everglades National Park waters. An 11.9 m immature fin whale, *Balaenoptera physalus*, apparently washed ashore dead on Man-o-War Key in Florida Bay (see Figure 1). It was discovered on 19 February 1974 and examined on 22 March 1974. It was badly decomposed. This is apparently the first record for this species in the Gulf of Mexico.

A large sperm whale, *Physeter macrocephalus*, stranded on Highland Beach, just north of the entrance to Whitewater Bay (see Figure 1) on about 7 April 1974. No data on sex or length was collected due to the inaccessability of the carcass.

A herd of 29 false killer whales, *Pseudorca crassidens*, stranded near Captiva Island, Lee County, Florida, on 22 July 1976. Five animals ultimately died, and 24 went back out to sea on their own accord. At 1330 hours, 24 July a herd of false killer whales stranded on Loggerhead Key, Dry Tortugas (near Fort Jefferson National Monument), several hundred km south of Captiva. One died and 29 were forced back out to sea. Based on a comparison of photographs of dorsal fins, the two strandings were considered to be the same herd. A similar occurrence has been reported for pilot whales, *Globicephala macrorhynchus*, in the same area (Fehring & Wells 1976). On 2 August 1976, 3 dead false killer whales were found floating off Cape Sable in the Everglades National Park. Again, on 23 August, 20 dead false killer whales were found on Cape Sable by Park rangers. The animals were badly decomposed and had probably been ashore for at least 2 weeks. In all proba-

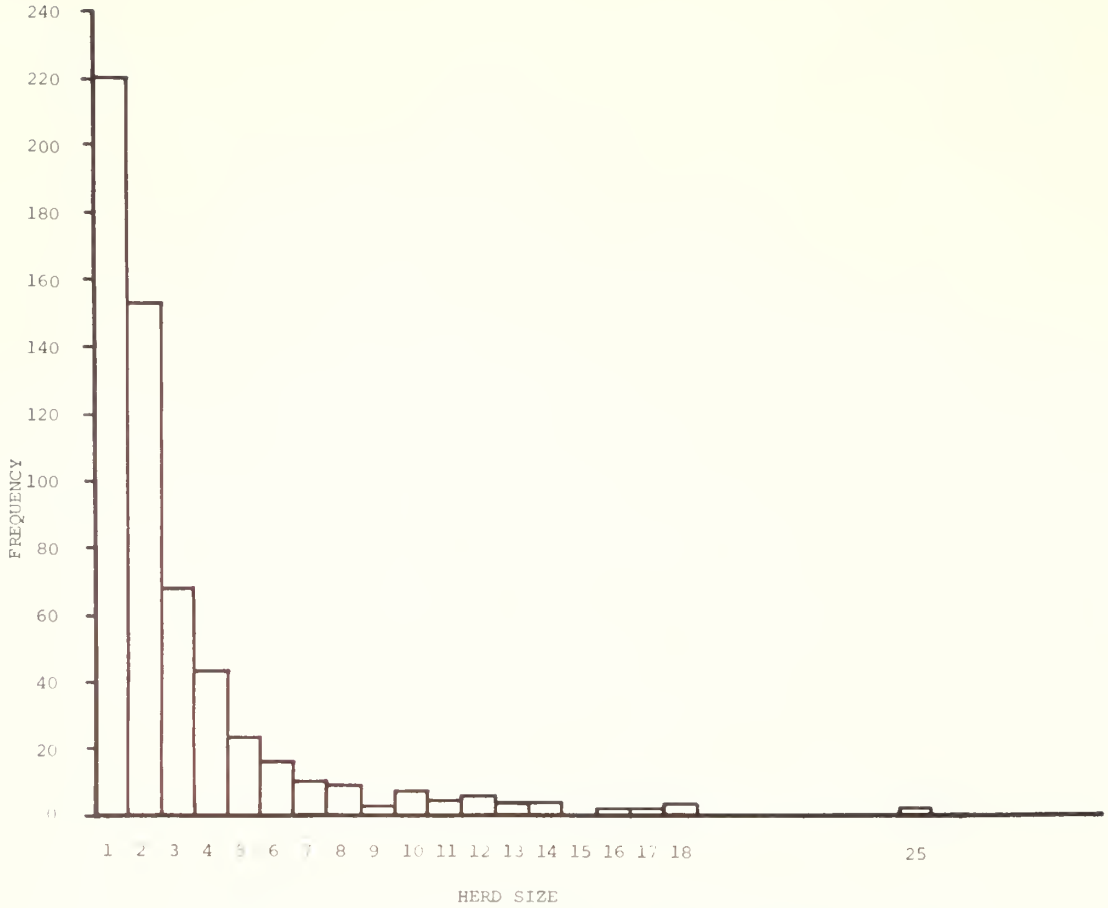



FIGURE 2. Frequency of sighting of dolphin herds of different sizes.

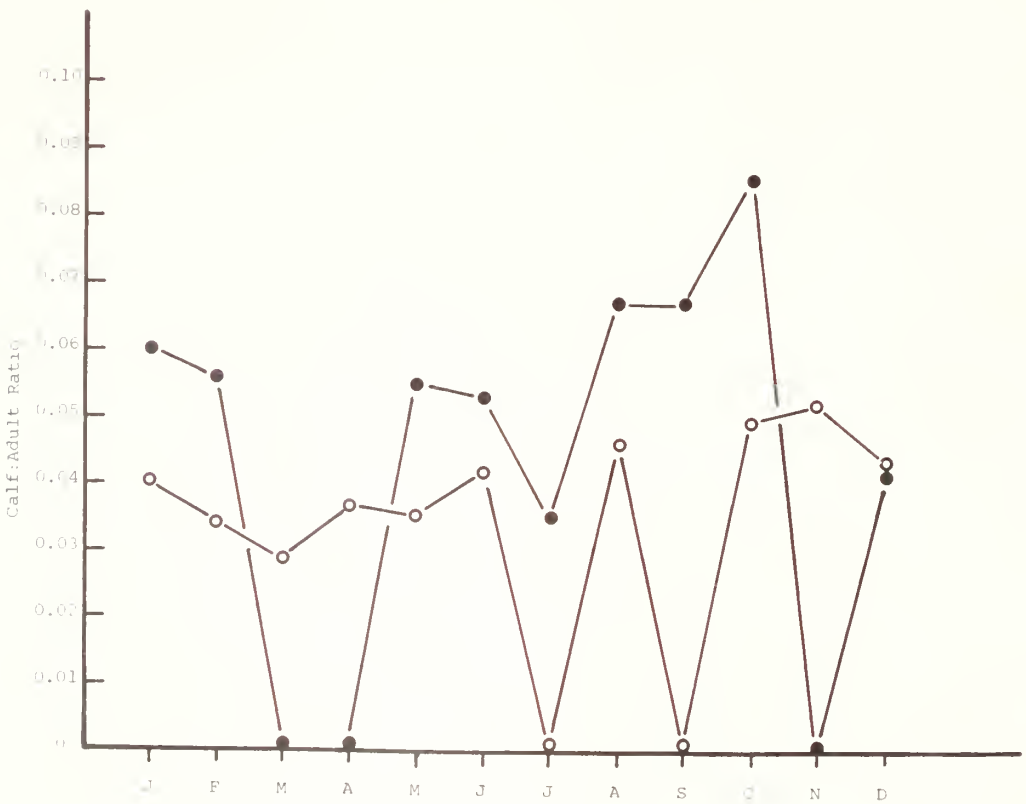



FIGURE 3. Calf-Adult ratios by month for dolphins (circles) and manatees (filled circles) in Park waters.

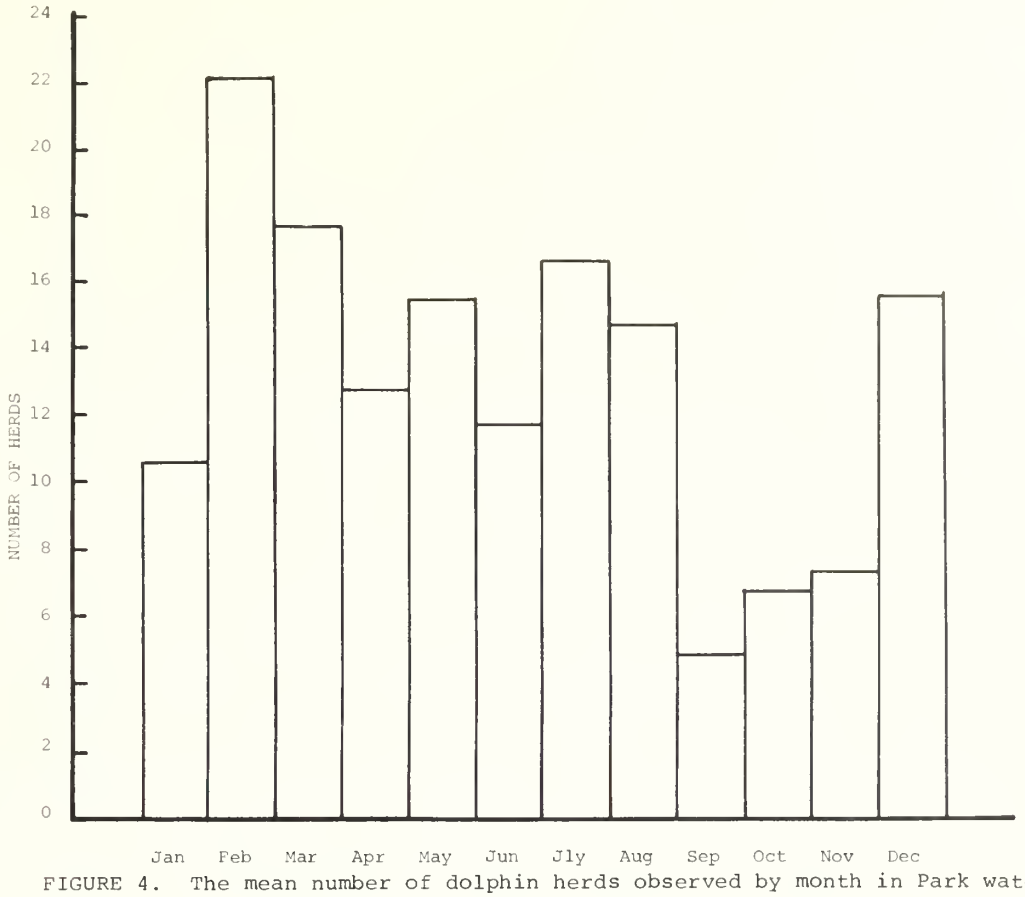



FIGURE 4. The mean number of dolphin herds observed by month in Park waters.

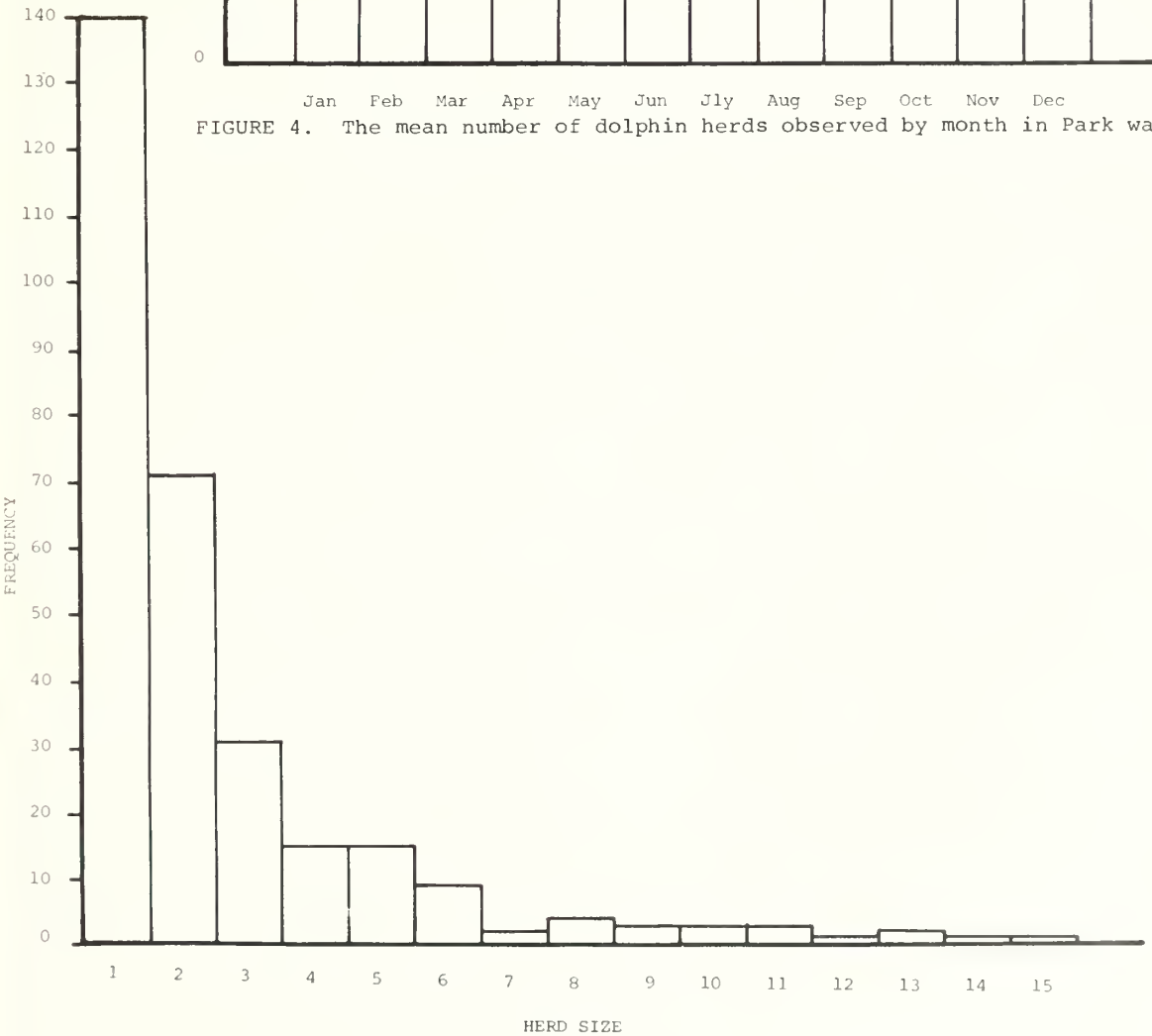



FIGURE 5. Frequency of sighting of manatee herds of different sizes.

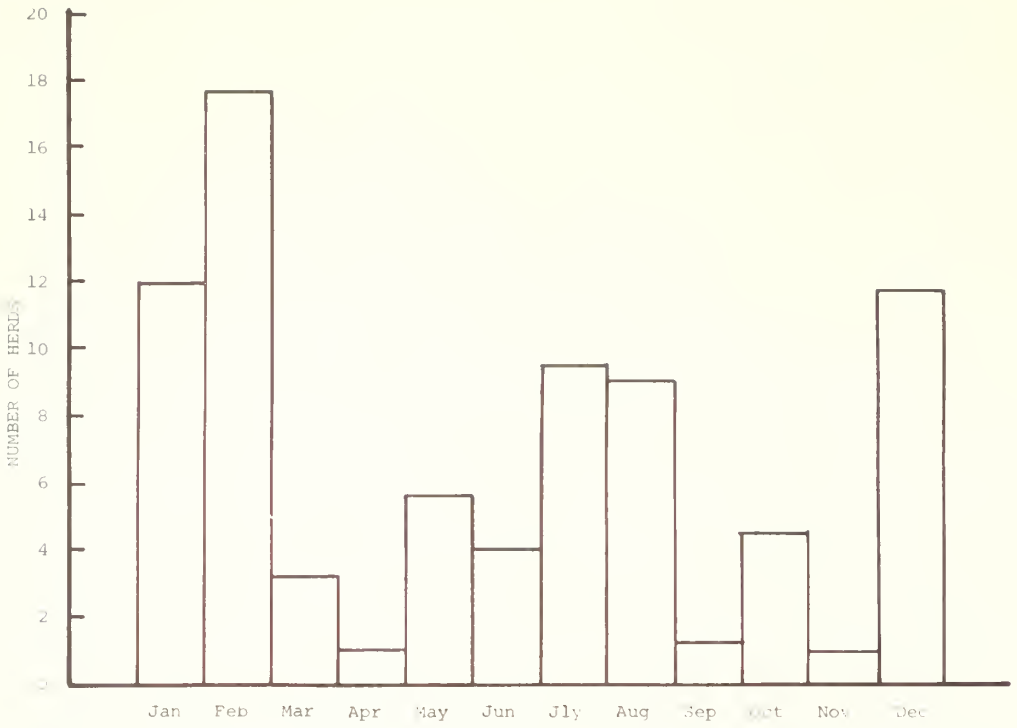



FIGURE 6. The mean number of manatee herds observed by month in Park waters.

bility, these animals were part of the herd pushed off Loggerhead Key 3 weeks earlier, but the advanced state of decomposition made positive identification impossible. The cause(s) of the strandings remain unknown.

## ACKNOWLEDGMENTS

The author was supported in part by U. S. Marine Mammal Commission Contracts MM4AC003 and MM5AC026; and U. S. Fish & Wildlife Service Contract 14-16-0008-930 during the field work and preparation of the report. E. Man and F. Williams, University of Miami, provided support to attend the conference. Aircraft time was provided by the Everglades National Park. The assistance of L. Purkerson, G. Hendrix, J. Stark, G. Davis, A. Lussier, and R. Miele (all of Everglades National Park); and E. Markoff, J. E. Reynolds, N. Chitty, and A. Baldridge (all of the University of Miami) is gratefully acknowledged.

## LITERATURE CITED

ANONYMOUS. 1975. Endangered and threatened wildlife and plants. Federal Register. 40:44417.

CALDWELL, D. K. and M. C. CALDWELL. 1976. Cetaceans. pp. 1144-1152. In: J. N. Layne (ed.), Florida Committee on Rare and Endangered Species. Inventory of rare and endangered biota of Florida (Interim microfiche edition). Florida Audobon Society and Florida Defenders of the Environment. Maitland, Florida.

HARTMAN, D. S. 1974 ms. Distribution, status, and conservation of the manatee in the United States. National Fish and Wildlife Laboratory, Washington, D. C. 247pp.

HUSAR, S. 1974 ms. Survey of the Order Sirenia. II. The West Indian manatee (*Trichechus manatus*). National Fish and Wildlife Laboratory, Washington, D. C. 114pp.

LAYNE, J. N. 1965. Observations on marine mammals in Florida waters. Bull. Fla. State Mus. (Biol. Sci.). 9(4):131-181.

LEATHERWOOD, S. 1975. Some observations of feeding behavior of bottlenosed dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops* cf. *T. gilli*) off southern California, Baja California, and Nayarit, Mexico, Mar. Fish Rev. 37(9):10-16.

MITCHELL, E. D. (ed.). 1975. Review of biology and fisheries for smaller cetaceans. J. Fish. Res. Board Canada. 32(7):889-983.

MOORE, J. C. 1951a. The range of the Florida manatee. Quart. J. Fla. Acad. Sci. 14(1): 1-19.

MOORE, J. C. 1951b. The status of the manatee in the Everglades National Park, with notes on its natural history. J. Mammal. 32(1):22-36.

MOORE, J. C. 1953. Distribution of marine mammals to Florida waters. Amer. Midl. Nat. 49:117-158.

ODELL, D. K. 1975. Status and natural history of the bottlenose dolphin, *Tursiops truncatus*, in Florida. J. Fish. Res. Board Canada. 32(7):1055-1058.

ODELL, D. K. 1976. Distribution and abundance of marine mammals in South Florida: Preliminary results. pp. 203-212. In: A Thorhaug and A. Volker (eds.). Biscayne Bay: Past/Present/ Future. Proceedings of a symposium. Special Rept. No. 5. Univ. of Miami Sea Grant Program.

ROBERTSON, W. B. JR. 1959. Everglades--The Park Story. Coral Gables (Florida). Univ. of Miami Press. 95pp.

# ENVIRONMENTAL STUDIES OF BUCK ISLAND REEF NATIONAL MONUMENT

Elizabeth H. Gladfelter and Rosemary K. Monahan[1]

## INTRODUCTION

Buck Island Reef National Monument is a unique area set aside in 1961 to preserve a spectacular coral reef and tropical island for the enjoyment of many thousands of visitors (tourists and local residents) annually. It is located in the Caribbean, 1½ miles north of St. Croix, U. S. Virgin Islands and can be reached only by boat. The Monument encompasses 880 acres; Buck Island is 1 mile long by ½ mile wide occupying 176 acres. There are two major recreation sites: the underwater snorkeling trail at the well developed bank barrier reef framing the eastern portion of the island, and the beautiful sand beach lying on the west and southwest shores of Buck Island. The east end of the Monument is a superb example of an *Acropora* dominated reef.

Prior to the project to be described below apparently no published marine research has been done at Buck Island, although rangers have been monitoring certain parameters of the reef ecosystem. Littlefield, unpubl. The National Park Service felt there was a need for documented research in the Monument to provide a sound basis for management decisions concerning future use of the area. Visitation to Buck Island is on the increase with 35,000 people recorded in 1975, while through October of this year, over 40,000 people have visited the area, with 75% of these snorkeling the underwater trail.

The West Indies Laboratory of Fairleigh Dickinson University is currently studying the marine ecosystem of the Buck Island Reef National Monument for the National Park Service. The laboratory is located on the northeast shore of St. Croix, a 15 minute boat ride from Buck Island, thus providing ready access for field studies. The research program is divided into three main areas:

(1) Structure of the marine ecosystem within the Monument boundaries;

(2) Growth and accrual of selected living resources and carbonate substrates; and

(3) Destruction of the above resources by natural elements and man.

The following account presents short descriptions of the major zones within the reef system, and a brief summary of the progress being made in other areas of the project.

## STRUCTURE OF THE REEF

A complete set of aerial photographs of the marine area of the monument has been taken, and from these a base map showing the major marine zones is in the process of being constructed. These zones have been characterized by depth, substrate and major faunal and floral components by means of radiating transects at various positions around the island, running from shoreline to the boundary line.

The reef system can be divided into three areas each with distinct characteristics: (1) the Southeast Reef which runs from the underwater trail westward to the boat cut, (2) the Northeast Reef which runs from the underwater trail westward for about 1000m grading into (3) the Leeward Reefs. To date transects of the Southeast Reef and of the Northeast Reef have been completed and analyzed. The zones which comprise them are: 1-Lagoon, 2-Backreef pavement, 3-Reef crest, 4-Forereef slope, and 5-the Bank.

### *Southeast Reef*

1-The Lagoon zone consists of a rubble area extending from shore out 20m and a sand channel area from that point to about 180m. The rubble area has a maximum water depth of 1 m and contains a substrate of angular cobbles and pebbles. There are a number of small colonies of *Acropora palmata* and *Porites astreoides* and many benthic algae. The channel (1-3 m in depth) has a uniform deep sand substrate. Near the backreef is a heavily bioturbated area, separated from the backreef by a barren area of calcareous pavement 2.5 m wide. A few calcareous green algae are found scattered in the channel.

2-The Backreef pavement zone, about 25 m wide, is underlain by a solid rock pavement formed from dead coral. There are scattered *Monastrea annularis* heads distributed evenly throughout the zone completely dominating the fauna. A few heads of *Diploria* and some gorgonians are also found.

3-The Reef crest is a well defined band 40 m wide, 0-0.3 m below the water's surface. *Acropora palmata* is the dominant coral in this zone. A large amount of *Millepora complanata* is present at the outer edges extending to the water surface.

4-The Forereef slope is gradual over about 20 m to depth of about 4 m below the surface, and is dominated by large colonies of *Acropora palmata* both living specimens and a large accumulation of dead branches. At this depth the *Acropora palmata* ends fairly abruptly and the area is dominated by *Acropora cervicornis-Porites porites and P. astreoides*, extending outward for another 50 m to a depth of about 11 m. There are a number of small colonies of other scleractinian corals located here as well as many gorgonians of various species. The deepest part of this zone (11-15 m), extending another 20 m was dominated by *Monastrea annularis*. This section, like the backreef also has a hard calcareous pavement. Many gorgonians are also growing here, ending abruptly at the next zone.

5-The Bank lies at 15 m depth and is a sand area which is relatively flat, moderately bioturbated, has deep sediment and contains scattered sea grasses. It extends to the Monument boundary.

### *Northeast Reef*

1-The Lagoon of this reef system is quite different from that of the Southeast Reef. Nearest shore the bottom is composed of cobbles and coarse sand. The cobbles are covered with many species of benthic algae. Just past this area is a hard substrate extending to 40 m from shore having a depth of 1-2 m. This substrate has many

[1]West Indies Laboratory, Fairleigh Dickinson University, P. O. Box 4010, Christiansted, St. Croix U. S. V. I. 00820.

small caves and cracks and is covered with a lush algal growth as well as many types of anthozoans. This platform drops abruptly to the sandy lagoon floor having a maximum water depth of 5 m. The floor is covered by a deep layer of sand. Scattered throughout this area are isolated corals and occasional patch reefs, whose crests are dominated by *Acropora palmata* and whose bases support many gorgonians. This area extends from 40 m to 150-200 m from shore.

2-The Backreef pavement zone is about 100 m wide with a water depth of 1-4 m. The pavement consists of consolidated coral which is lushly covered with zoanthids (both *Palythoa* and *Zoanthus* in about equal area coverage). In some spots adjacent to the lagoon this zone contains dense, healthy *Acropora cervicornis* in a 30 m wide band.

3-The Reef crest of the Northeast Reef breaks up with an increasing number of gaps as one proceeds leeward (west). Near the underwater trail this is a fairly well defined zone, similar to that described for the Southeast Reef, dominated by *Acropora palmata* with *Millepora complanata* at the seaward edge. To the leeward the crest becomes more ill-defined, wide (40-50 m) and shallow in some spots and narrow (15 m) in others. The water depth of this zone varied from 0 m to a maximum of 3.5 m through the gaps.

4-The Forereef slope is an abrupt drop from the reef crest to a depth of 6-10 m. The wall of the Forereef is dominated at shallow depths by *Acropora palmata,* and at the deepest portion by *Monastrea annularis* which grows along the base. The wall consisted of much dead *Acropora palmata* covered with coralline algae, forming many small caverns and crevices. The base had many species of scleractinian corals, zoanthids and a number of species of gorgonians. This zone is only 10-15 m wide but has much vertical relief.

5-The Bank in front of the Northeast Reef extends from the base of the Forereef slope to the Monument boundary and beyond. There is a proximal band (of up to 100 m in width) of barren sand. The depth gradually reaches a maximum of 11-15 m (being shallower in the west). Scattered throughout this zone are haystacks, large columns of coral reaching the water's surface. The crest has *Millepora complanata,* while the next 5-7 m are dominated by *Acropora palmata,* growing lushly all around the haystack. Below this are many dead branches of *A. palmata,* which provide a suitable substrate for many species of corals and a profuse growth of gorgonians.

The zones in the Leeward Reef system and the bank off the beach have not been as well studied to this date. The remainder of this paper will give a brief account of the progress being made in a number of other studies related to this project.

### *Structure of the Marine Ecosystem*

The dynamics of the beach are under study by determining the profile of the beach at 10 stations. These profiles are taken every three weeks or after a major storm, whichever occurs first after the previous readings. A gradual eroding of the northwest shoreline, resulting in the undercutting and toppling of manchineel trees is being systematically watched. Preliminary results have shown an erosion of the north section of the beach, and a deposition on the southwest section during the fall months.

The underwater trail is being monitored to show seasonal variability in water temperature, water clarity and wind, wave and weather conditions. Monthly fish censuses are taken in selected areas of the Monument to determine composition and estimate standing crop.

### *Accrual of Resources*

The rate of calcium carbonate deposition has been determined for the warm fall months in four species of coral: *Acropora palmata, A. cervicornis, Porites astreoides, Monastrea annularis* and one species of hydrocoral: *Millepora complanata.* In addition, the rate of primary production has been determined in *Acropora palmata.* Since this coral is so important in the Buck Island reef system, the above determinations are being made on colonies growing on the shallow Backreef, the Reef crest on the seaward side, and the base of the Forereef slope. Additional measurements will be made in January, and April-May, thus determining short day, cold water and long day cold water rates.

*Monastrea annularis* has been cored and its growth rings are under investigation. These bands, in addition to aging the coral, can provide information on climatic changes in the area in the past century (Hudson et al. 1976). One study has been conducted to determine the rate of bioturbation in the sand areas; estimates of the amounts of sediment mixed by this process have been determined. Finally, aspects of the biology of certain important invertebrates in the reef system are under investigation, including the relationship of the sea urchin *Diadema antillarum* to the dynamics of the reef, and a determination of the factors which influence the distribution of *Palythoa* and *Zoanthus* in the reef system.

### *Destruction of Resources*

Aerial photographs and mapping will provide a basis for determining large scale damage due to storms and other natural disasters. Hurricanes can cause massive damage to a reef system (Stoddart 1974); Buck Island reef has yet to feel the effects of a major storm (at least within this century). Man can cause direct damage to coral by breaking or scraping living colonies, either intentionally or not. Coral which is easily broken (such as the species of *Acropora*) have fast recovery rates with new growth forming soon after damage, and wounds repaired within a month. These and the corals which suffer from chronic abuse (such as rubbing, or being a rest stop for snorkelers) are being systematically studied to determine the point at which irreversible damage occurs. In relation to this, we are monitoring the activities of the visitors to the underwater trail to see how a greater impact at a given area can accelerate destructive forces.

### *Summary*

Completion of this project should provide the National Park Service with the information necessary to guide future policies within the Monument. Buck Island Reef National Monument is a unique part of the National Park System and should be maintained in its natural state for the education and enjoyment of future generations.


### ACKNOWLEDGMENTS

The authors wish to thank W. Gladfelter for help in preparation of the manuscript, the 1976 Fall semester class of West Indies Laboratory for aid in some field studies, and C. Schell for helpful information on the visitor use in the Monument.

## LITERATURE CITED

HUDSON, J. H., E. A. SHINN, R. B. HALLEY, and B. LIDZ. 1976. Sclerochronology: A tool for interpreting past environments. Geol. 4: 361-364.

LITTLEFIELD, R. G. 1975. Buck Island Reef National Monument. Photo Study of Injured Coral 1971 to 1975. NPS report.

STODDART, D. R. 1974. Post-hurricane Changes on the British Honduras Reefs: Re-survey of 1972. Proc. of the Second Intl. Coral Reef Symp. 2:473-483.



☆ U.S. GOVERNMENT PRINTING OFFICE 1978 O—283-901

NOV 3 0 1988