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Preface

The papers in this proceedings were selected from the 63 presentations given at the Fourth Biennial Conference on Research in National Parks in California. The overall theme for this meeting was a recurring one: "The Integration of Research into National Park Service Resource Management Decisions." The conference was held at the University of California, Davis, on 10–12 September 1991 and was sponsored by the National Park Service Cooperative Park Studies Unit and the Institute of Ecology at the University of California, Davis.

This proceedings highlights a variety of research and resource management efforts to improve the stewardship of our most treasured landscapes. In the future, it will become increasingly important for federal and state agencies, university scientists and students, and the public to cooperate fully to improve the quantity and quality of science and resource management programs in units of the National Park System. As many of the papers in this proceedings attest, we must look beyond the political boundaries of protected landscapes to incorporate entire ecosystems. Competing resource uses inside and outside parklands must be reexamined to weave a common thread of biological conservation. As scientists, our studies must bridge the gap from plots to landscapes and from landscapes to regions. Our studies must build on information from species and populations to ecosystems and the processes that influence them. The papers in this proceedings are a modest but important contribution to those ideals. Each paper represents original research and has been peer-reviewed.

Many agencies, institutions, and individuals contributed in the development of this product. In the planning stages, National Park Service Western Region scientists provided advice and assistance in structuring the conference format. University of California, Davis, graduate students, directed by Sharon Lynch, assisted with logistics at the meeting, and provided general assistance with the paper sessions. We thank the students, technicians, and support staff who labored unselfishly behind the scenes to collect data and transfer information important to the completion of each paper.

Financial support for this publication was provided with funds from the Western Region Resource Management and Research Program and the Washington Office Servicewide Publications Program of the National Park Service. We thank Denny Fenn, Stan Albright, Bruce Kilgore, Dave Cherry, Gene Hester, and Donna O'Leary of the National Park Service and Charles Goldman of the University of California, Davis, Institute of Ecology for their support throughout the development of the proceedings.

Finally, we are entering into a new age of research in the U.S. Department of the Interior. Recently, plans were announced for the creation of the National Biological Survey, dedicated to improving the quantity and quality of research

necessary for the wise stewardship of our natural resources and wildlands. We welcome our new partners and pledge our full support to both the new and old agencies. The papers presented here—and past research efforts in national parks—provide an important stepping stone to the future. While many of us will be transferred administratively to the National Biological Survey, our emotional ties to the National Park Service mission of preserving resources for future generations will remain with us forever.

April 1993
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Status of Summer Steelhead Trout in Redwood Creek, Redwood National Park, California

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Abstract. Summer steelhead (*Oncorhynchus mykiss*), a declining stock of rainbow trout in Redwood National Park, have been monitored in Redwood Creek by snorkelers since the summer of 1981. The adult fish migrate upriver in spring, hold in pools during summer, and spawn during winter. Large and numerous pools have been filled in as a result of record floods and land-use activities. The resultant high water temperatures ($\leq 25°$ C) and lack of pool habitat and cover have restricted the distribution of summer steelhead in Redwood Creek. Schools of fish are rare and observed only in pools adjacent to tributaries where cooler water enters Redwood Creek. A 25.9-km reach of the creek's best habitat was used to index trends in the population. Numbers of fish observed peaked at 44 in 1984–85 but have since declined. Summer steelhead face several problems: habitat degradation, poor water quality, sport-fishing and poaching, and small population size. The prospect for recovery of the summer steelhead of Redwood Creek is poor and long-term.

Key words: Habitat, *Oncorhynchus mykiss*, summer steelhead, stock decline, Redwood Creek, water temperature.

Summer steelhead (*Oncorhynchus mykiss*) are an anadromous race of rainbow trout. Their life cycle differs from that of the more numerous winter-run steelhead. Adult summer steelhead ascend the rivers in spring, hold over in deep pools in summer, then spawn during winter. This cycle isolates them both spatially and temporally from winter-run fish. Because adult summer steelhead hold in freshwater for 8–10 months (Roelofs 1983), they are vulnerable to detrimental environmental and human-caused factors including high water temperatures, low summer flows, and poaching.

Redwood National Park personnel have been monitoring the status of adult summer steelhead in Redwood Creek since 1981. To ascertain that the fish we observed were summer-run fish, two females were sacrificed in 1986. Their gonads were in an immature state of development, and they had a low gonad to body weight ratio indicative of summer steelhead.

Approximately 25 summer steelhead populations are known in California. In 1990, almost 1,900 adults were counted; over half were observed in two rivers (E. Gerstung, California Department of Fish and Game, personal communication). Most rivers had less than 100 adults. The species, though not federally or state listed as threatened or endangered, is classified as a sensitive species by the U.S. Forest Service and as a species of special concern by the California Department of Fish and Game. Roelofs (1983) and, most recently, the summer steelhead management advisory committee (under the auspices of the California Department of Fish and Game) have documented the status of summer steelhead populations in California.

Study Area

The 108-km-long Redwood Creek drains a 730-km^2 watershed in Humboldt County, California (Fig. 1). The basin is steep-sided and narrow with a total basin relief of 1,616 m. The climate is Mediterranean, with an estimated average precipitation of 203 cm per year (Janda et al. 1975). Mainstem stream flow is lowest between August and October. Vegetation in the basin consists of coast redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*) forests, their associated flora, and ridge-top prairies (Janda et al. 1975). Commercial timber harvest is one of the major land use practices in the basin. By 1978, 66% of the basin drainage, composing 81% of the original conifer forests, had been logged (Best 1984). Logging no longer occurs in the lower one-third of the watershed, site of Redwood National Park. The park was established in 1968, and its boundaries were expanded in 1978 to protect park resources.

Methods

A 25.9-km reach (Fig. 1), 24% of Redwood Creek, is surveyed by snorkelers during summer, usually around the first week of August, to index the population. This reach includes a majority of the deep pool habitat in Redwood Creek. Expanded surveys showed that almost all summer steelhead were within the reach during the period of observation. Of the 25.9 km, 16.1 km is in Redwood National Park, and 9.8 km is upstream of the park on private property commercially harvested for timber. The reach was divided into smaller sections and surveyed in 3–4 days. Following procedures of Roelofs (1983), crews of three–five people dove in the creek using mask and snorkel to count adult summer steelhead trout. While proceeding downstream, the swimmers looked under ledges, root wads, and other large organic debris; at the base of boulders; and in the bubble curtains of turbulent water. Numbers and locations of fish observed were recorded on waterproof U.S. Geological Survey topographical maps. Water temperatures (°C) were obtained where summer steelhead were observed and where tributaries enter Redwood Creek.

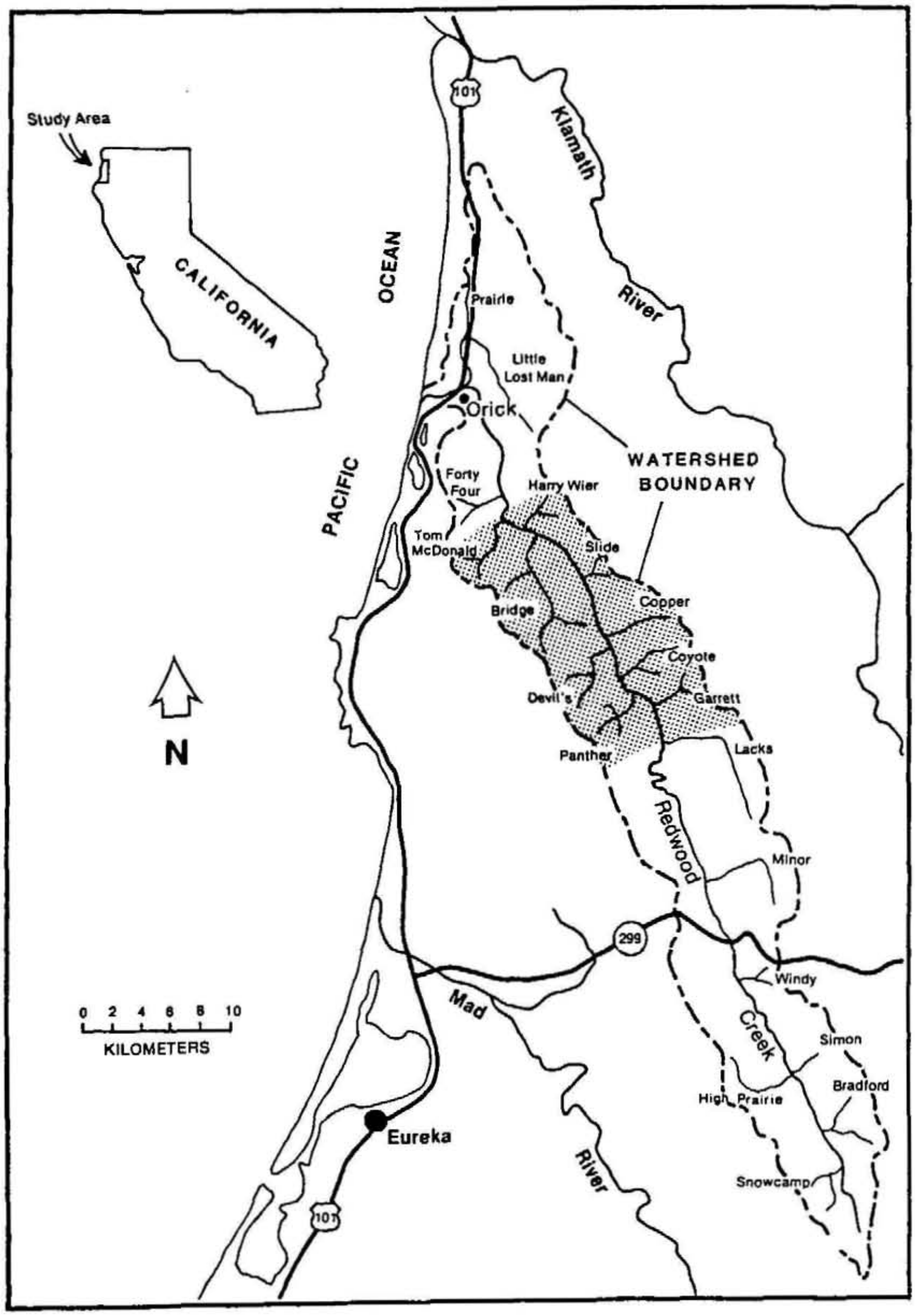


Fig. 1. Redwood Creek, Humboldt County, California. *Shaded area* represents the stream reach surveyed by snorkel swimmers as a population index for summer steelhead.

Results

Numbers of fish observed over the 11 summers of surveys declined from 44 in mid-decade to 0 in 1989 (Fig. 2). The observation of 15 fish in 1991 was the highest recent count.

Summer steelhead numbers and estimated depths of pools where fish were observed for seven of the surveys indicate an avoidance of shallow (30–60-cm) and mid-depth (275–400-cm) pools (Fig. 3). Other variables, including cover provided by boulders and large organic debris and nearby low-temperature tributaries (with cooler water temperatures than the mainstem), influence their occurrence.

Mainstem and tributary water temperatures from the 1990 summer steelhead survey were representative of conditions measured in previous surveys. The highest water temperatures, ranging from 20.5 to 24.5° C were measured in mainstem Redwood Creek. East-side tributaries were cooler, with a mean of 18.0° C ($n = 8$) and ranging from 15.5 to 20.0° C. West-side tributaries were coolest, with a mean of 15.2° C ($n = 17$) and ranging from 12.0 to 18.0° C.

Discussion

The majority of summer steelhead were observed in pools. Forty-five percent of the fish were sighted where a deep pool and inflow of cooler water

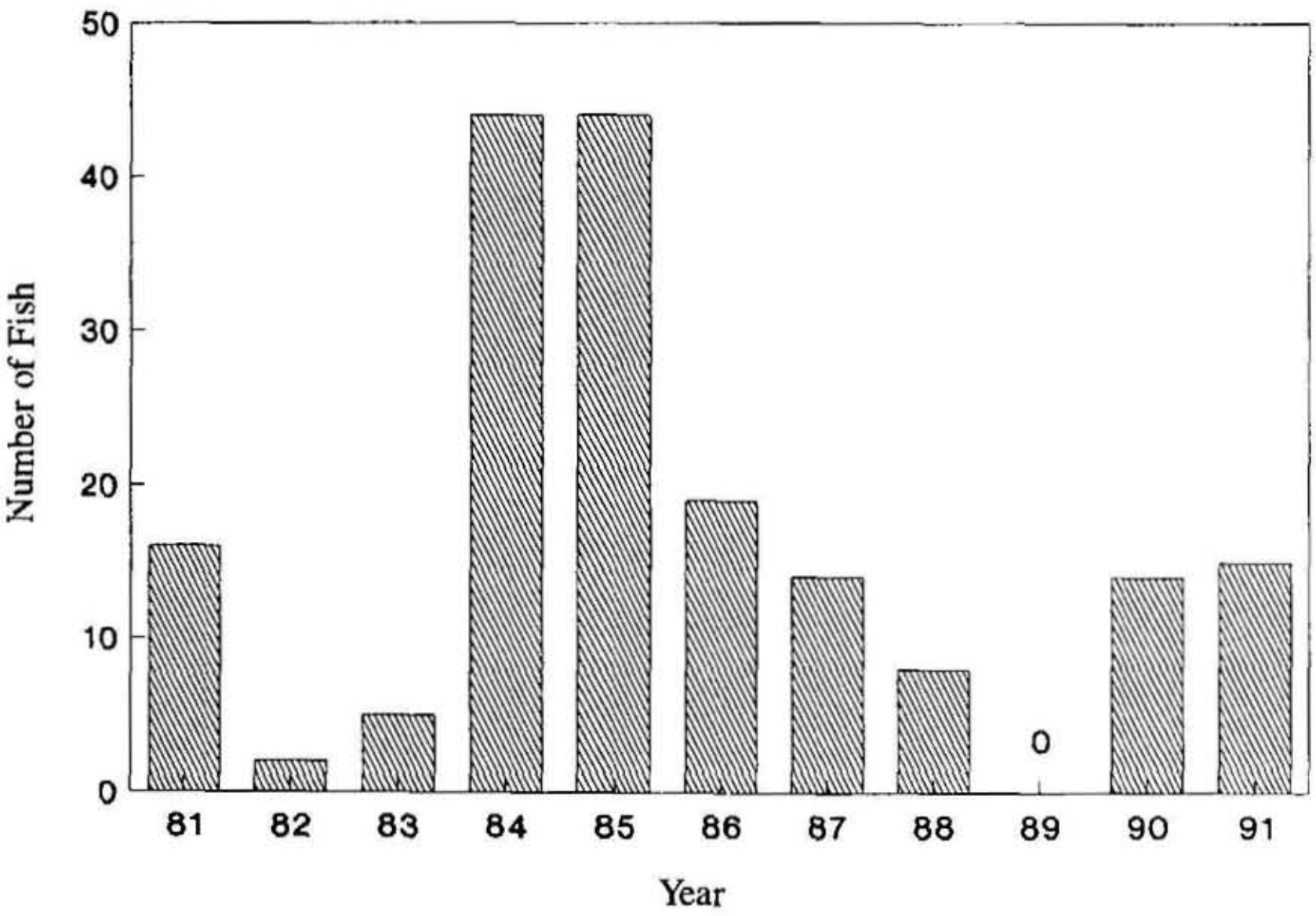


Fig. 2. Numbers of summer steelhead observed each summer since 1981 on a 25.9-km reach of Redwood Creek, Humboldt County, California.

from a tributary occurred together. The highest concentration of fish was usually in a pool at the confluence of one large west-side tributary and Redwood Creek. Otherwise, fish were generally found singularly and not in schools.

In the 3 years (1981, 1983, 1987) the survey was expanded to include more of Redwood Creek, 92% of summer steelhead were found in the index reach. This reach represented the best habitat in the stream for summer steelhead trout. Suitable holding pools were generally lacking in the upper and lower reaches of Redwood Creek, presumably because of sedimentation, lack of cover, or both.

Summer steelhead in Redwood Creek face several problems: habitat degradation, water quality, sportfishing and poaching, and population size. Geologically, the Redwood Creek basin is highly erodible (Janda et al. 1975). Also, large portions of the Redwood Creek basin have been logged. Together, the combined effects of timber harvest (i.e., removal of forest cover and road building) and significant storms have deposited large amounts of sediment in Redwood Creek and degraded fish habitat. Both erosion and hillslope mass wasting caused sedimentation of the mainstem that filled deep pools, the preferred habitat of summer steelhead. Major flood events like the record flood of 1964 caused significant channel adjustments—channel widening, aggradation, and bank erosion. The resultant widened streambed and accompanying shallow riffles provided little or no cover for fish.

The stream received more insolation with less riparian canopy cover over a wider channel, with an accompanying increase in water temperature and a decrease in water quality. Summer mainstem water temperatures are well above the preferred temperature range reported by Reiser and Bjornn (1979) for

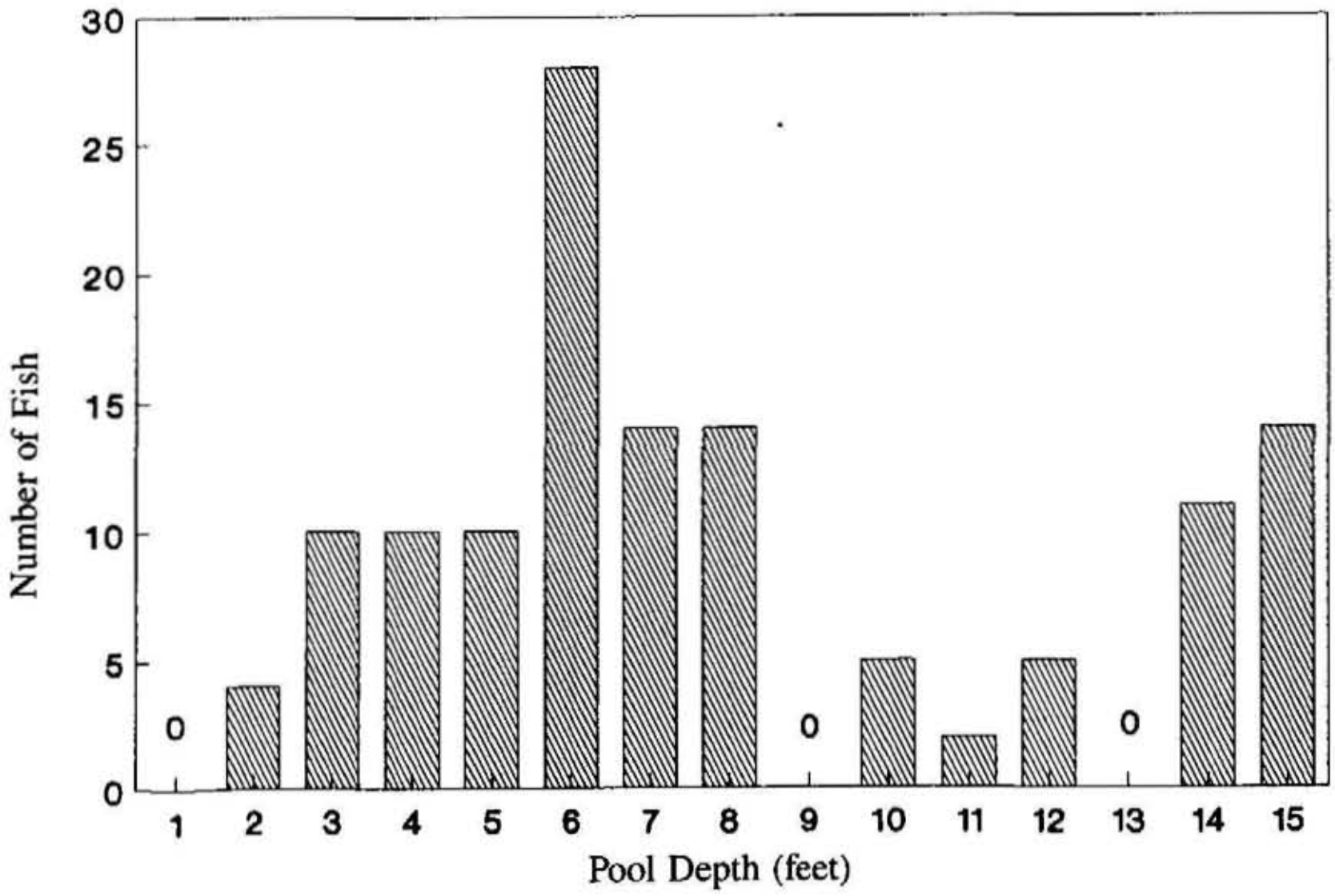


Fig. 3. Summer steelhead numbers and estimated pool depths where fish were observed for seven of the snorkel surveys of Redwood Creek, Humboldt County, California.

steelhead of 7.3–14.6° C. Greater numbers of steelhead were found where water at 15° C entered Redwood Creek from a major west side tributary. The entering flow cooled portions of the pool. This 'cold' pool area was partially thermally stratified because the cooler water sank to the bottom. Though not meeting the definition of a typical cold pool—where physical features such as a gravel bar isolate large volumes of cool water from the warmer mainstem (Ozaki 1988)—the resulting cooler water in the pool provided habitat for summer steelhead.

Sportfishing may be adversely affecting the summer steelhead population. Though the pools are somewhat inaccessible, a few knowledgeable people could deplete the small population present. Further, fishing in the lower river adversely affects the numbers of fish that can migrate in spring to the holding areas upstream. The extent of poaching on this reach of Redwood Creek is unknown. The holding pools are remote and not patrolled, and poaching activities have not been detected but, because of the small population size, poaching would have an inordinate effect on summer steelhead.

A factor making summer steelhead susceptible to poaching is its hiding behavior. When approached by a diver in the water, it may only partially hide. For example, its head will be under a log but its body will be visible, or it may rest in the open on the substrate at the base of a boulder. The fish is easy to approach and usually does not move until touched. This behavior makes it susceptible to spearfishing.

Most summer steelhead in California are found in remote canyons not readily accessible to people (P. B. Moyle and M. D. Morford, California Fish and Game Commission, unpublished data). On Redwood Creek, a hike of approximately 9 km is necessary to reach the holding pools, and on the private timber land, public access is restricted. This may indicate that, besides habitat distribution, public access and the accompanying fishing pressure may influence their distribution.

The small population size and potential concomitant loss of genetic diversity of the summer steelhead of Redwood Creek may also affect their chances for recovery. The optimum effective size of the population for the long-term survival of this run needs to be determined.

The small population size makes this run more prone to be severely affected should a catastrophic natural or human-caused event occur—an event from which the population would not recover. The natural recovery of this population would also be longer because of a catastrophe. In their review of salmonid stocks at risk, Nehlsen et al. (1991) rated the summer race of steelhead of Redwood Creek at a high risk of extinction, based primarily on the small adult escapement and threats of further habitat destruction and overutilization of the fish.

The likelihood of recovery of summer steelhead of Redwood Creek is poor and long term. The National Park Service has invested 15 years and approximately $11 million in a comprehensive watershed rehabilitation program of erosion control and rehabilitation of timber-harvested lands in the Redwood Creek basin and in restoration projects on Redwood Creek, its tributaries, and its estuary. These programs will benefit the fish in the long run by decreasing

erosion and sedimentation and increasing in-stream cover and spawning gravels. However, changes in present fishing regulations and watershed management practices are necessary in the interim. Closing the index reach to fishing and implementing more restrictive angling regulations downstream, including catch-and-release, would increase upstream migration and immediately protect summer steelhead.

Most of the basin is already logged, and vegetative recovery needed to decrease insolation and erosion will be slow. Upstream of the park, better timber-, road-, and erosion-management practices to protect the inner gorge area and riparian canopy are needed to maintain and conserve the remaining habitat.

The California Department of Fish and Game is writing a statewide summer steelhead management plan to address problems facing these fish and to aid their recovery. Creating additional holding pools by installing in-stream structures and implementation of artificial propagation using small on-site hatch-box programs have been proposed. These proposals will need to be evaluated for their potential effectiveness in Redwood Creek and their appropriateness in a national park (Meffe 1992).

The future for the summer steelhead is uncertain. The situation on Redwood Creek is not an isolated one. Most summer steelhead stocks in California are at risk. Decisions, some unpopular, that further protect the stocks and their habitat may be the answer.

Acknowledgments

I thank the many Redwood National Park employees, volunteers, and California Department of Fish and Game personnel that participated in summer steelhead surveys over the past 11 years. I also appreciate access to private land permitted by the Stover family and Simpson Timber Company.

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Nine Thousand Years of Coastal Prehistory on Santa Rosa Island, California: A Radiocarbon Chronology for CA-SRI-1

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Abstract. Twenty-five years ago, Phil Orr described several shell middens on Santa Rosa Island he believed dated to the late Pleistocene. The existence of Pleistocene middens on Santa Rosa Island would have major implications for a number of current anthropological issues, including the possibility of an early coastal migration route for the peopling of the New World. In this paper, we discuss Orr's claims in the context of our recent field work at CA-SRI-1 (Garanon Point), an archaeological site where shell-bearing strata have now been dated to about 2,000, 7,150, and 9,050 years ago. The earliest of these dates, on marine shell of probable cultural origin, took place well within the age range of known coastal California sites. Natural processes, including the transport of shellfish by carrion-eating birds, may account for occasional marine shells found in Pleistocene terrestrial sediments along the California coast.

Key words: Archaeology, Santa Rosa Island, shell midden, Pleistocene.

From 1947 to 1968, Phil Orr of the Santa Barbara Museum of Natural History studied archaeological and paleontological sites of Santa Rosa Island,

40 km off the Santa Barbara coast (Fig. 1). Santa Rosa Island is one of four northern Channel Islands. During glacial periods, lowered sea levels connected these into a single island called Santarosae (Orr 1968). The Channel Islands have been separated from the mainland throughout the Quaternary and contain a very limited range of land mammals. The only indigenous land mammal able to sustain permanent human settlement would have been the dwarf mammoth (*Mammuthus exilis*), which became extinct near the end of the Pleistocene. On the northwest coast of Santa Rosa Island, stratified and highly dissected sediments span much of the past 100,000 years (Orr 1967). These sediments contain abundant fossils and archaeological remains that are invaluable in reconstructing the prehistory of the island.

In a number of controversial publications, Orr and Berger (e.g., Orr 1956, 1967, 1968; Berger and Orr 1966; Orr and Berger 1966; Berger 1980, 1982) argued that associations between mammoth bones, fire areas, and occasional stone tools suggested that humans were present on Santa Rosa Island for 40,000 years or more. The cultural origin of these localities has been questioned by many scholars (e.g., Johnson 1972; Glassow 1977; Moratto 1984; Cushing et al. 1986; Erlandson 1991) and accepted by few (e.g., Carter 1980; Goodman 1981).

Nearly lost in the debate about the contemporaneity of mammoths and humans on Santa Rosa Island were several Pleistocene shell middens that Orr reported finding on the northwest coast of the island. According to Orr (1968), charcoal samples from shell-bearing soils at Survey Point and Tecolote Point

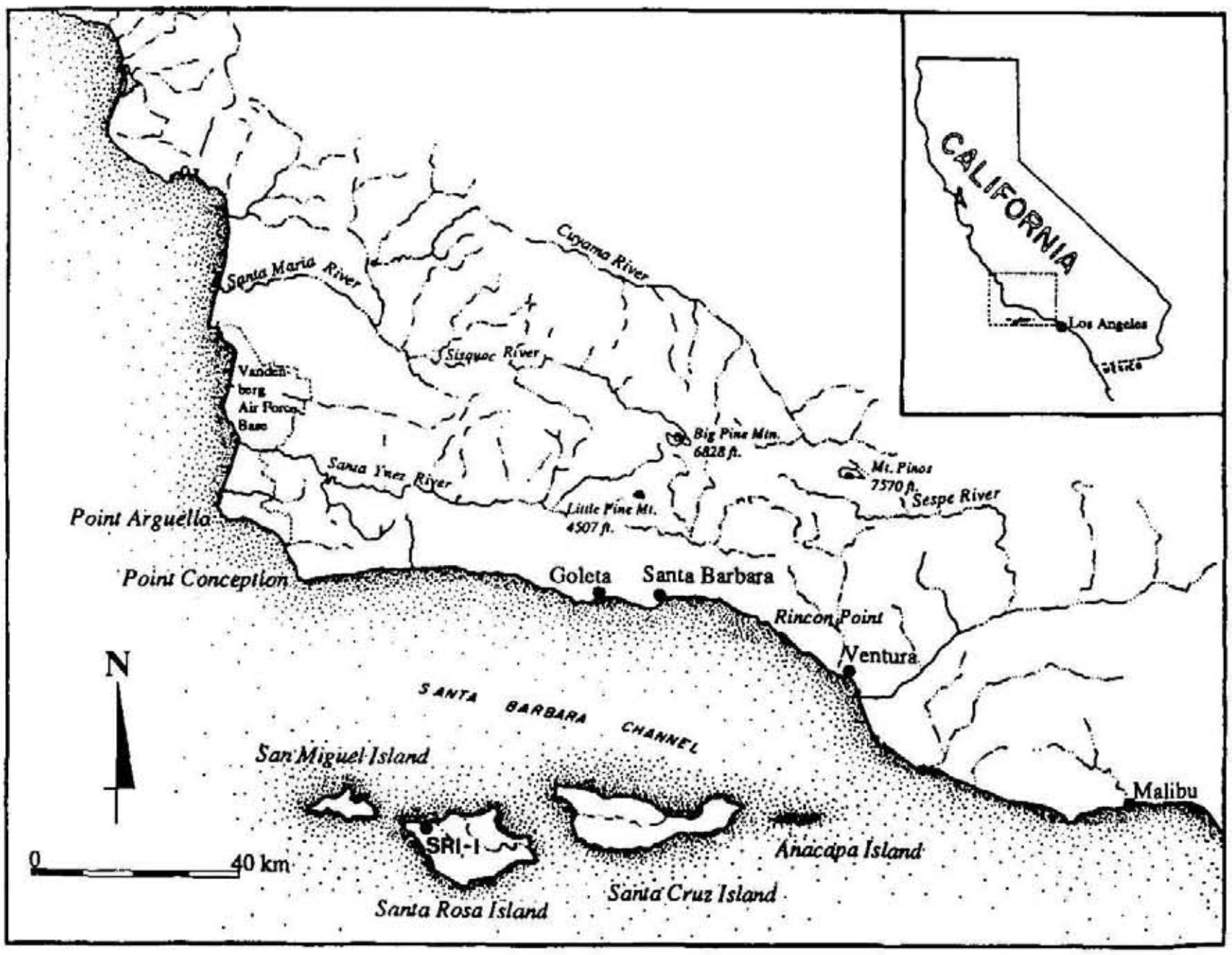


Fig. 1. The Santa Barbara Channel region and the location of CA-SRI-1.

were dated to 12,620 ± 200 and 11,900 ± 200 radiocarbon years before present (RYBP), respectively. Considerably younger than the controversial mammoth kill and fire areas, these shell deposits have received little scientific attention. As research pushes the age of California's earliest coastal sites back to 10,000 or more years (e.g., Simons et al. 1985; Erlandson et al. 1987; Jones 1991; Salls 1991), however, the antiquity of Orr's proposed Pleistocene middens becomes less anomalous and their contents potentially more important. If their age and cultural origin were confirmed, for instance, they would be the earliest coastal sites in the Americas, predating the widespread Clovis tradition and supporting Fladmark's (1979) theory that an early coastal migration contributed to the peopling of the New World.

Given the importance of these issues, we reexamined Orr's early shell-bearing deposits on Santa Rosa Island and his arguments for their potential antiquity and cultural origin. Orr described Pleistocene middens at Garanon Point (CA-SRI-1), Tecolote Point (CA-SRI-3), Survey Point (CA-SRI-5), and Radio Point (CA-SRI-26). We completed preliminary surveys of Tecolote and Survey points, with carbon 14 (C14) dates on the lowest middens of 6,585 ± 60 (Beta-33936) and 7,360 ± 100 RYBP (Beta-33937). Both sites are very large and complex, however, and additional research is needed to rule out the presence of earlier midden deposits in sea cliff exposures.

In this paper, we present new data on the age and stratigraphic context of a previously undated multicomponent shell midden (CA-SRI-1) located near Garanon Canyon. At CA-SRI-1, we almost certainly have identified features described by Orr (1968), dated three shell midden strata in a thick sedimentary sequence exposed in sea cliff and canyon wall exposures, and made observations on the distribution of artifacts and shellfish remains in various strata of Holocene and late Pleistocene age. Our results lead us to question Orr's claims about the age and cultural origin of his Pleistocene middens of Santa Rosa Island.

Garanon Point Locality (CA-SRI-1): Stratigraphy and Chronology

Orr (1968) described CA-SRI-1 as a stratified midden where marine shells and human bones potentially of Pleistocene age were observed more than 9 m below the surface of an uplifted marine terrace covered with fluvial and eolian sediments:

> West of the mouth of Canada Garanon and on the east bank of Jaw Gulch is a large site composed of water-laid sediments and sand dunes built on the Dume platform with the usual "black" humus midden lines in the Pleistocene deposits. . . . Weathered human bone has been found at a number of places during the past 20-odd years since the site has been under observation but, while a human cranium was found at a depth of 20 feet and human limb bones found only 6 inches above mammoth bones, all we can say now is that the site is very old and, in spite of various

other evidences suggesting association of mammoth with human bones, they cannot be proved.

Elsewhere, Orr (1968) referred to shell midden deposits 15 cm above mammoth bones exposed in the sea cliff at CA-SRI-1.

In 1989 and 1991, we visited the site and found many of the features described or depicted in Orr's book, field notes, and photographs. We found at least four discrete shell-bearing eolian or fluvial strata in the complex and highly dissected sea cliff and canyon wall exposures near the mouth of Jaw Gulch (Fig. 2). Three of these have been C14 dated, providing the first absolute dates for the shell-bearing strata at the site.

The uppermost of these is an extensive shell, bone, and artifact-bearing midden that extends for more than 100 m along the canyon rim and sea cliff. A single black abalone (*Haliotis cracherodii*) shell removed from the lower part of this midden stratum was dated by Beta Analytic, Inc., to 2,770 ± 70 RYBP (Beta-56703). After calibration and various corrections (Stuiver et al. 1986), this date is equal to about 2,200 ± 100 calendar years before present (cal B.P.). Roughly 1 m below this upper midden is another extensive shell midden depicted in one of Orr's photographs. This midden extends for at least 80 m in sea cliff and canyon wall profiles. The density of shell refuse is relatively low in areas, but concentrated in others. Bone refuse and artifacts are rare, but several crudely flaked cobble tools were found in situ within the nearly vertical sea cliff exposures. A red abalone (*H. rufescens*) shell from this intermediate



Fig. 2. Sea cliff profile at CA-SRI-1 (*A* = midden dated to 2,200 cal B.P., *B* = midden dated to 7,150 cal B.P., *C* = midden dated to 9,050 cal B.P., and *D* = approximate location of abalone shell in Pleistocene deposits).

midden was dated to 6,420 ± 95 RYBP (Beta-34923), equal to about 7,150 cal B.P.

Another 1 m or so below this intermediate midden, confined to sea cliff exposures extending for no more than 15 m, is a thin lens of marine shell fragments. The shells are primarily from large California mussels (*Mytilus californianus*), though black abalone and barnacle (*Balanus* spp.) shells also were noted. The shells are found in the upper 5–10 cm of a well developed paleosol, including some at the contact with overlying sediments—dune sand to the west and yellow alluvium to the east. Some shells are just 10 cm above a scatter of mammoth bones found in situ near the top of the well-developed soil. This stratum seems to correspond to Orr's locality where midden and human bones reportedly were found about 15 cm above mammoth bones. Mussel shell fragments collected from this shell lens were C14 dated to 8,320 ± 105 RYBP (Beta-34922), equal to about 9,050 cal B.P. No artifacts were found clearly associated with this shell lens, but the concentrated nature of the shells suggests that they may be of cultural origin (cf. Erlandson 1991). Until further data are forthcoming, however, the cultural origin of the 9,000-year-old shell at CA-SRI-1 will remain uncertain. For the purpose of this paper, our main point is that the shell deposit Orr associated with mammoth bones dates not to the Pleistocene, but to the early Holocene, well within the known period of human occupation of the Channel Islands (Erlandson 1993).

An even older shell-bearing stratum exists at CA-SRI-1, one that may shed some light on Orr's thinking about the cultural origin of marine shells found in Pleistocene deposits on Santa Rosa Island. We identified an isolated black abalone shell exposed in the sea cliff near the base of the sequence, clearly in situ within a stratum of fluvial sediment several meters below the mammoth bone-bearing soil. Unfortunately, this abalone shell was lost to erosion before it could be collected, but its stratigraphic position below a heavily calichified eolianite leaves little question about it's late Pleistocene age. Lithified fossil shell fragments from raised beach deposits located upslope are found in this same stratum and there is no evidence that this lowest abalone shell was deposited by humans.

Discussion

Orr (1968) believed that isolated shells in the Pleistocene terrestrial sediments of Santa Rosa Island provided clear evidence of human occupation. Human deposition of such abalone shells is one possibility, but others should be considered. One alternative is fluvial redeposition from abalone shell-bearing fossil beaches described by Orr (1968) for raised marine terraces at elevations of about 8, 23, and 75 m above sea level. Shells found in the lowest of these terraces, which probably dates to the Last Interglacial, are unlithified and well preserved, and include many species common in Holocene middens of the area.

Some of Orr's critics suggested that animals transported abalones and other shellfish from the beach to upland landforms, leading to the incorporation of shells in terrestrial sediments. Orr ridiculed this idea, claiming no animal could pry a large abalone from the rocks and carry it a substantial distance inland. Facetiously, he suggested that

> . . .the dwarf mammoth, a lover of water, equipped with long tusks which are ideally suited as prize bars and with a long proboscis with its sensitive "finger," was the only quadruped capable of securing the abalones and carrying them inland. Anyone familiar with the necessity of pounding the meat of an abalone to make it tender will immediately recognize that the heavy molar teeth of the elephant are ideal for this purpose (Orr 1968).

What Orr did not consider was natural mortality in shellfish populations, and the scavenging and transport of dead invertebrates off the beach by a variety of carrion-eaters. We have observed relatively fresh abalones and other marine shellfish on coastal terraces of the Channel Islands, some suspended in bushes with scraps of meat still attached. These almost certainly were transported by non-human agencies. Some of the smaller shells may have been dropped by carrion-eating ravens and sea gulls which still live on the island. Potential scavengers for red abalones and other large shellfish include condors, which lived on Santa Rosa Island prehistorically, and bald eagles, which occupied the island into historic times. On the northwest coast of North America, bald eagles eat abalones and other shellfish, and routinely steal food from other shellfish-eaters such as gulls and sea otters (Stalmaster 1987). Furthermore, bald eagles sometimes fly inland with food to escape competitors and can carry objects weighing 5 kg or more, considerably more than the proverbial 6-pound abalone Orr (1968) thought only humans could carry.

Conclusions

In the past, many archaeologists (ourselves included) have assumed uncritically that marine shells in archaeological sites are of cultural origin (Claassen 1991). Having completed a cursory review of a number of Pacific coast birds and mammals that eat shellfish and transport the remains onto land, it is clear that such assumptions often are tenuous. This is particularly true in the absence of substantial midden accumulations or other evidence of associations between artifacts, features, and the shell refuse found in a deposit. Before concluding that scattered marine shells found in open air or cave sites are of cultural origin, archaeologists should carefully evaluate a range of biological and geological processes that might account for their origin.

Thanks to Orr and other researchers, there is fairly conclusive evidence that humans occupied California's Channel Islands by at least 10,000 years ago. The earliest well-documented archaeological site on Santa Rosa Island may be the Arlington Man skeleton (CA-SRI-173) from which charcoal and human bone

samples have been dated to about 10,500 years ago (Orr 1962; Berger and Protsch 1989; Erlandson 1993). Three samples of gelatin or amino acids extracted from human bone from CA-SRI-116 on the northeast coast of the island produced an average age of about 8,700 RYBP, or about 9,600 cal B.P. As noted above, the earliest potential shell midden at CA-SRI-1 has been dated to about 9000 years ago, well within the known period of human occupation for the California coast and the Channel Islands.

Unambiguous evidence for an earlier occupation of the Channel Islands remains elusive. More work is needed before Orr's Pleistocene middens can be confidently rejected as archaeological sites. With the data presently available, however, Orr's arguments against a natural origin for marine shells in late Pleistocene terrestrial sediments are not convincing. There are both geological and biological sources for such shells that seem to be more plausible than human intervention.

Acknowledgments

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Conducting a Biological Survey: A Case Study From Sequoia and Kings Canyon National Parks

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Abstract. In 1985, we initiated a plot-based parkwide survey of vascular plants using a randomized systematic sampling design based on 1-km grid intersections. We emphasized an exhaustive enumeration of plant species on 0.1-ha circular plots, took additional measurements of dominance, and recorded abiotic environmental factors. The sampling methodology selected was intended to cover the full geographic extent of the parks and to test the validity of existing vegetation classification systems at the cost of some efficiency in species detection. We reviewed the advantages and limitations of conducting such a survey without developing a priori hypotheses; data management and quality control; and linkages with geographic information systems. Surveys of this kind, while suffering from significant limitations, can contribute substantially to the understanding and management of park systems.

Key words: Biological survey, resources inventory, Sequoia, Kings Canyon.

The National Park Service faces accelerating challenges in protecting the natural resources in its charge. Accelerating regional and global anthropogenic forces — insularization, air pollution, loss of natural fire regimes, and global climate change, for example — are insidious in their behavior and ominous in their long-term influence on wild ecological processes. If resource protection programs within parks and policies designed to protect natural resources are to be successful, they must be supported by knowledge of the state of those resources, the direction and rate of change, and the nature of the processes affecting those resources. Moreover, advances in scientific understanding of community and ecosystem ecology, particularly if conservation is the goal, must be based on accurate and comprehensive empirical data.

In 1987, the National Park Service formally adopted a policy that mandates programs of systematic inventories and long-term monitoring of natural resources. Minimum and preferred standards of information resolution and accuracy have since been developed (National Park Service 1991, 1992). In 1985, research biologists at Sequoia and Kings Canyon national parks initiated a biotic survey of vascular plants and vertebrate animals based on 0.1-ha plots placed at 1,000 m Universal Transverse Mercator (UTM) grid intersections. This Natural Resources Inventory is the most ambitious element in a program designed to gather and organize data about the resources of the parks, and to array them first as relational computer databases and thence within the framework of a geographic information system (GIS; Graber 1987; van Wagtendonk and Graber 1990). Other elements in the program include incorporation of data from published literature and archival materials containing geographically-referenced natural resources data; validation, enhancement, and compilation of the parks' plant and animal collections; incorporation of nonsystematic records of biota; and integration of past and current vegetation cover maps.

In this paper we review the botanical aspects of the biological survey. We discuss our objectives for the survey, the basis of the methodologies selected, and the degree to which the survey has been successful at meeting the initial objectives and responding to new questions.

Site Description

Sequoia and Kings Canyon national parks are located in the south-central Sierra Nevada of California (Fig. 1). The two parks are contiguous and form an International Biosphere Reserve of 349,525 ha that falls within the Sierra Nevada–Cascade biogeographic province of Udvardy (1975). Altogether, 95.6% of the reserve is either designated or proposed statutory wilderness; an additional 2.4% is without development and is managed as wilderness.

The parks are bounded on the north, east, and south by National Forest lands mostly designated as wilderness but used also for timber harvest, grazing, reservoirs, and recreation. Lands to the west are largely private, are devoted to ranching and farming, and contain villages. The eastern boundary is delineated by the crest of the Sierra Nevada; the remaining boundary is a combination of watershed, river, and artificial demarcations. The reserve ranges from 400 to 4,418 m elevation, constituting a portion of the western slope of the Sierra Nevada that rises gently to the Pacific Crest. The eastern slope of the range is an escarpment that drops sharply into the Owens Valley and the Great Basin. Four river systems, the Kaweah, Kern, Kings, and San Joaquin, drain the parks to the west into the San Joaquin Valley. The terrain of the reserve is largely mountainous: 83% of park lands are above 2,100 m elevation. The climate is Mediterranean with warm, dry summers and cool winters, during which most precipitation falls. Above 2,000 m, the bulk of precipitation is snow. Vegetation is varied and includes chaparral, oak woodland, upland hardwood forest, conifer forest, meadows, and alpine plant communities (Vankat 1982).

History of Biological Survey and Related Activities at Sequoia and Kings Canyon National Parks

For these national parks, as for other large natural-area parks established long ago, much of our information about natural resources was collected during the first half of this century. Before the present decade, the systematic collection of information about most park resources in Sequoia and Kings Canyon national parks was largely the product of short-term, specialized efforts by a few individuals. That data base is no longer adequate to manage the parks: It lacks

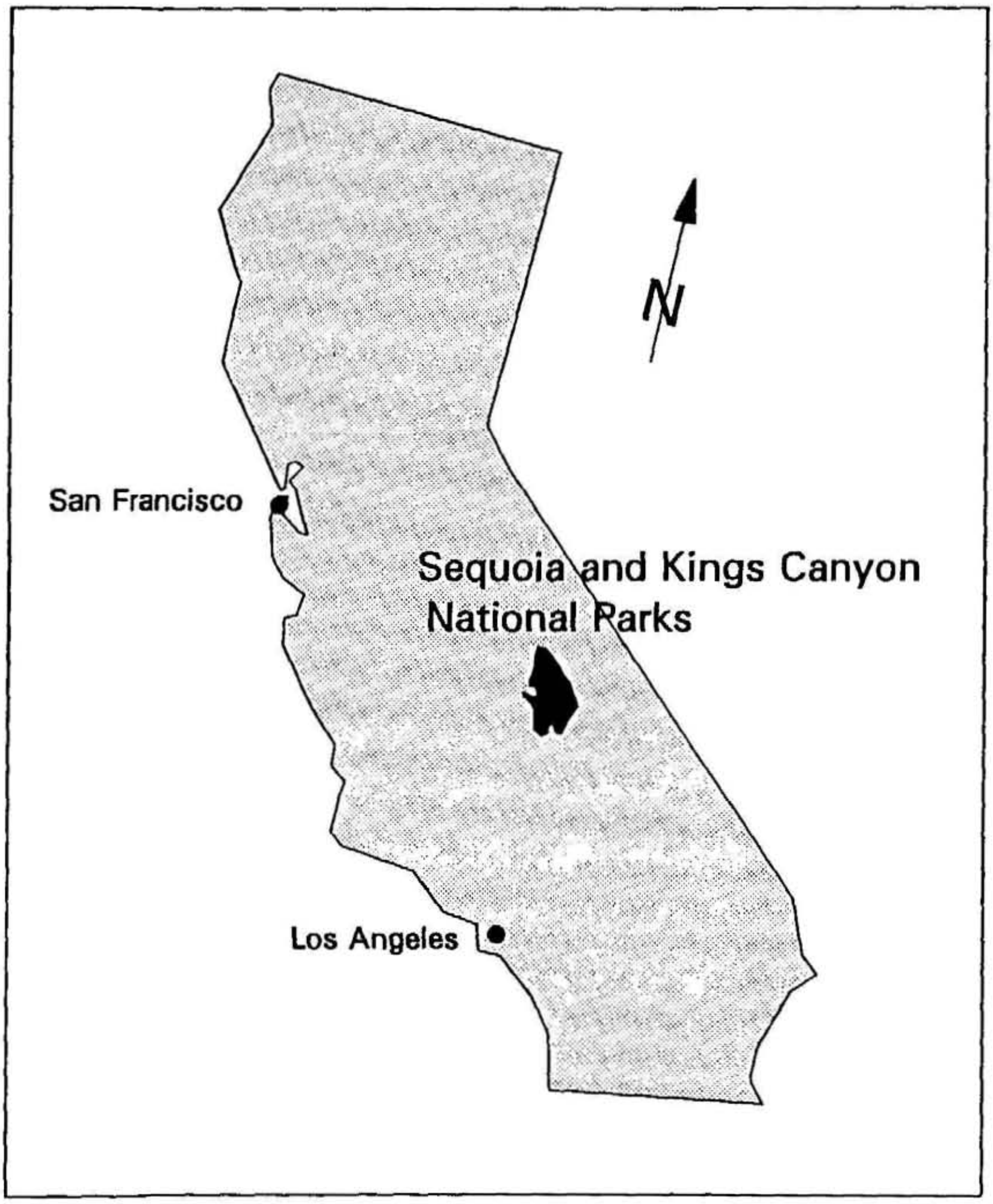


Fig. 1. Location of Sequoia National Park and Kings Canyon National Park in the southern Sierra Nevada of California.

the technical sophistication and theoretical underpinnings of modern science and is frequently inaccurate and incomplete (Stohlgren and Quinn 1992).

Early descriptions of vegetation were developed in conjunction with Sierra Club outings over the first half of the 20th century (Eastwood 1902; J. T. Howell, Sierra Club reports, National Park Service, Three Rivers, California, unpublished data), as well as through pioneer investigations by field botanists including Frank Smiley (1921), Carl Sharsmith (National Park Service, Three Rivers, California, unpublished report), and Peter Raven (1961). The first efforts at mapping vegetation of Sequoia National Park took place during the late 1920's and early 1930's, leading to a published map (Frost 1935) that was used for several decades and remains important as the earliest record of park vegetation patterns. Using their field observations and available records, two park naturalists compiled a listing of the park's flora during the 1960's. They also used general range maps as surrogates for empirical data (Rockwell and Stocking 1969). Vankat (1970) conducted one systematic scientific study of vegetation change in the parks during this time.

The giant sequoia (*Sequoiadendron giganteum*) was surveyed under contract during the 1960's and 1970's (Hammon, Jensen, and Wallen Mapping and Forestry Services, National Park Service, Three Rivers, California, 1964, 1975, and 1976 unpublished report; Western Tree Service, National Park Service, Three Rivers, California, unpublished report). During the same period, the National Park Service contracted for production of conventional timber type maps from aerial photographs and a contemporary map base covering both Sequoia (Natural Resource Management, National Park Service, Three Rivers, California, unpublished report) and Kings Canyon (Hammon, Jensen, and Wallen Mapping and Forestry Services, National Park Service, Three Rivers, California, 1970 unpublished report) national parks. A reconnaissance survey of plant species with potential for listing under the Endangered Species Act was completed for portions of the parks (Norris and Brennan 1982; Norris and Parsons 1984). A comparison with International Biosphere Reserves in other Mediterranean ecosystems (Macdonald et al. 1988) found a relatively low level of invasion by alien vascular plants and vertebrate animals, but a comparatively low level of confidence was given to the information on which that finding was drawn.

In 1982–83, J. F. Franklin and a team of scientists based at Oregon State University conducted a so-called pulse study of forest structure at two sites in mixed conifer forest. That work developed exhaustive plant lists and diagrams of forest composition and structure (Riegel et al. 1988). Based in part on this example, the National Park Service established permanent terrestrial vegetation plots in subalpine, montane, and foothill elevation zones as part of research on the effects of acid precipitation on terrestrial ecosystems (Evison 1985; Parsons and Graber 1985; Stohlgren et al. 1991). Also during this period, Stephenson (1988) conducted an environmental gradient analysis of park vegetation, and Anderson (1990) began reconstructing vegetation change over the past 10,000 years using pollen analysis.

In 1952, J. Moore (1963) of the Geological Survey initiated systematic mapping of surficial geology of the entire parks region, an effort now nearing completion. As part of acid precipitation studies pursued during the 1980's, Huntington and Akeson (1987) developed Order 4 soil maps for a portion of the Kaweah River watershed—the only significant soils maps available for the parks.

The studies listed above, as well as many other more narrowly focused efforts at resource information gathering, are documented in the parks' research bibliography (Parsons and King 1980; Parsons and Haggerty 1986). This bibliography has been compiled as a computer data base.

Objectives

From the outset, this biological survey was designed to serve four distinct objectives. These were an inventory of vascular plants, establishing a baseline for monitoring vegetation change, providing a basis for establishing correlative autecological relations, and constructing and evaluating vegetative land cover classification models.

Inventory of Vascular Plants

We decided to enumerate all vascular plant taxa (to subspecies level) and to establish their geographic and ecological distribution throughout the parks. Such a data set is necessary to support the intent of the Endangered Species Act of 1973 (U.S. Code 87 Stat. 884; 16 USC 1531 et seq.) as amended and is now required by Natural Resources Management Guidelines (National Park Service 1991). This basic listing is a prerequisite of planning for development or other landscape disturbance where prior knowledge of the biota is necessary for protective interventions or if an area is subject to disturbance.

There is pedagogical basis for this enumeration as well. The more accurate and comprehensive a picture of park biota developed, the more valuable a source of information it is for park naturalists and others who use knowledge about the parks as a platform for instruction, dialogue, or simply to enhance the pleasure of visitors. This constitutes the social value of biological survey.

Baseline for Monitoring Vegetation Change

We originally intended that a subset of plots would be revisited periodically to record change. This objective was revised (as explained below) so that the intention became to provide an empirical basis for stratifying the parks by vegetation and then selecting long-term monitoring plots. Thus, the initial biotic survey, which would require a decade or longer to complete, would provide geographic breadth and capture the parks' biological diversity, while sites selected for long-term monitoring would be designed to capture the portion of that diversity most amenable to and appropriate for monitoring. However, all plots would be marked permanently so that any of them could be revisited.

Basis for Establishing Correlative Ecological Relations

By collecting information about the presence and relative importance of vascular plants, vertebrate animals, substrate, terrain, and other ecological elements at a matrix of sites, we intended to provide the basis for describing and understanding species–environment (and species–species) relations. This was to include, for example, estimating the realized environmental niche of each vascular plant species and determining if there are predictable guilds of understory plant species associated with specific overstory species. This a posteriori approach to ecological analysis is less powerful than research driven by a priori hypotheses. It serves, however, as an effective first-stage filter—where hundreds of species and a substantial number of environmental variables are involved—for the later construction of efficient hypotheses.

Construction and Evaluation of Vegetative Land Cover Classification Models

High-resolution, geographically rectified vegetative land cover or plant community maps are highly desirable for a variety of management and scientific purposes. For large land areas, these often can be produced most economically by employing satellite-based remotely-sensed images produced by Thematic Mapper or SPOT sensors combined with terrain data in a geographic information system (Davis and Dozier 1990). Because of the physiographic as well as vegetative complexity of the parks, a large number of points of empirically-measured vegetation are required to develop and to test classification models. The biological survey was intended to provide such ground truth points. Conversely, our decision to select sample plots independently of perceived vegetative composition, by using the UTM grid as our sole selection criterion, was intended to permit testing of vegetation classification systems and to evaluate the objective reality of nominal plant communities as well as their boundaries or ecotones.

Literature

Sampling and subsequent description of vegetation are intrinsically influenced by the underlying philosophy and objectives of the investigator. The development of vegetation science during the last century has been marked by the emergence of two dominant approaches. Most widely accepted (outside North America) for the classification of vegetation associations is the floristic approach of the Zurich–Montpellier School of Phytosociology, developed by Braun-Blanquet and Rübel in the 1930's (Barbour et al. 1987). The fundamental tenet of this school is that distinct species combinations exist (i.e., plant communities), which repeat themselves regularly in nature. Samples (relevés) are chosen subjectively, and plot size varies with the scale and complexity of the

vegetation studied (Becking 1957). Traditionally, sites are placed in vegetatively homogeneous stands, avoiding transitions and edges of types.

This contrasts with the North American School, which found its origins in work by Gleason and Ramensky, and was formalized by Whittaker (Barbour et al. 1987). The North American approach rests on the principle that most communities intergrade continuously with one another along environmental gradients, rather than forming distinct, clearly separated zones. Using this approach, emphasis is placed on studying the relations of vegetation to environment along gradients (Whittaker 1975). Samples are consequently selected objectively in relation to perceived vegetation types, but in environmentally homogeneous locations.

Both of these approaches have been used to describe vegetation patterns in the Sierra Nevada. As a part of the Vegetation Type Map Survey of California begun in the 1930's (Wieslander 1935), hundreds of subjectively placed plots were established throughout the Sierra Nevada (Colwell 1977). Under the direction of J. Major, subalpine and alpine vegetation has been described by Pemble (1970), Taylor (1976), Burke (1982), and Benedict (1983) using the phytosociological techniques of the Zurich–Montpellier School (Parsons 1982). Vankat used subjective techniques to place transects in homogeneous vegetation along an elevational gradient in Sequoia National Park (Vankat 1970, 1982). Rundel et al. (1977) built on this work and others to describe Sierran vegetation types relative to elevation and moisture. Following the approach of R. H. Whittaker, Stephenson (1988) used a strict gradient analysis approach to describe the relation between climate and vegetation in Sequoia National Park. Work by Parker (1989) in Yosemite National Park also relied on gradient analysis techniques in describing forest types.

Sampling Design

Sampling was based on a randomized systematic design. The units of sampling were points and their neighborhoods, located on 1-km UTM grid intersections, as indicated on the USGS 7.5– topographic map series. Final plot location was determined by traveling a random distance (0–99 m) in a random direction (0–359 degrees) after a selected UTM intersection had been located. This randomization served to remove the effect of observer bias on plot location. All vegetation measures were conducted within a 17.84-m radius of the plot center, thus yielding a 0.1-ha circular plot.

Sampling Rationale

The resource inventory is a neighborhood description wherein sampling radius about the coordinate point varies according to the scale and mobility of each class of organism (Lund 1982). Thus, large organisms, such as trees, and mobile organisms, such as birds, were sampled over a greater area than were

herbs or amphibians. Sampling was center-weighted (Fig. 2). No effort was made to place sampling points in homogeneous habitat, as is done conventionally with relevés (Mueller-Dombois and Ellenberg 1974:46). That would bias sampling against ecotones, underreport variability of the physical and biotic environment, and undermine the value of the sampling to test existing classification schemes.

Plot Design

We selected 0.1-ha circular plots as the principal sampling unit for several reasons. Conceptually, we are describing the neighborhood of a point at varying degrees of resolution and scale. Therefore, fine resolution measures, such as cover of herbaceous species, were taken relatively close to the origin using 1-m^2 quadrats, while large-resolution measures, such as plant community types, were taken within a radius of 100 m, describing about 3 ha. In addition to the convenience of establishing only a single point in the field, selection of a circular plot yields increased accuracy, as there is less perimeter to consider than when working with square or rectangular plots (Barbour et al. 1987). However, to maintain our freedom to compare results with traditional plot-based vegetation sampling, as many measures as were feasible were taken within a radius of 17.84 m to yield a 0.1-ha sample unit. We elected to calculate distance and area projected along the ground surface rather than as a map projection. Our system more accurately reflects growing space for herbs and shrubs where canopies are generally parallel to the ground surface. It is less accurate for trees, where access to light is best described by map-projected area.

Dominance

We measured cover independently for each of three strata of vegetation: herbs, shrubs, and trees. Cover was selected as the principal index of within-plot

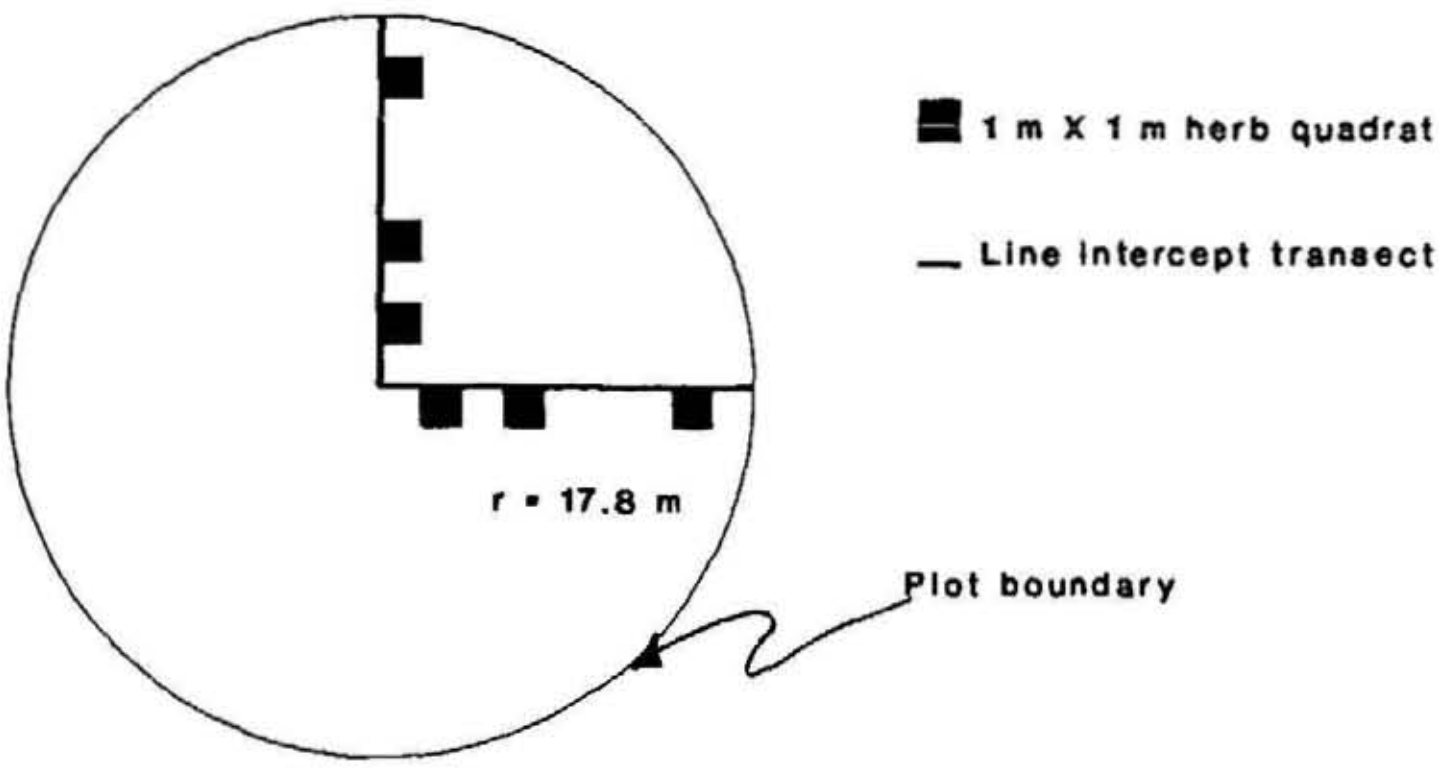


Fig. 2. Schematic diagram of 0.1-ha circular plot used in vegetation sampling.

biological dominance: It is more easily quantified than is density (Shimwell 1972) and is a better measure of plant biomass. Biomass reflects the ability to fix energy and is directly related to influences on the surrounding environment such as light, moisture, nutrient flux, and temperature (Mueller-Dombois and Ellenberg 1974). We accept Daubenmire's (1959) restatement of Lindsey (1956) that "canopy coverage is the most important single parameter of a species in its community relations." It is also most frequently measured, providing the opportunity to compare with other studies. Cover is, however, substantially less useful than is density of individuals in comparisons of biological diversity (Magurran 1988). As a consequence of time and budget constraints, we declined to measure density of herbs and shrubs.

Sampling Intensity

An initial sampling density of one point per square kilometer was selected, yielding approximately 3,500 possible plots covering 0.1% of the parks' areas. This initial approximation was derived from the assumptions that, under ideal budgetary conditions, no more than 300 plots could be completed in a field season, and that it was unwise to design a project that would take more than a decade to complete. Conversely, we chose a grid of convenient scale that was sufficient to capture the underlying terrain variation of our region. We used this design and stratified the initial sampling to approximate physiographic diversity and the geographic extent of the parks—we lacked the information to stratify by vegetation type. We assumed that we could later safely reduce the number of potential plots based on the development of an accurate vegetation map and an assessment of variability among existing plots within each vegetation type.

Sampling Methodology

General Plot Data

We intentionally clustered plots to reduce backcountry travel costs. We attempted to distribute these clusters as evenly as possible throughout the parks and to sample exhaustively within an affordable travel radius of each base camp over 3–12 days. Additional constraints on plot selection included inaccessibility of potential plots because of terrain, high water, or poison oak (*Toxicodendron diversilobum*). Safety was the most important factor in this type of inaccessibility. The date selected for sampling a plot cluster was determined largely to yield optimal phenological conditions for plant identification. Plots otherwise accessible but markedly retarded in phenological development because of elevation or aspect may not have been sampled. The park GIS was used in latter years to indicate underrepresented terrain classes and thus suggest locations for sampling.

Plot Location

Location of each plot was documented through the use of USGS topographic maps and the UTM grid system, with the northing and easting of the original UTM intersection and the offset from this point recorded for each plot. Because we used traditional orienteering methods to find grid intersections, accuracy of plot location varied. Uncertainty of the location was described by estimating the maximum possible distance, in meters, between the calculated ground location of the UTM intersection and its true location.

We marked each plot near its center either with a numbered stainless steel stake, tagged fiberglass stake, or numbered aluminum tag attached to a stable rock surface with epoxy. Plot markers were located such that they were protected by a boulder or tree from exposure or trampling; the distance and direction to actual plot center was recorded. Measurements were always taken from calculated plot center, not marker position. We used topological (ground surface) distances, not map-projected distances, for all measurements.

Photographs were taken from plot center, facing each cardinal direction, to document fuel cover type and provide a visual record of the plot. We took additional photographs when appropriate to aid in relocation.

Site Description

A physical characterization of the plot was constructed by recording descriptive site characteristics including slope, aspect, and elevation; evidence of fire and of natural or anthropogenic influences; and area of the plot covered by standing or flowing water.

The edaphic environment of the plot was described in three ways. A small soil pit was dug as close to plot center as possible; an approximately 50-g sample of each discernible horizon was collected (for potential future analysis) and its depth measured. Soil depth over the entire plot was estimated in two ways: An ocular estimate of percent of exposed rock was made, and depth was measured using a steel bar at 10 points along the north-south diameter. Finally, we noted the origin of the geologic parent material.

Each site was also described in a detailed narrative that identified the general characteristics of the plot. All vegetation types that appeared on the plot, as well as those that occupied at least 0.10 ha and fell within 100 m of the plot center, were identified and recorded. A modified version of the California Department of Fish and Game Descriptions of the Terrestrial Natural Communities of California (R. F. Holland, California Department of Fish and Game, unpublished data) was used for classification.

Fuels

Downed fuels that intersected a transect congruent with the north radius were tallied in three diameter-size classes and measured in a fourth, according to the methods described by Brown (1974). We measured depth of litter (undecomposed organic material) and duff (decomposed organic material) at five 2-m intervals along the same transect.

Vegetation Data

Herbaceous Layer

A 17.8-m tape was laid due north along the surface of the ground from the plot center. A 1-m^2 frame was placed alongside and right (as viewed from plot center) of this line at distances of 1 m, 5 m, and 15 m (Fig. 2). Relative percentage of cover by each herbaceous species was then estimated by eye. Cover by bare ground, rock, fallen wood, and low shrubs were accounted for, so total cover was 100%. We repeated this procedure on the east radius of the plot, for a total of six herb quadrats.

Shrub Layer

Absolute shrub cover by species was measured along the entire lengths of the north and east radii (17.8 m) and recorded as centimeters of intercept by each shrub or nonshrub category (Fig. 2). Nonshrubs, such as rocks, herbs, trees, or bare ground, were recorded only when acting as placeholders where shrubs were absent. Total cover was therefore at least 1,780 cm but was greater when there were multiple layers of shrubs.

Tree Layer

Diameter at breast height (dbh; 1.3 m) was recorded by species for each tree greater than or equal to 1.3 m height on the plot. Saplings (between 10 cm and 1.3 m height) were tallied only and listed by species. Seedlings (less than 10 cm height) were not counted. Consequently, density of tree species on each plot was recorded for all but seedlings.

Some plots contained shrubby, multistemmed forms of trees. If a species was nominally a tree, but was taking the form of a shrub, it was treated as a shrub and measured on the shrub transect. If it was multistemmed, the diameters at breast height of any stems greater than or equal to 1.3 m in height were measured. If a species exhibited both forms—that is, a multistemmed tree emerging from shrubby branches—the stems were measured as trees and the lower branches measured on the shrub transect. This situation was most often encountered in the mixed north slope (hardwood) forest and in alpine areas that contained krummholz conifer trees.

Additional Species

After the vegetation measurements were taken, a careful search of the entire plot was made for any vascular plants not otherwise recorded. Thus we completely enumerated all species within the 0.1-ha radius area.

Results

Distribution of Plots

From 1985 through 1990, we sampled 517 plots. An additional 29 were completed in 1991 and used for some analyses.

Physiography

We used digital terrain data for the entire parks' areas (30 m spatial resolution, 3–15 m vertical RMS error) in a GIS to measure the physiographic representativeness of the plots completed. The terrain data have a pixel size of 0.09 ha, close to that of plot size; however, calculation of slope and aspect using these data produces significant nonsystematic error when terrain is very steep. As expected, we found an acceptable fit of elevation, except for significant oversampling in the 1,828–2,133-m class (Fig. 3). Similarly, the distribution of plot aspects was similar to that for the entire study area (Fig. 4). As we knew from field experience, we substantially undersampled slopes greater than 30° because we lacked the techniques to sample steep slopes safely (Fig. 5).

Vegetation

We progressively adapted R. F. Holland's (California Department of Fish and Game, unpublished data) hierarchical vegetation classification system to physiognomic–species arrays (associations, such as lodgepole pine–whitebark pine forest) as we discovered them, but occasionally we resorted to distinctive physiographic conditions, such as low angle rock slabs and ledges, that we encountered during fieldwork. From 1985 to 1990 the number of vegetation classes expanded from an initial 24 to 40.

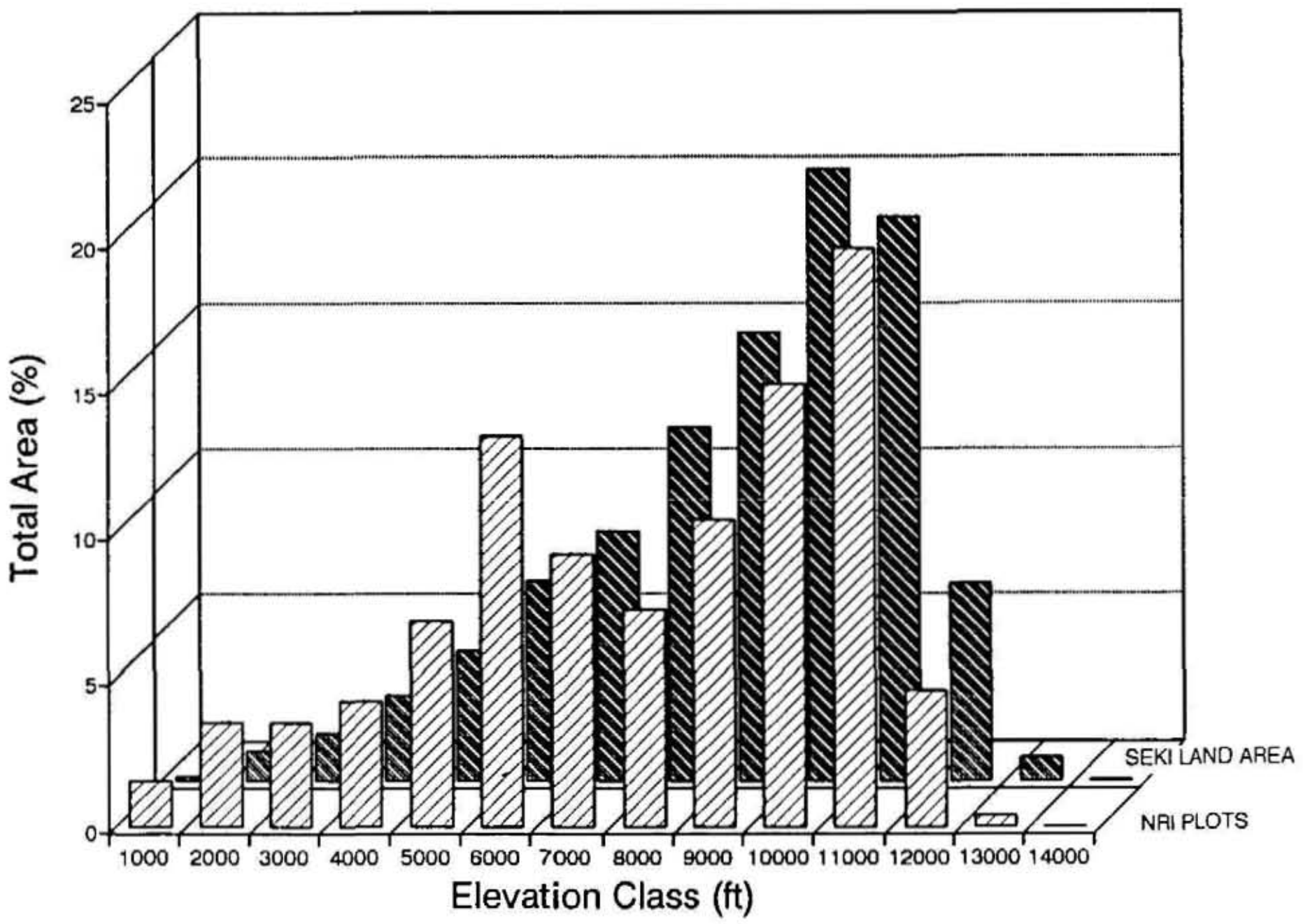


Fig. 3. Distribution of Sequoia and Kings Canyon (SEKI) national parks land area and Natural Resources Inventory (NRI) plots ($n = 547$) by 1,000-foot elevation increments ($\chi^2 = 37.6$, d.f. = 13).

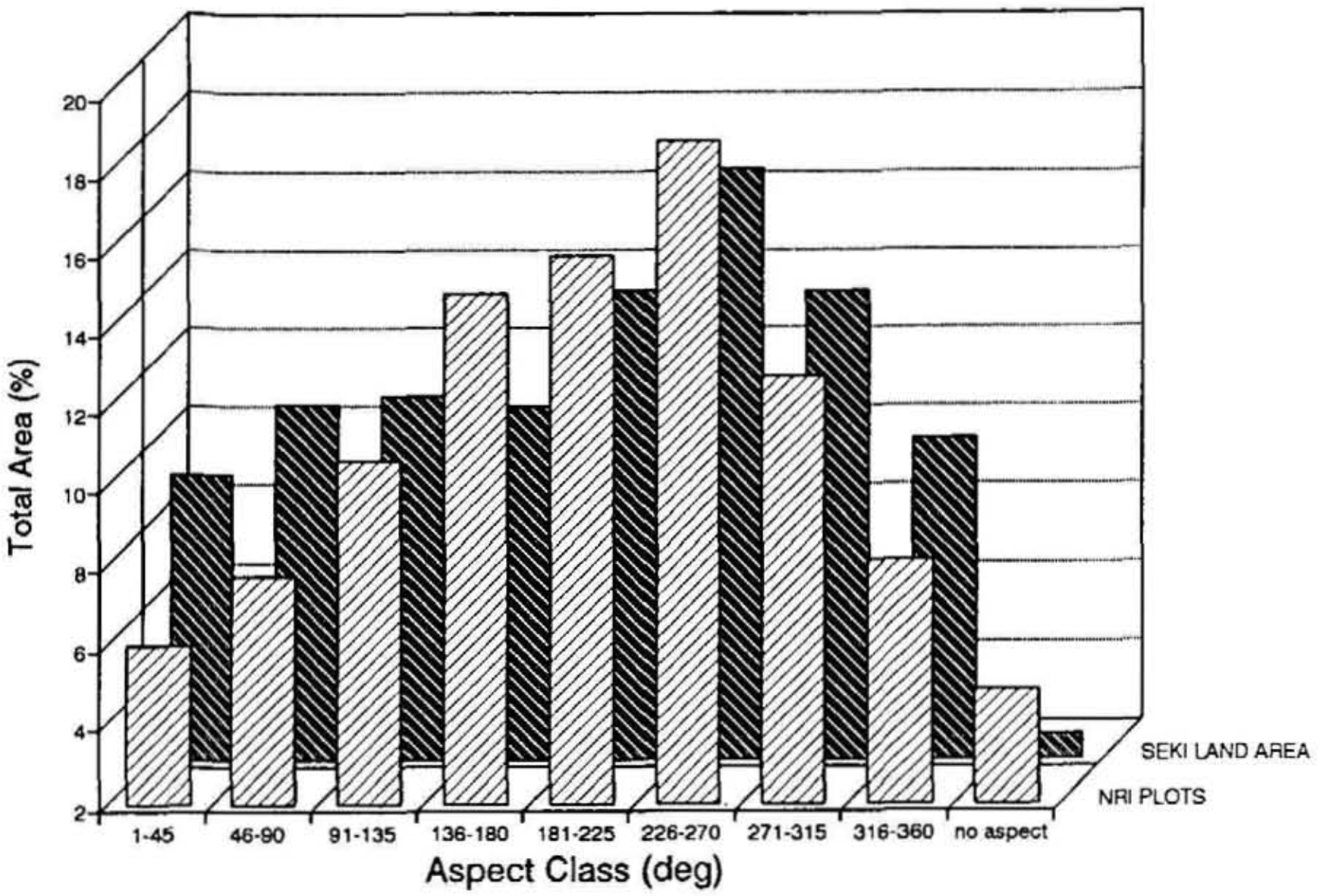


Fig. 4. Distribution of Sequoia and Kings Canyon (SEKI) national parks land area and Natural Resources Inventory (NRI) plots ($n = 517$) by aspect ($\chi^2 = 24.2$, d.f. $= 8$).

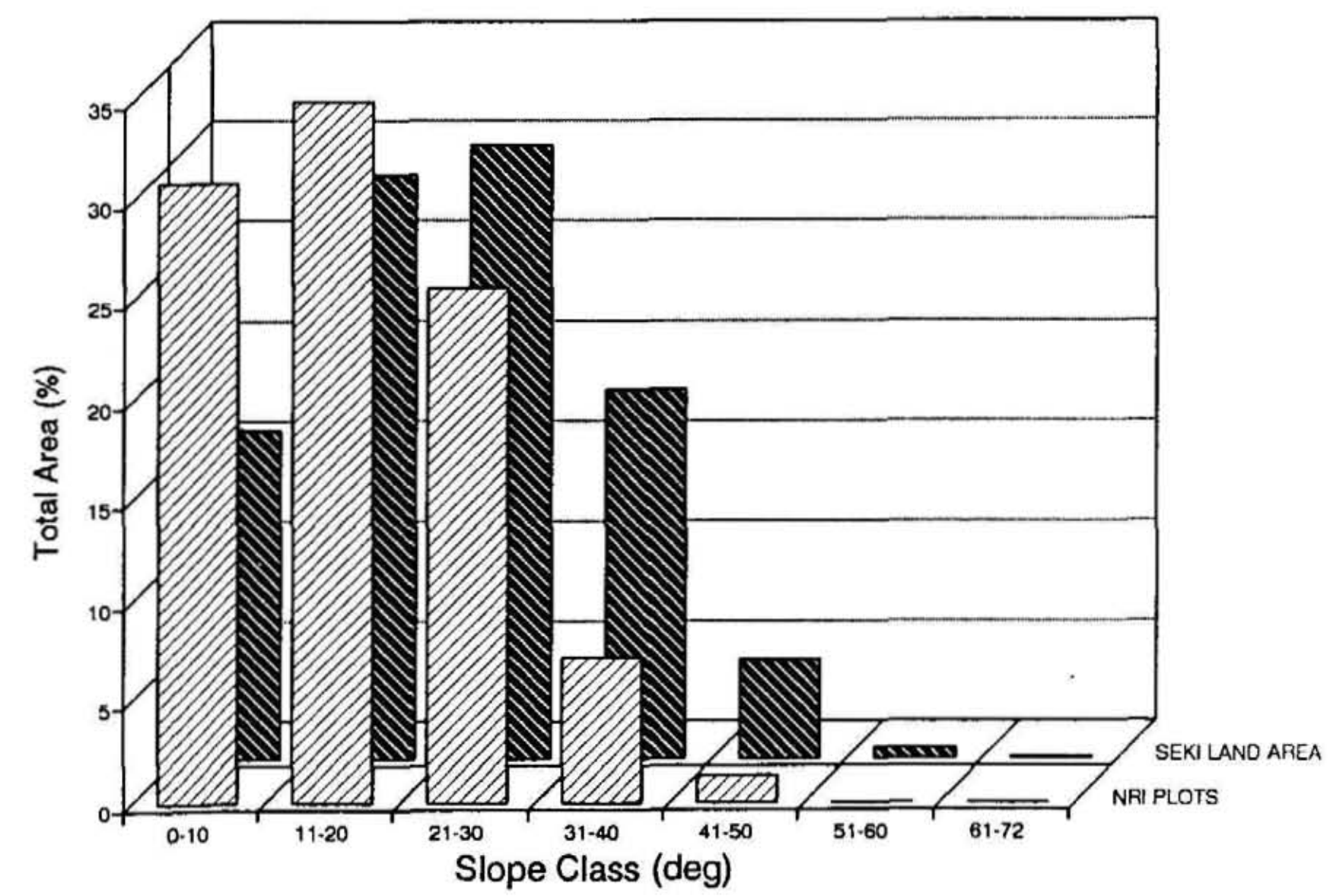


Fig. 5. Distribution of Sequoia and Kings Canyon (SEKI) national parks land area and Natural Resources Inventory (NRI) plots ($n = 517$) by slope ($\chi^2 = 125$, d.f. $= 6$).

Species Discovery

On 517 plots we encountered 860 vascular plant species, 68% of the 1,268 species known from the parks. A plot of the accumulation of species encountered against number of plots, in random plot order to produce a homogenized landscape, reveals that the rate of novel encounters continues to decline with additional area (Fig. 6) in the classic pattern described by Macarthur and Wilson (1967).

The study plots yielded 42 vascular plant species not previously recorded from the parks (Fig. 7). New species were concentrated in the lower elevations where dense chaparral conditions and a limited trail network are not congenial to botanists. Eleven (26%) of those new species were alien, compared with 3 (7%) for the park flora as a whole, suggesting that alien invasions may presently be taking place in the lower elevation boundary zone adjacent to development, where alien species are adapted to its Mediterranean climate and may have benefitted from the past century of disturbance.

Cost of Survey

The biological survey cost $265,300 for 1985–90. This was a mean cost of $513 per plot (one visit), including 33 h of labor. These costs reflect travel and plot sampling time, transportation, specimen identification and preparation,

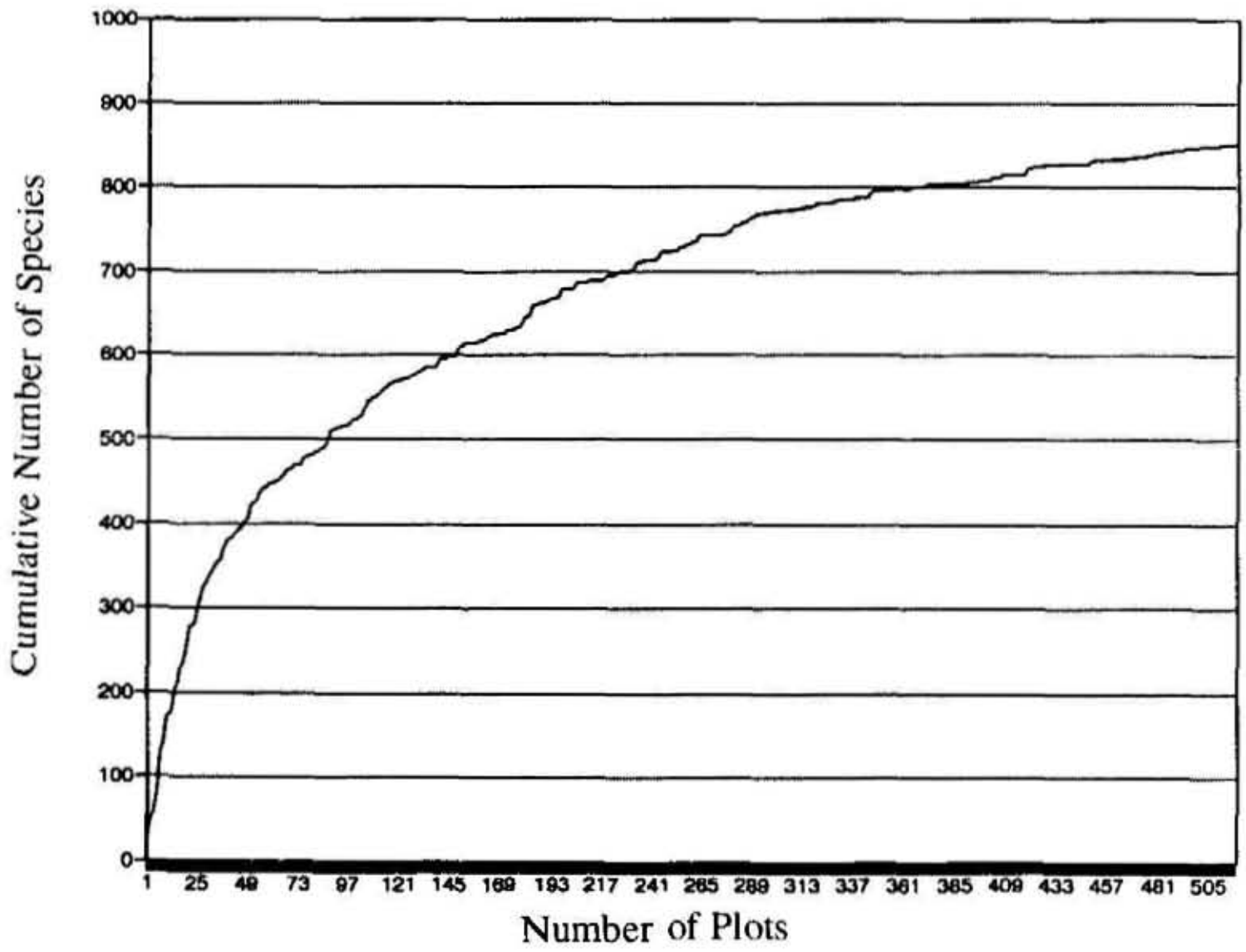


Fig. 6. Cumulative numbers of novel (not previously encountered) species with increasing sample size ($n = 517$). Plots were selected in random sequence to generate the curve.

field equipment, data processing, and data management. They do not include $60 per plot dedicated to faunal work. Fieldwork costs were approximately half the total. Data management, including data entry, quality assurance, and quality control, represented one-third of expenses.

Discussion

The biological survey described here was a compromise among several a priori objectives. As a result, like any general-purpose tool, it accomplished each objective less successfully than a study specifically designed for that objective. However, we believe the combined approach was much more economical than using a series of independent study designs.

Biological Diversity

The power of our survey in measuring ecological diversity (as opposed to simple species richness) would have been substantially increased had we counted individuals of each species (Magurran 1988). This task would have added field time, but judicious sampling could mitigate that problem.

Our decision to describe biomass by measuring cover of herb and shrub layers, but basal area (at dbh) of the tree layer, made it impossible to fully compare plots using all three layers simultaneously. Although estimating cover of the tree canopy is an uncertain and potentially time-consuming business, it would have been preferable to standardize on one parameter. This was addressed in 1992 when woody canopy cover by species was also recorded along the length

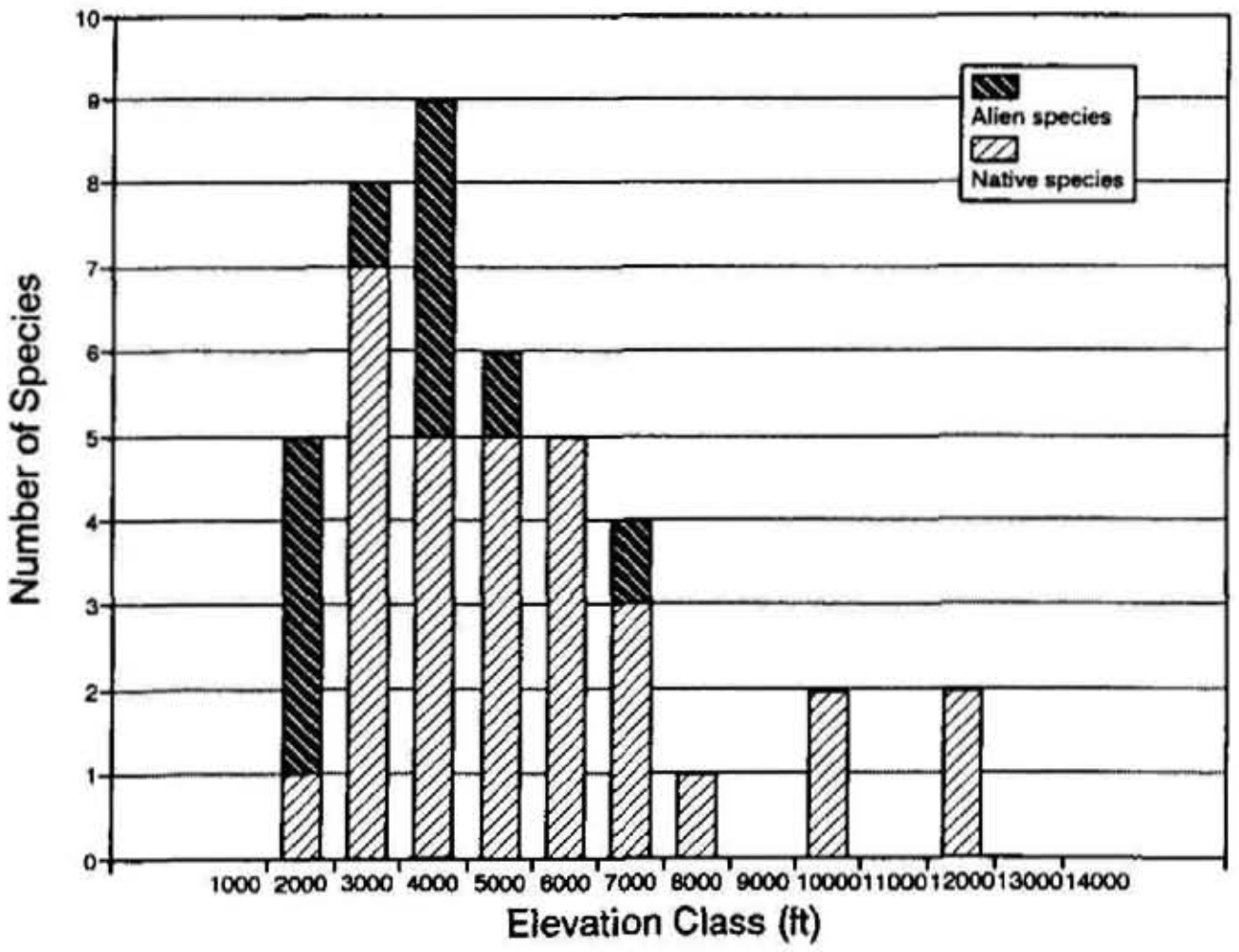


Fig. 7. Distribution of species not previously known from the study area by elevation.

of the north and south radii as 30 points of interception directly above and below the observer at 1-m intervals. Interception was defined as the object hit in the crosshairs of a Canopy Sighting Device. This is a small periscope device with pitch and yaw levels to ensure that aiming it is approximately vertical and unbiased. Simultaneously, ground cover hits at each point were also recorded as bare, rock, litter, wood, herb, or woody species; this will provide a more rigorous estimate of the extent of exposed rock or bare ground on the plot as well as an estimate of woody seedling cover.

Species Enumeration

After more than 500 plots, representing 0.015% of the Sequoia and Kings Canyon national parks area, the survey encountered two-thirds of the vascular plant species known in the parks. Although the survey seems ideal for describing both the geographic and environmental distributions of most species, the classic species-abundance curve (Magurran 1988) indicates that locating rare species may require directed searches or sampling a vastly greater proportion of the reserve. This is reflected by our discovery curve (Fig. 6). On the other hand, the rate of encountering species previously unrecorded in the parks was almost constant through the course of the study.

Remote Sensing Corroboration

Using random plots such as ours to supervise classification of remote sensing imagery is less efficient than either selecting blocks of a common vegetation type and deriving a statistic of reflectance signatures for each a priori type or selecting contiguous blocks of pixels of a common reflectance signature and determining their vegetative composition in the field (J. van Wagtendonk, National Park Service, personal communication). One approach attempted requires one to discard plot neighborhoods that are heterogeneous at a scale of less than 9 pixels (0.81 ha) or for which the signature of the 9-pixel block is heterogeneous. When close correspondence between geographically rectified imagery and ground points is important—as in this exercise—the use of a global positioning device (GPD) with an accuracy of half a pixel (15 m) is highly desirable. A GPD also obviates the need for a highly visible plot marker, which can be lost as some of ours were, and ensures that all plots can be relocated for future comparisons. Many of our plots will be difficult or even impossible to relocate with assurance.

Vertebrate Sampling

We attempted to combine the botanical work described here with comparable vertebrate investigations on the same plots for later species–environment investigations. We found that botanical investigations disturb the plot, affecting the success of small-mammal trapping. Moreover, given the high travel cost of visiting many backcountry areas, detection would be more efficiently accomplished by stratifying animal sampling to capture the scale of local habitats and

the average home ranges of the target species. More work on methods of cost-effective, multispecies detection remains to be done.

Substrate

Although soil is an important environmental parameter because of its moisture-holding and nutrient-bearing capabilities, there was substantial uncertainty associated with our methods for determining meaningful soil depths in the thin and stony soils typical of the Sierra Nevada. We were constrained by time and the weight of tools from collecting enough penetrations at sufficient depth to characterize soil fully on the plots.

Conclusion

The biological survey has serendipitously generated numerous new hypotheses, including questions about the dynamics of alien invasions and the environmental factors underlying observed species distributions. It has stimulated new questions about the nature of biological communities as entities in space and time. Preliminary work on most of these questions can proceed with the existing sampling design, but specialized study designs will be required eventually to test hypotheses with a satisfactory level of discrimination. Nonetheless, in the context of National Park Service budget constraints, an approach similar to the one we have taken does seem to advance important ecological knowledge along a broad front and provides an excellent framework for more narrowly-focused studies.

Acknowledgments

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A Stable Isotopic Study of the Effect of Fog-drip Water on the Point Reyes National Seashore, California

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Abstract. Fog and rain were collected for stable isotopic analysis for 4 years from three locations at the Point Reyes National Seashore in California. The yearly weighted averages of the isotopic compositions of fog water ranged from −16 to −8 per mil in δD and from −2.9 to −2.0 per mil in δ^{18}O. Those of the rain ranged from −45 to −30 per mil in δD and from −7.6 to −5.8 per mil in δ^{18}O. Coastal fogs on the peninsula are consistently and predictably more enriched in deuterium and oxygen-18 than rain because the fog is an early stage condensate produced from a single cycle of evaporation over the ocean with condensation at the coast.

Tree water from the same three locations was collected for stable isotopic analysis to determine the importance of fog-drip water to coastal conifers. Tree cores were collected at the end of the rainy season in June and again at the end of the foggy season in October 1990. The tree core water ranged from −34 to −20 per mil in δD and from −5.2 to −2.5 per mil in δ^{18}O, and seasonal variations were observed. The results indicate dependence by the conifers on fog-drip water at least during the foggy season.

Peninsular groundwater samples were also collected for isotopic analysis to determine whether fog drip plays a role in groundwater recharge. Groundwater ranges from −32 to −29 per mil in δD and from −5.8 to −5.2 in δ^{18}O and plots on a mixing line between the fog and rain, indicating that fog drip may be a partial source. An observed geographic variation of almost 5 per mil in the δD of fog on the peninsula is explained by the loss of about 5% of the condensing atmospheric vapor in the form of fog drip. Coupled with the observed isotopic composition of groundwater, this indicates that a small portion of fog-drip water may recharge the groundwater system.

Key words: Fog-drip, rain, groundwater, Point Reyes National Seashore, deuterium, isotope, conifer, tree cores.

Coastal fogs, such as those observed on the Point Reyes peninsula north of San Francisco, California, are produced when moist air is blown landward over an area of coastal upwelling. Upwelling is the process whereby cold, deep ocean water wells upward to replace surface water that has been driven offshore. Coastal fogs associated with upwelling are commonly observed along the west coast of North America between June and October (Goodman 1977).

Between July and October, fog is observed on the Point Reyes peninsula about 30% of the time, more often than at any other San Francisco Bay area station. Fog is observed at this station up to 37% of the time during August (Goodman 1982). The fog is blown onshore by northwesterly winds. The winds are lightest in the early morning and strongest during the afternoon, when the greatest temperature gradient occurs between the coast and the interior.

Fog drip is the raining to the ground of large water drops formed by the coalescence on foliage of blowing fog droplets. The amount of fog drip that can be produced is related to the duration and liquid water content of the fog; the type, density, and cross-sectional area of the collecting vegetation; and prevalence of the wind. Large amounts of fog-drip water have been measured at the ground surface, either by outfitting rain gages with special collectors or by simply placing the gages under trees. Using a rain gage outfitted with a cylindrical screen 80 cm high, Azevedo and Morgan (1974) caught as much as 42.5 cm of fog water during summer dry periods on ridges bordering the Eel River Valley in northern California. Similar results were obtained by Parsons (1960) who collected as much as 25.4 cm of fog water during the dry summer months by placing rain gages under Monterey pines (*Pinus radiata*) and eucalyptus (*Eucalyptus* sp.) trees in the Berkeley hills. Oberlander (1956) caught up to 150 cm of precipitation on Cahill Ridge in the San Francisco Bay area during a rainless period of about 6 weeks using a rain gage placed under a tanbark oak (*Lithocarpus densiflorus*).

Several researchers have discussed the importance of fog drip to the survival of vegetation. Byers (1953) considered fog drip to be too spotty to be a limiting factor in coastal redwood distribution, but Oberlander (1956) stated that seedlings of Monterey cypress (*Cupressus macrocarpa*), among others, seem to be encouraged beneath fog-drip-producing trees. Azevedo and Morgan (1974) determined that fog drip influences nutrient cycling, species composition of forests, and the character of forest soils. However, the importance of fog drip as a water source for large conifers has never been ascertained.

This study is designed to better quantify the relative importance of fog drip on the Point Reyes peninsula. Point Reyes was selected because of the existence of fog-drip-producing vegetation and common summer fogs.

Methods

Rain and Fog Collection

Rain and fog were collected for stable isotopic analysis at three locations on the Point Reyes peninsula (Fig. 1) from 1987 through 1990. The specially

designed collectors are made of 12.7-cm PVC pipe protecting a 2.5-L glass jug (Fig. 2). Each fog collector has a 0.14-m^2 fine mesh screen mounted vertically with PVC pipe over the collection tank. The screens are set about 0.6 m above the ground and positioned approximately perpendicular to the prevailing winds. The blowing fog collects on the screens, and the resulting water is channeled into the collection tank. The rain collectors are similar in design but without the fog collecting screen. The 12.7-cm opening is reduced to 5 cm. All collection tanks contained 100 mL of mineral oil to control evaporation.

Rain is collected during the rainy season, between mid-October and late June, whereas fog is collected during the rainless summer fog season from late

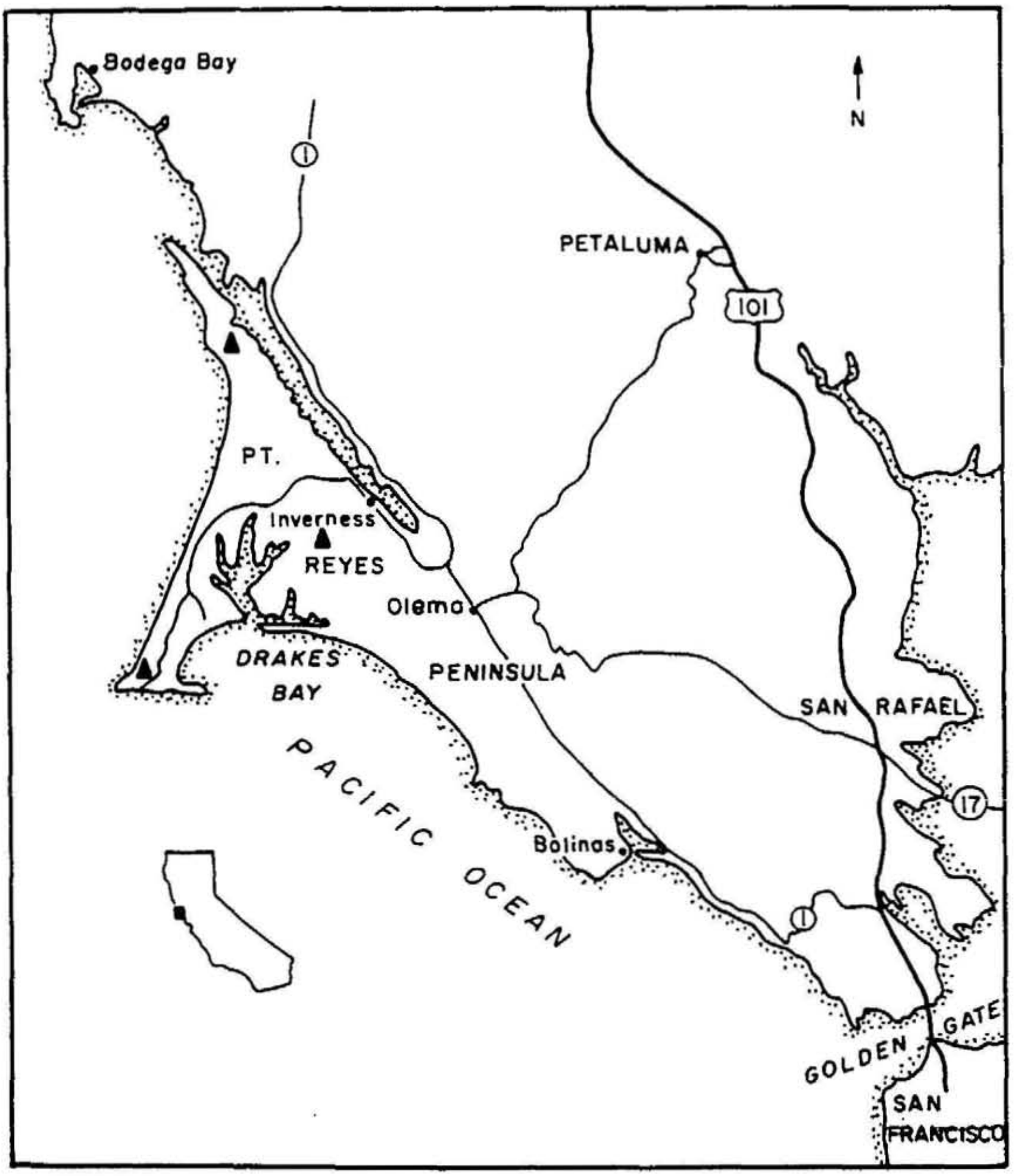


Fig. 1. Location map of the collection sites of the fog, rain, and tree cores on the Point Reyes peninsula.

June through mid-October. In addition, five groundwater samples for stable isotopic analysis were collected from springs, shallow wells, and holes drilled with an auger. Some locations of groundwater sampling were near drip-producing trees, whereas others were not.

Tree Water Collection

Tree and soil cores were collected at each of the three locations following the rainy season in June 1990 and at the end of the foggy season in October 1990. Bishop pine (*P. muricata*) and Monterey cyprus were cored, with selection depending on occurrence. The tree cores were collected using a standard 1.3- × 45.7-cm increment borer. The 1.3-cm bore was chosen to provide the largest possible volume of sample, whereas the 45.7-cm length was to ensure the collection of heartwood (White et al. 1985). The innermost portion of the core was sealed in a 2- × 10-cm glass vial with a poly-sealed lid. The core-removal and sealing were performed quickly because, soon after sealing, condensate forms on the inside walls of the vials. Eventually a considerable amount of water evaporates from the wood core and becomes attached to the inside of the bottle. Because this evaporation would fractionate the portions, collection of both parts

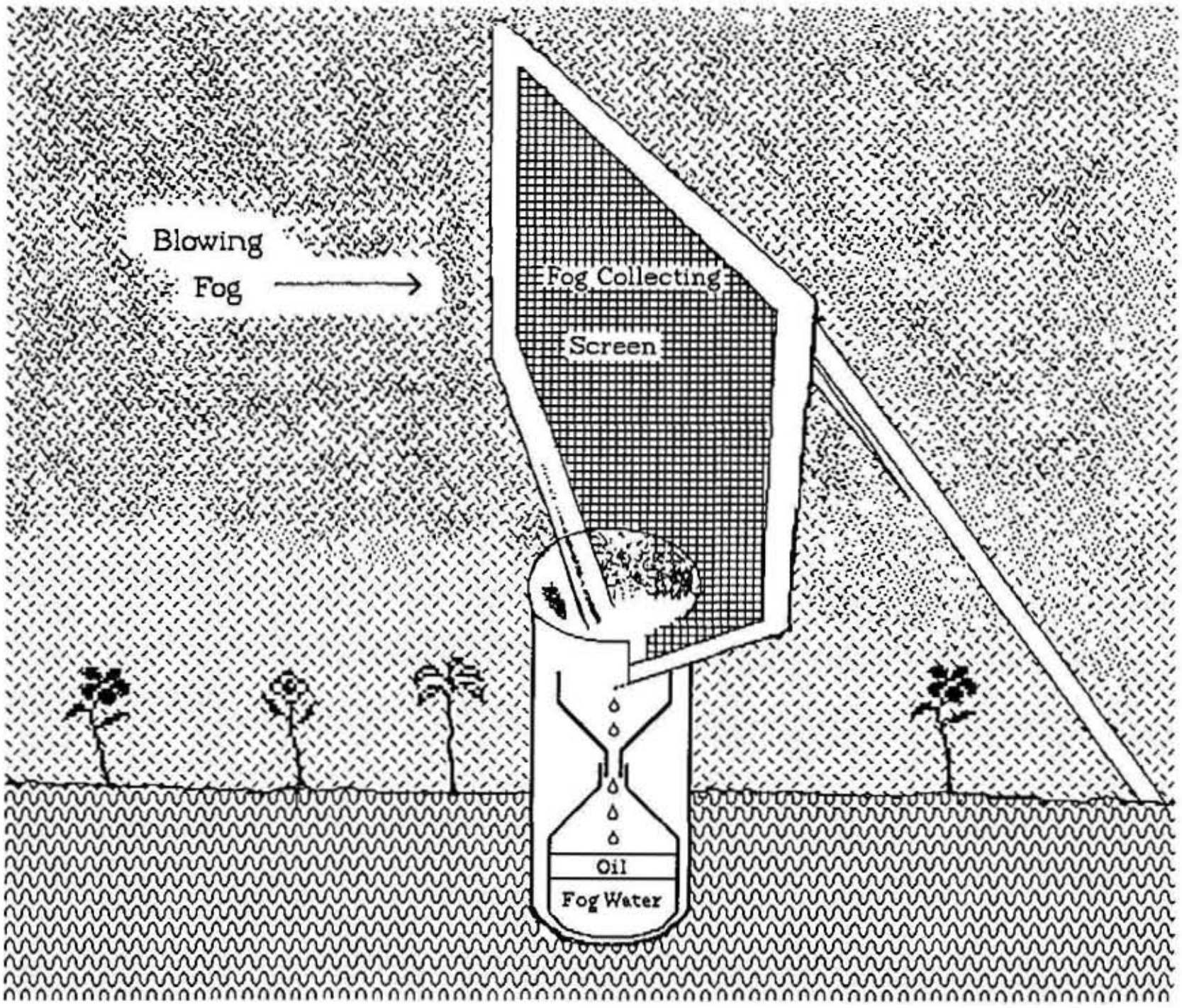


Fig. 2. Fog collector designed for this study.

of the sample—that from the wood core as well as from the bottle—was necessary.

Quantitative extraction of the tree water was performed by azeotropic distillation using toluene (Revesz and Woods 1990; Ingraham and Shadel 1992) in a still that could accommodate both the wood core and the bottle in the boiling chamber. The distillation process was allowed to proceed for about 6 h, after which the water sample was collected for stable isotopic analysis. Each wood core segment generally provided about a 1-mL water sample.

Sample Analysis

The hydrogen isotope ratios were determined by the quantitative conversion of a 5-μL aliquot of the water sample to hydrogen gas using uranium (Bigeleisen et al. 1952) as a reducing agent. The hydrogen gas was then analyzed in a mass spectrometer. The oxygen isotope ratios were determined by reacting 10 μL of the sample with guanidine hydrochloride (Dugan et al. 1985) and analyzing the resultant CO_2 in a mass spectrometer.

The isotopic data are reported in terms of variations from the SMOW (standard mean ocean water) in delta (δ) notation where

$$\delta \text{ per mil} = ((R_{sample} - R_{SMOW})/R_{SMOW}) \times 1{,}000$$

and where

R is the isotope concentration ratio (e.g., $^{18}O/^{16}O$ or D/H).

The δ values are precise to approximately ± 1.0 per mil for hydrogen and ± 0.2 per mil for oxygen.

Results

The yearly weighted averages of the stable isotopic compositions of the precipitation samples and amounts of fog water collected on the Point Reyes peninsula are shown in Table 1. Also shown in Table 1 are the stable isotopic compositions of the groundwater collected on the peninsula. The stable isotopic compositions of fog water range from -16 to -8 per mil in δD and from -2.9 to -2.0 per mil in $\delta^{18}O$. These values are consistently more enriched than those of the collected rain, which range from -45 to -30 per mil in δD and from -7.6 to -5.8 per mil in $\delta^{18}O$. Small variations are also observed in the stable isotopic compositions of the fog from the three collection sites. The stable isotopic compositions of the fog collected at Vision Peak, the most inland site, are generally about 5 per mil more depleted in δD than are those of fog from the lighthouse, the most coastal site, as described by Ingraham and Matthews (1990).

The yearly weighted averages of the stable isotopic compositions of the precipitation samples from all collection sites are plotted in Fig. 3, along with

Table 1. The stable isotopic compositions of the fog, rain, and groundwater samples collected on the Point Reyes peninsula and used in this study.

Fog				
Sample site	1987	1988	1989	1990
Vision Peak	−15(−2.7)9.4[a]	−16(−2.9)4.5	−14(−2.9)2.8	−15(−2.8)5
Lighthouse	− 8(−2.4)1.65	−10(−2.0)1.35	−10(−2.5)1.0	−13(−2.7)4.5
Pierce Ranch	−12(−2.3)2.6	− 9(−2.2)3.6	− 9(−2.1)2.0	−12(−2.6)5.2
Rain				
Sample site	1987–88	1988–89	1989–90	1990–91
Vision Peak	−37(−6.9)	−36(−6.4)	−43(−7.6)	−45(−7.3)
Lighthouse	−35(−6.2)	−30(−5.8)	−35(−6.6)	−43(−6.7)
Pierce Ranch	−40(−6.3)	Lost	−37(−7.0)	−37(−6.1)
Groundwater[b]				
Sample site	Date collected	δD		$\delta^{18}O$
Bass Lake Spring	7-07-88	−31		−5.7
Lighthouse well	7-16-88	−29		−5.4
Galagher Ranch	7-16-88	−30		−5.3
Stockwater well	7-16-88	−29		−5.2
Vision Peak	7-16-88	−32		−5.8

[a]The δD values are shown first, the $\delta^{18}O$ values are shown in parentheses, and the amount of water collected, in liters, follows the isotopic data of the fog samples (e.g., for Vision Peak 1987: δD = −15 per mil, $\delta^{18}O$ = −2.7 per mil, and 9.4 L were collected).
[b]Samples from holes drilled with an auger.

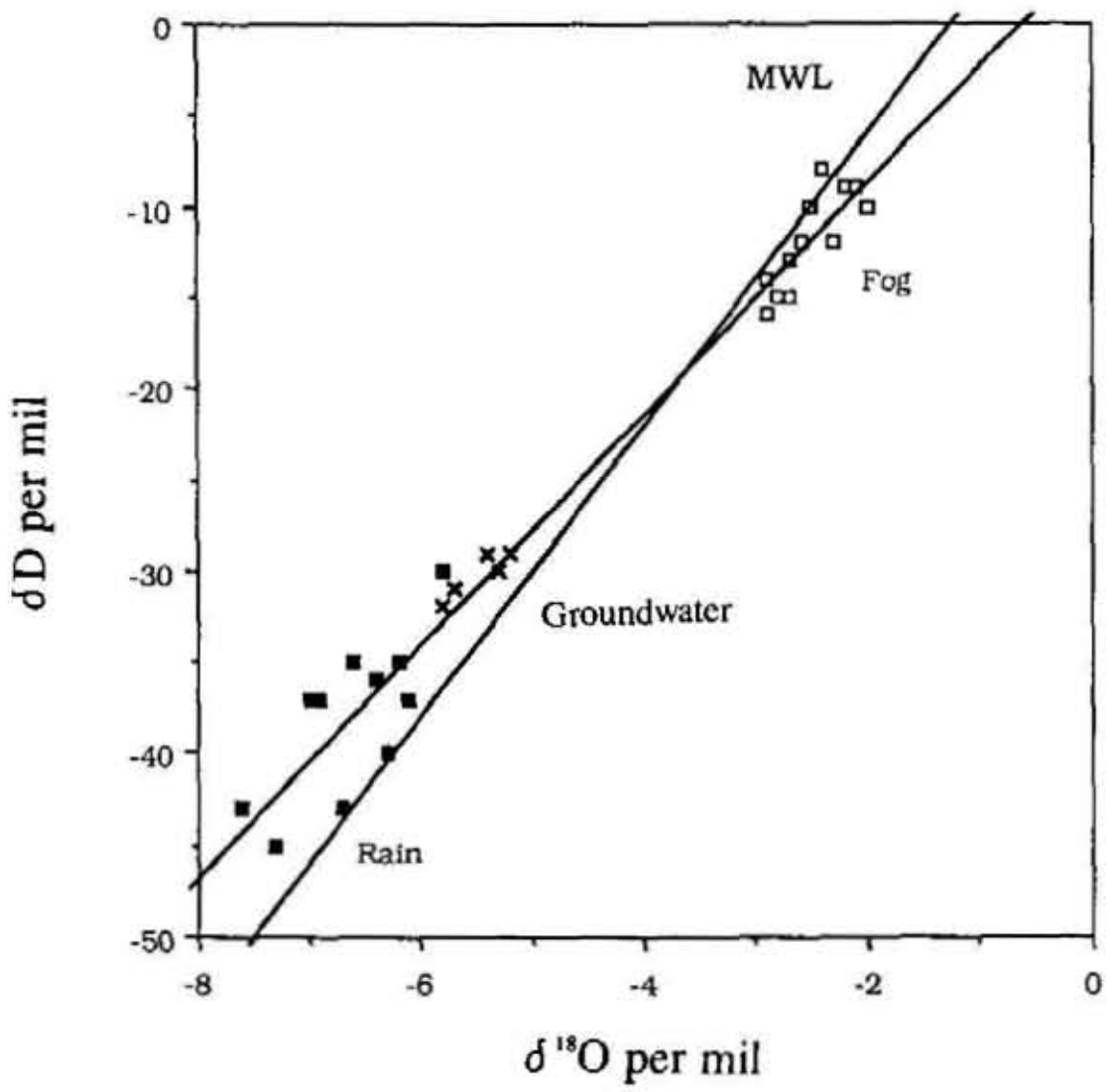


Fig. 3. The yearly weighted averages of the stable isotopic compositions of the precipitation samples from each collection site and the best fit regression line through the data. Also shown are the global meteoric water line (MWL) first described by Craig (1961) and the stable isotopic composisions of five groundwater samples.

the global meteoric water line (MWL) and the best fit regression (mixing) line for the fog and rain. The MWL, first described by Craig (1961), represents the loci of the stable isotopic values of meteoric water and is commonly used as a baseline for comparison. The fog water commonly plots below the MWL, whereas the rain generally plots above it. Also shown in Fig. 3 are the stable isotopic compositions of the five peninsular groundwater samples, which plot close to the mixing line between the fog and rain, at a location approximately 5 per mil more enriched in δD than the rain and 15 per mil more depleted than the fog.

The stable isotopic compositions of the water extracted from tree cores of Bishop pine and Monterey cyprus are shown in Table 2. The range in the composition of the samples collected in June is from -32 to -20 per mil in δD and -5.2 to -3.9 per mil in δ^{18}O. Those collected in October range from -34 to -24 per mil in δD and from -5.2 to -2.5 per mil in δ^{18}O.

Discussion

The basis for using stable isotopes to study the importance of fog drip is the understanding that fog and rain at any location have differing stable isotopic ompositions (Ingraham and Matthews 1988a, 1990). To be effective as fog drip, fog must condense at an altitude no higher than the collecting vegetation, which is much lower than the level of rain formation. Thus, the condensation of fog ccurs at higher temperatures than that of rain and so is accompanied by a smaller isotopic fractionation. Because coastal fog is formed when the warm moist air blows over the cold upwelled water, it is an early stage condensate. The air mass that produces rain, however, continuously condenses out water across the ocean, resulting in isotopic compositions of more advanced stages. The coupling of warmer condensation temperatures and an early stage condensate

Table 2. The stable isotopic compositions of the water obtained from tree cores of Bishop pine (*Pinus muricata*) and Monterey cyprus (*Cupressus macrocarpa*) collected on the Point Reyes peninsula.

Location	Species cored	δD per mil	δ^{18}O per mil
	Sampled 6-12-90		
Vision Peak	*Pinus muricata*	−30	−4.9
Vision Peak	*Pinus muricata*	−32	−4.9
Lighthouse	*Cupressus macrocarpa*	−20	−3.9
Pierce Ranch	*Cupressus macrocarpa*	−30	−5.0
Pierce Ranch	*Cupressus macrocarpa*	−31	−5.2
	Sampled 10-4-90		
Vision Peak	*Pinus muricata*	−25.5	−2.5
Vision Peak	*Pinus muricata*	−31	−3.8
Lighthouse	*Cupressus macrocarpa*	−24	−3.8
Pierce Ranch	*Cupressus macrocarpa*	−34	−5.2

would produce more isotopically enriched fog than the opposite rain producing conditions of colder condensation temperatures and a later stage condensation.

Geographic Variation of Fog

Small differences in the stable isotopic composition of fog have been observed among the three collection sites. The largest difference is between the most inland collection site (Vision Peak) and the most coastal site (lighthouse). The stable isotopic compositions of Vision Peak fog are consistently more depleted than those of lighthouse fog and have a difference in their weighted δD averages of almost 5 per mil. This difference has been attributed by Ingraham and Matthews (1990) to the loss of fog water between the two sites and was investigated using two models. These researchers assumed similar isotopic compositions of the condensing parent vapors at the lighthouse and Vision Peak and used a moist adiabatic model to predict the temperatures necessary to produce the fog. The results were compared to the lapse rate of a moist adiabatic curve. Ingraham and Matthews (1990) also developed a rain-out model (a model of moisture lost through rain). In the model a constant temperature of condensation is assumed, and the fraction of water vapor remaining in the atmosphere at the lighthouse and at Vision Peak may be calculated using a distillation equation. The results from both models indicated that fog water, in the form of fog drip, is lost from the air blowing across the Point Reyes peninsula.

Stable Isotopic Composition of Groundwater

The stable isotopic composition of groundwater on the Point Reyes peninsula, as shown in Fig. 3, is approximately 5 per mil more enriched in δD than the rain, 15 per mil more depleted than the fog, and plots close to the mixing (regression) line for the fog and rain. The stable isotopic composition of groundwater might be explained by evaporation of rain before infiltration; however, the groundwater does not display any obvious evaporative effects as the data plot close to the MWL rather than on an evaporation line. An additional explanation of the isotopic difference between the rain and groundwater on the Point Reyes peninsula is that some of the fog drip may be infiltrating and recharging the groundwater system (Ingraham and Matthews 1988b, 1990).

Importance of Fog Drip to Conifers

The consistent and predictable differences in the stable isotopic compositions of fog and rain are used here to aid in determining the dependence of vegetation on fog-drip water. The stable isotopic compositions of the fog, rain, and tree water collected on the peninsula are shown in Fig. 4.

The tree core water samples collected on the peninsula in June plot close to the MWL and most plot close to the groundwater. Thus, during the rainy season, most trees seem to consistently use groundwater that may or may not contain fog-drip water. One sample, collected at the lighthouse in June, plots

closer to the fog, indicating that trees at this location do use fog-drip water during the rainy season. Two questions are unanswered by our study: Is enough fog-drip water stored in the soil zone to supply the trees through June? Is the effective foggy season at the lighthouse longer than our collection periods?

The stable isotopic compositions of the tree water samples collected on the peninsula vary by season. Those collected in October, after the foggy season, tend to fall on evaporation lines emanating from the MWL; these samples show effects of evaporation, but also seem to contain some fog-drip water. Peninsular trees seem to depend, in part, on fog-drip water during the summer fog season.

Conclusions

California coastal fogs are early stage condensate representing a single cycle of evaporation over the ocean with condensation at the coast and are isotopically more enriched than local rain. The rain is produced from an air mass that has experienced continued rain-out over the ocean before reaching the California coast and, thus, is consistently more depleted than the fog. The isotopic compositions of fog and rain collected on the peninsula are predictably and consistently different.

The stable isotopic composition of the groundwater collected on the Point Reyes peninsula plots directly between those of rain and fog. The stable isotopic

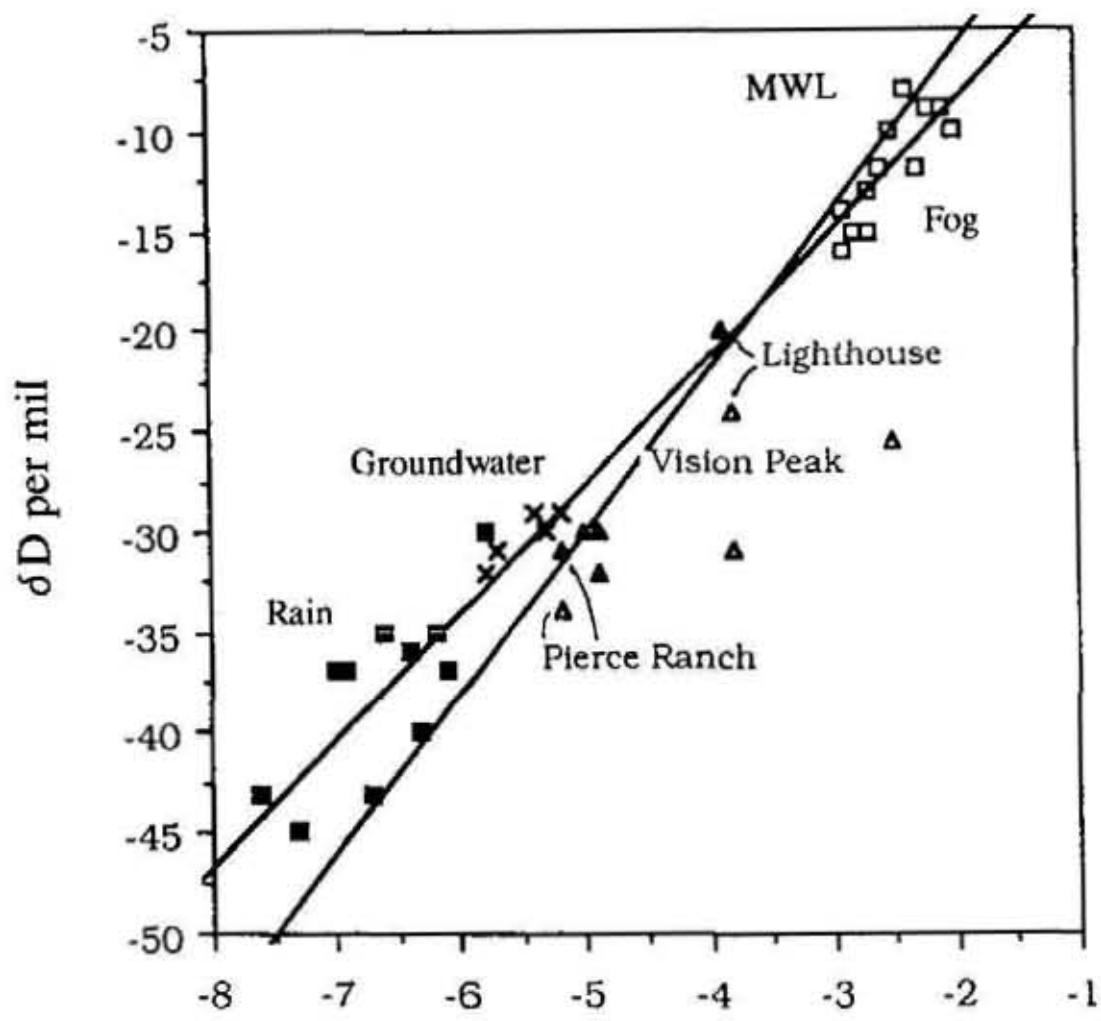


Fig. 4. The stable isotopic compositions of precipitation and groundwater, the mixing line between the fog and rain, and the meteoric water line. Also shown are the isotopic compositions of the tree core water at the three sites collected in June (*closed triangles*) and October (*open triangles.*)

composition of groundwater may be explained simply in terms of evaporation of the rain before infiltration; however, the stable isotopic compositions do not display isotopic effects normally associated with evaporation. An alternate explanation is that some of the fog water lost over the peninsula as fog drip may infiltrate and recharge the groundwater system. This hypothesis is supported by an observed geographic variation across the peninsula in the isotopic compositions of fog; this was suggested as being caused by a loss of about 5% of the atmospheric water vapor in the form of fog drip.

The conifers on the peninsula display varying dependence on fog-drip water. Some of the conifers may depend on fog-drip water year-round, whereas others may depend only partially on fog-drip water and only during the foggy season.

Acknowledgments

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Effects of Fine Sediment on Salmonid Redds in Prairie Creek, a Tributary of Redwood Creek, Humboldt County, California

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Abstract. We studied the effects of fine sediment derived from a highway construction alignment on salmonid redds in Prairie Creek, a creek flowing through Redwood National Park and Prairie Creek Redwoods State Park, California. We used infiltration bags, permeability standpipes, and colander mesh baskets filled with gravel and eyed steelhead trout (*Oncorhynchus mykiss*) eggs, to measure changes in fine sediment, gravel permeability, dissolved oxygen, and egg survival to hatching in artificially constructed redds. Infiltration bag results indicated fine sediment was greatest in a Prairie Creek tributary affected by highway development, next greatest in Prairie Creek mainstem, and the least in the control stream. However, fines smaller than 1 mm in the egg-containing baskets placed in the mainstem were low (1−8% by volume) and did not differ significantly from the control stream. Permeability decreased over the season at all Prairie Creek sites, including a site that received minor amounts of sediment from the highway alignment. Intragravel and surface dissolved oxygen decreased over the winter, but never below 7.7 ppm. Survival of steelhead eggs was high in affected and control streams. Fine sediment did not seem to be the major factor affecting these parameters. These results were obtained during a low rainfall year. Streamflows were too low to move sediment into the cleaned gravel of the redds; consequently, egg survival was probably less adversely affected than it would have been in a year of more normal streamflow. Similar studies will be conducted to document effects of higher flows.

Key words: Salmonid, egg survival, redd, dissolved oxygen, gravel permeability, fine sediment.

In October 1989, a storm delivered tons of fine sediment from an unprotected highway construction alignment into Prairie Creek and many of its tributaries. A layer of silt- and clay-textured sediment settled on the surface of the streambed and infiltrated into subsurface gravels of this relatively pristine salmonid stream system (Redwood National Park 1991). Infiltration of large amounts of fine sediment into salmonid redds can reduce reproductive success

(Everest et al. 1987). Sediment can reduce gravel permeability and intragravel water flow (Cooper 1965) and, thus, availability of dissolved oxygen (DO; Coble 1961). Low DO can cause direct egg mortality (Alderice et al. 1958). We studied the effects of fine sediment in Prairie Creek, beginning in December 1989. The objective was to determine if the fine sediment reduced gravel permeability, DO, and salmonid egg survival in the creek. During the first year of this multiyear study, we specifically addressed the effect on survival to hatching of eyed steelhead trout (*Oncorhynchus mykiss*) eggs. We present the results of the first year of study in this paper.

Study Area

Prairie Creek is in Redwood National Park and Prairie Creek Redwoods State Park near the town of Orick in northern California. Prairie Creek, tributary to the coastal stream Redwood Creek, is 22 km long. The average stream gradient in the study area is 1%, and the drainage area is 35 km^2. Much of the Prairie Creek watershed vegetation is old-growth redwood (*Sequoia sempervirens*) forest. Anadromous and resident stocks of cutthroat trout (*Oncorhynchus clarki*) are common in Prairie Creek and its tributaries (Anderson 1988). The creeks support large runs of anadromous coho salmon (*O. kisutch*), steelhead trout, and chinook salmon (*O. tshawytscha*).

A four-lane highway was being constructed upslope and parallel to Prairie Creek on the east side for 10 creek km in second-growth redwood forest. The terrain of the highway alignment was steep and highly erodible. During the October storm, sediment was delivered into Prairie Creek from the tributaries Ten Tapo, Brown, Big Tree, Boyes, and May creeks. The study area included the affected Prairie Creek reach, the affected Brown Creek tributary, and a control stream, Lost Man Creek (Fig. 1). Lost Man Creek is a large tributary to Prairie Creek that was unaffected by highway sediment inputs. This stream was not an ideal control because it has been affected by some logging and is somewhat dissimilar geologically. However, it is identical climatologically, has supported successful salmonid spawning, and was the best control available.

Methods

To test permeability, fine sediment infiltration, and egg survival, we constructed artificial salmonid redds and measured the cumulative effect of subsequent storms on those three parameters. To simulate a redd, we sifted pockets of gravel to clean out fine sediment using a shovel or sieve at potential spawning sites. For the egg survival experiment, we also mimicked the shape and pot of a natural redd. We recorded Prairie Creek water and sediment discharge near the sites (Fig. 1) during the study.

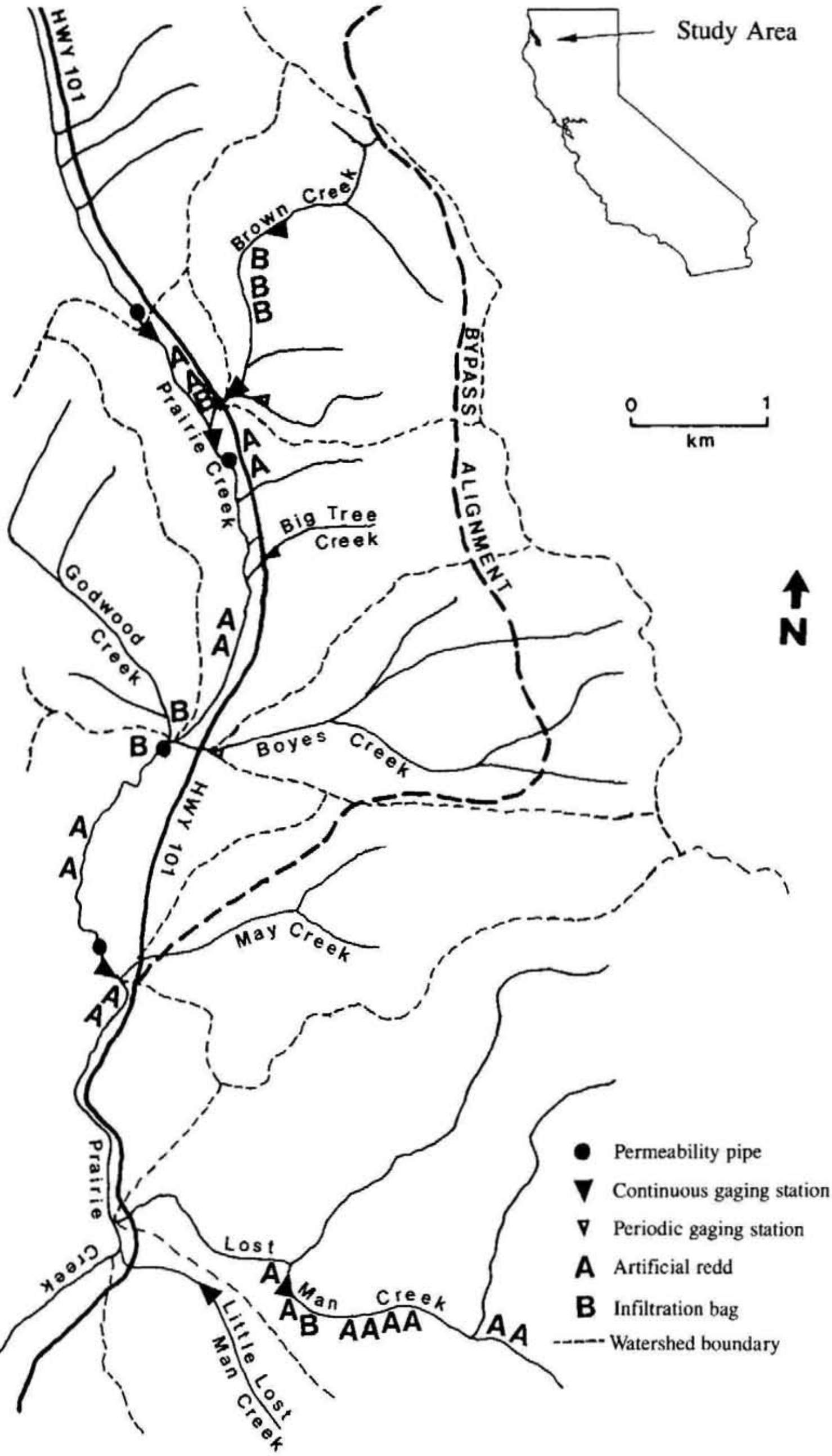


Fig. 1. Study area showing Prairie Creek, its tributaries, the highway bypass alignment, water and sediment discharge gaging stations, and location of artificial redds containing clusters of permeability pipes.

Fine Sediment Infiltration in Redds

In December 1989, we placed three infiltration bags on Prairie Creek, one on the control stream, and three on Brown Creek, a sediment-affected tributary to Prairie Creek (Fig. 1). These collapsible, waterproof bags with floats were placed beneath columns of stream gravel sieved of all fines smaller than 4 mm in Prairie Creek and smaller than 2 mm in Brown Creek. All bags were removed with a winch and tripod by June 1990 and sieved to determine percent of the total sample weight in various particle size classes smaller than 4 mm. Sample size was only one in the control stream because of time constraints, therefore little could be inferred statistically. Differences found were interpreted as apparent trends.

Redd Gravel Permeability and Dissolved Oxygen

In January 1990, we placed four clusters of four permeability standpipes, modeled after those of Gangmark and Bakkala (1958), in shovel-cleaned artificial redds in Prairie Creek. The most upstream cluster was in the least affected section of Prairie Creek, which was above the Brown Creek confluence. The other three were downstream of Brown Creek and other tributaries known to have contributed large amounts of sediment (Redwood National Park 1991; Fig. 1).

Permeability testing procedures followed those of Terhune (1958). Pipes remained in the streambed throughout winter, and subsurface gravel inflow rates were measured in January and July 1990. Beginning in February, we also lowered a probe into the standpipes to measure DO concentrations in the subsurface gravels. Dissolved oxygen was measured in the adjacent surface water at the same time.

Inflow rate was used as an index of permeability. Differences in inflow rate and DO between the standpipe clusters and over time were tested using two-way analysis of variance. One-way analysis of variance and Tukey's multiple range tests (Neter et al. 1990) were performed to determine which groups differed significantly ($P < 0.05$). We used paired *t*-tests to test differences between intragravel and surface water DO.

Egg Survival

We constructed 10 artificial steelhead redds in Prairie Creek and eight in the control stream. Three enamel-coated colander baskets (0.31-cm mesh), filled with shovel-cleaned stream gravel and eyed steelhead eggs, were covered with a fiberglass screen mesh and buried in each redd. The eggs were incubated between mid-February and April 1990, similar to the natural incubation period. After eggs were expected to have hatched, we removed the baskets and counted the number of alevins.

During removal, baskets were slid into a dishtub underwater to minimize loss of fine sediment. Basket gravel was wet-sieved to determine percent volume

of fines smaller than 1.0 mm. Differences in survival and fines between Prairie Creek and the control stream were tested using analysis of variance. To reduce nonnormality, all percentage estimates were converted by an arcsine square root transformation. Additionally, percent egg survival was regressed on percent basket fines.

Results

Peak streamflows following artificial redd construction were low. The highest flows to which the permeability and infiltration redds were subjected were 20–40% of the stream's 2-year recurrence interval flow (RI), respectively (2-year RI = 17 m^3/s downstream of the Brown Creek confluence). The egg-survival redds were exposed to even lower flows, the highest being 10% of this RI.

Fine Sediment Infiltration in Redds

Brown Creek infiltration bags received a greater proportion of fine sediment than bags in Prairie Creek or the control stream. The control sample had the lowest percent fines (Fig. 2). Mean percent by weight of fines smaller than 1.0 mm ranged from 4.9% (SE = 1.9) in Brown Creek to 2.9% (SE = 0.28) in Prairie Creek and 1.9% (n = 1) in Lost Man Creek.

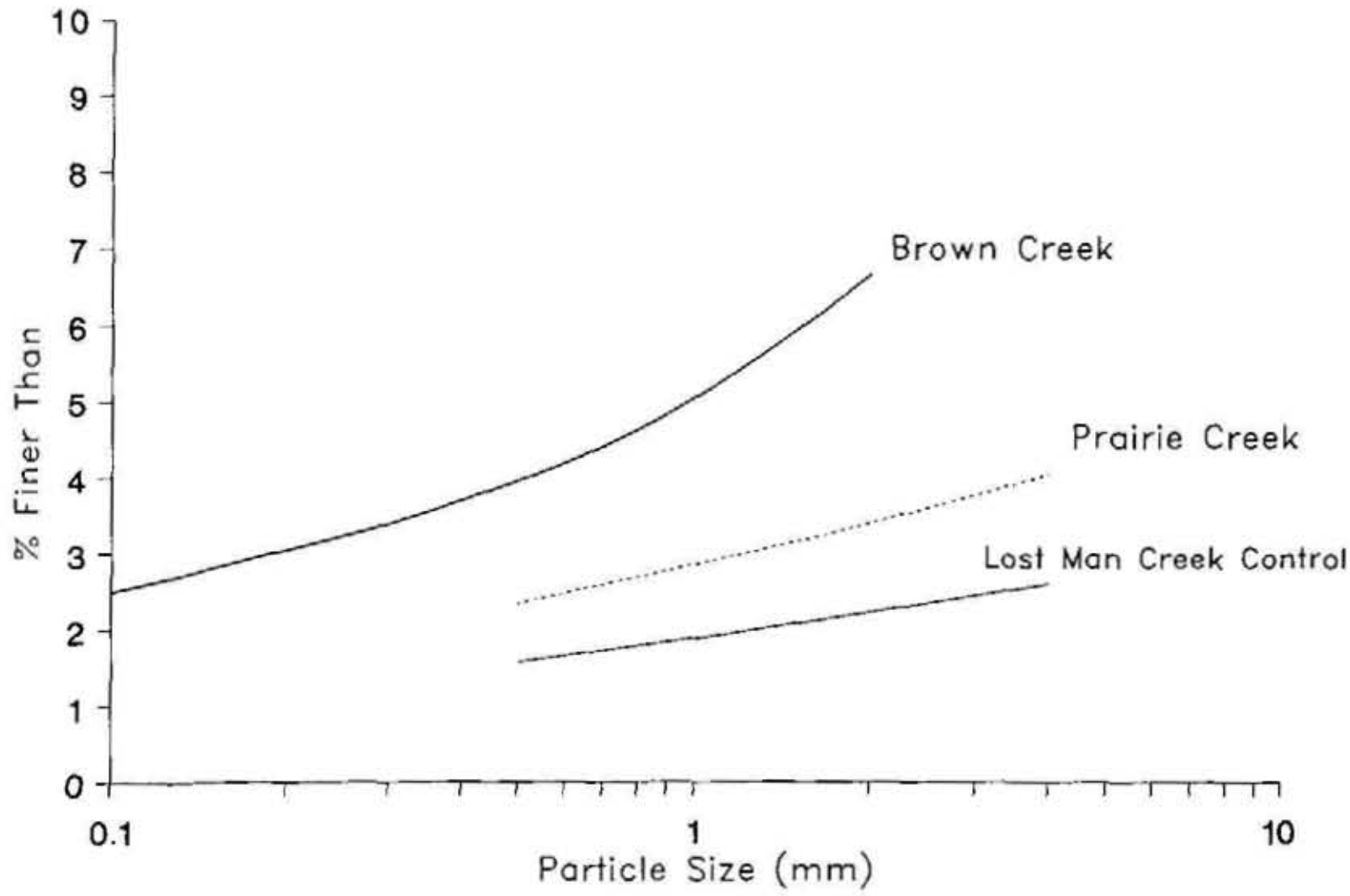


Fig. 2. Distribution of fine particle sizes in redds artificially constructed in Prairie, Brown (affected streams), and Lost Man (control stream) creeks, northern California, in late May and early June 1990. In December 1989, the redds were cleaned of fines smaller than 4 mm in Prairie and Lost Man creeks and smaller than 2 mm in Brown Creek.

Redd Gravel Permeability and Dissolved Oxygen

One standpipe in the third downstream cluster was damaged and not included in the results. Inflow rate decreased in all but one of the 15 pipes from January to July. Mean inflow rate significantly decreased over this period ($P = 0.002$) and varied between clusters ($P < 0.001$). Two-way interactions were insignificant ($P = 0.84$). Means were lower in pipe clusters below Brown Creek confluence (clusters 2–4) than above during both sampling months (Tukey's test, $P < 0.05$). However, the winter decrease in the upstream cluster did not differ significantly ($P > 0.05$) from downstream clusters (Table).

Dissolved oxygen decreased in all but two standpipes from February to July. Mean DO significantly decreased over this period ($P < 0.001$), and varied between clusters, although not at the 95% confidence level ($P = 0.10$). Two-way interactions between time and location were significant ($P < 0.001$). In February, the lowest mean concentration was in the cluster just downstream of Brown Creek confluence (Tukey's test, $P < 0.05$). However, unlike the other clusters, the mean in this cluster increased over the winter, becoming similar to all but the most downstream cluster by July (Table). Average decrease over time did not differ significantly ($P = 0.20$) between intragravel water ($\bar{x} = 12\%$, SE = 3) and surface water ($\bar{x} = 15\%$, SE = 1). Surface DO ranged from 0.1 to 1.0 ppm greater than intragravel DO. Intragravel DO never dropped below 7.7 ppm in any of the pipes.

Egg Survival

Egg survival to hatching was relatively high for all but two redds (Fig. 3). Mean percent survival was 71% (SE = 12.0) in Prairie Creek and 85%

Table. Mean inflow rates and dissolved oxygen concentration measured from clusters of four standpipes placed in artificial salmonid redds constructed on Prairie Creek in January 1990.[a]

	January		July		Decrease (%)	
Pipe cluster	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
			Inflow rate (cm^3/s)			
1	108[b]	7	87[b]	10	−20[b]	5
2	57[c]	9	35[c]	3	−32[b]	12
3	47[c]	8	35[c]	5	−22[b]	13
4	67[c]	5	54[c]	3	−19[b]	10
			Dissolved oxygen (ppm)			
1	10.4[b]	0.3	8.2[b,c]	2.5	−20[b]	3
2	8.6[c]	0.4	9.1[b]	0.1	+3[c]	5
3	10.7[b]	0.3	9.0[b]	0.1	−16[b]	2
4	10.5[b]	0.1	8.7[c]	0.1	−17[b]	2

[a]Pipe clusters were ordered from upstream to downstream.
[b,c]Similarly superscripted values in the same column did not differ significantly at the 0.05 level (Tukey's test).

(SE = 2.5) in the control stream. This difference was not statistically significant ($P = 0.36$). Two redds on Prairie Creek had 0% survival. These two redds were heavily infested with oligochaete worms. Fines smaller than 1.0 mm in the baskets of these two redds fell within the range of the other redds, 1.2 to 8.1% by volume. Means for fines were 2.6% (SE = 0.6) of the basket gravel for Prairie Creek and 3.7% (SE = 2.8%) for the control stream; those values did not differ significantly ($P = 0.24$). Basket fines did not explain much of the variance in egg survival ($r^2 = 0.06$, $P = 0.089$).

Discussion

Rainfall during the winter of 1989–90 was low, averaging 114 cm at Prairie Creek Redwoods State Park compared with the 19-year average of 170 cm. Stream discharge was low during all experiments. Scour and fill studies showed that very little of the streambed was mobilized during this period (Redwood National Park 1991). Consequently, flows were insufficient for scouring and moving much sediment into the cleaned artificial redds. This accounts for the low mean value of fines found in the redds toward the end of winter.

Infiltration bag results indicated that fines were greatest in the Brown Creek tributary, least in the control stream, and intermediate for Prairie Creek. This was expected because eastern tributaries, such as Brown Creek, received direct inputs of sediment from the highway alignment. Surface and subsurface

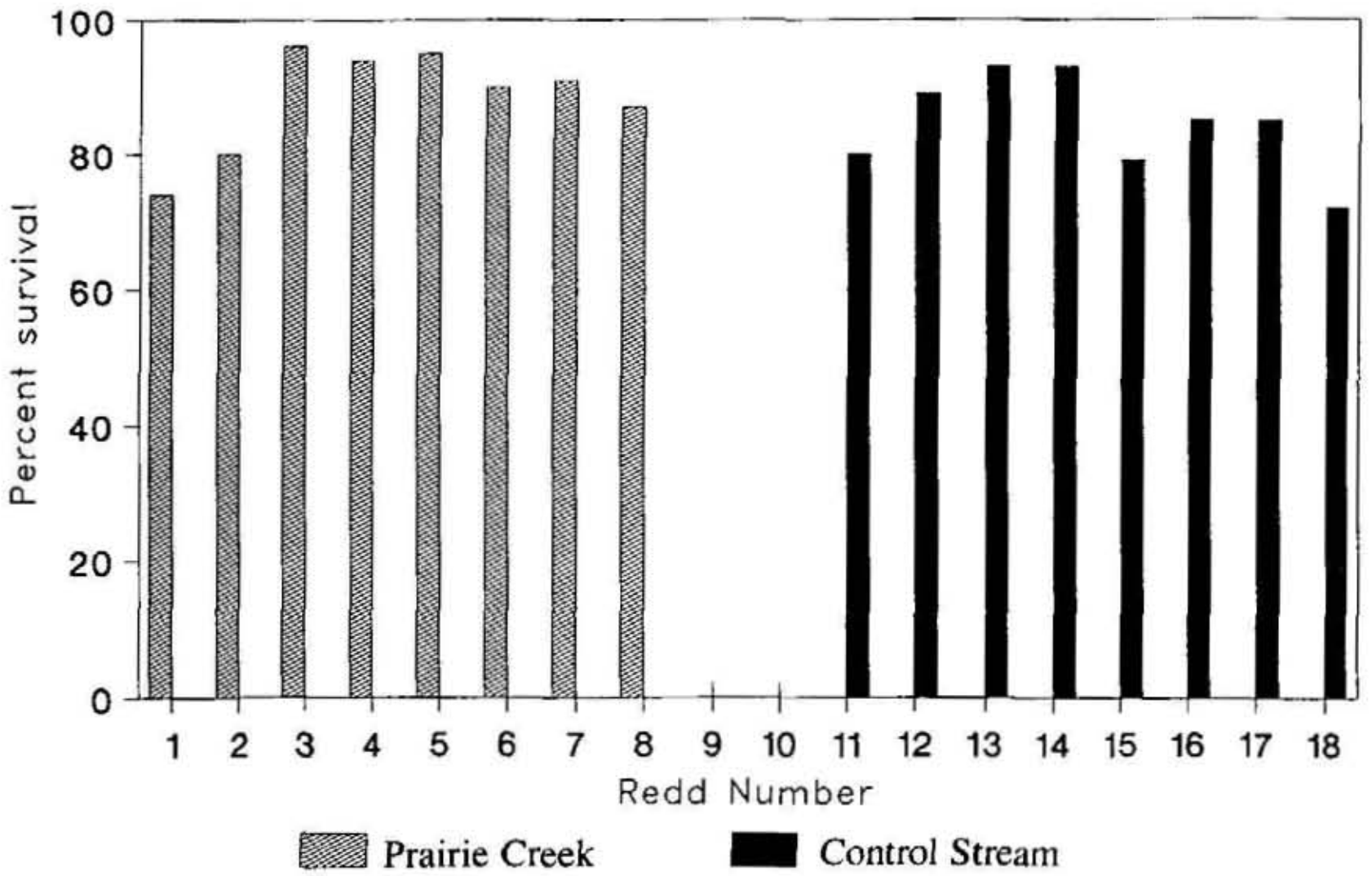


Fig. 3. Percent of eyed steelhead eggs (200 eggs/redd) that survived to hatching when incubated in artificial redds from February to April on Prairie Creek (affected stream) and Lost Man Creek (control stream) in northern California, 1990.

fines were found in greatest amounts in the tributaries (Redwood National Park 1991) and would, therefore, provide a larger source of infiltrating sediment on mobilization.

In contrast, levels of fine sediment in the egg survival redds in the affected stream were similar to the control stream. These redds, however, were subjected to smaller flows than redds with infiltration bags, which may explain the different results. Levels of fines reported to be deleterious to salmonid egg survival have varied (Chapman 1988) but are generally higher (at least 10% fines) than levels found during this study.

At the end of winter, permeability was lower in Prairie Creek redds exposed to sediment inputs from Brown Creek tributary than the most-upstream redd. This difference, however, was present immediately after installing the pipes and cleaning the gravel in January. Factors other than fines seem to be affecting permeability. Dissolved oxygen similarly decreased over the winter; but this seemed to be a function of decreasing surface water DO, which, in turn, was probably caused by increasing water temperature. Dissolved oxygen concentrations were above those reported in the literature as causing egg mortality (generally < 5 ppm; Alderice et al. 1958), although decreases below 11 ppm have restricted embryonic growth (Chapman 1988). Finally, steelhead egg survival to hatching was largely unaffected by fines or changes in permeability; instead, worm infestation seemed to be responsible for the two cases of high mortality. Further investigation is needed to determine if presence of worms is related to fine sediment.

We expect different results in the future if large storms occur. Most of the fine material in the system was still present in the gravel at the end of winter (Redwood National Park 1991). Following a large storm, we would expect these fines to be deposited in redds, increasing fines and reducing permeability to a greater extent than found in 1989–90, which could, in turn, adversely affect egg survival. Even during 1989–90, species such as coho and chinook salmon, which spawned earlier in the season and were exposed to more storms, may not have had as high egg survival as steelhead trout. For these reasons, we are repeating a refined version of this study for the years 1991–93, which addresses the effect of sedimentation on coho salmon egg survival and emergence.

Acknowledgments

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Preliminary Report on an Archaeological Resources Survey of Wreck Canyon, Santa Rosa Island: Channel Islands National Park, California

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Abstract. Recent emphasis on understanding prehistoric subsistence-settlement systems through knowledge of a complete inventory of archaeological site types has underscored the need to consider the traditionally overlooked category of sites at the smaller end of the size scale. When all site types, regardless of size or potential significance, are considered, studies of the range of artifact classes, environmental context, and spatial patterning of each site category in relation to the others can reveal important information about aboriginal subsistence strategies, demographics, and social organization.

While some early survey efforts on California's Channel Islands have taken the complete inventory view into account, the smaller sites on San Clemente Island and Santa Rosa Island were ignored. We undertook an intensive, focused, resurvey of the Santa Rosa Island archaeological site record to examine the number and types of sites in Wreck Canyon. We did this to determine site distribution, abundance, and function within certain geologic formations in the island drainages. The survey provided a model for a more thorough islandwide effort to identify sites not recorded during previous reconnaissance and survey.

Thirty-two new sites were added to the two sites originally recorded for Wreck Canyon. Most of the new sites were small and associated with rock shelters. Assessment of the distribution, abundance, and function of the island's numerous small sites will add to the understanding of Santa Rosa's entire settlement system and enable the island's resource managers to make informed decisions regarding research goals and visitor access. Site information is protected from public disclosure by federal law and National Park Service policy.

Key words: Chumashan Indians, California, Channel Islands, Santa Rosa Island, small sites, rock shelters, antiquities.

Santa Rosa Island, second largest of the four northern Channel Islands, is part of a group of eight islands lying off the coast of California, extending from Point Conception to the Mexican border (Fig. 1). More than 27 km long and 16 km wide, Santa Rosa Island's nearly 215 km^2 make up some 78% of the land area of Channel Islands National Park (National Park Service 1985).

A limited area survey using volunteers was proposed in 1988 for Santa Rosa Island to gain a better understanding of the nature and distribution of the island's sites through a more complete sample. The low number of sites recorded

previously compared to numbers for neighboring islands suggested a much higher density of sites on the island (Glassow et al. 1983). Wreck Canyon in the southeast quadrant was chosen as a target area because a reconnaissance of southside canyons in December 1988 revealed a number of unrecorded rock shelter sites. The entire canyon was selected as a survey area because it represented a more natural environmental unit to be used by aboriginal populations. Several major site types were included within varied physiographic zones, namely coastal terrace midden, open valley floor sites, and rock shelter sites along the canyon walls.

Investigations from 1947 to 1968 by Phil Orr of the Santa Barbara Museum of Natural History provided the most substantial record of Santa Rosa Island's archaeology (Orr 1952). They are the basis for evaluation of the island's archaeological potential. Orr identified 182 site/localities from all sectors of the island, defined a site typology based on seven different classes, and established a chronology for island sites.

The first archaeological investigation of Wreck Canyon began in 1901 with Philip Mills Jones, sponsored by the University of California, Berkeley, Department of Anthropology. Jones excavated skeletal material and artifacts at cave locations he numbered as camps 12, 13 and 14, which were approximately 3 km from the mouth of the canyon near Orr's Santa Rosa Island (SRI)-154 (Jones 1956). Jones removed 55 burials with artifacts from within cave 1 and burials without associated artifacts below and in front of this and two other rock shelters. He noted skeletal material and a burial slab eroding from the banks of

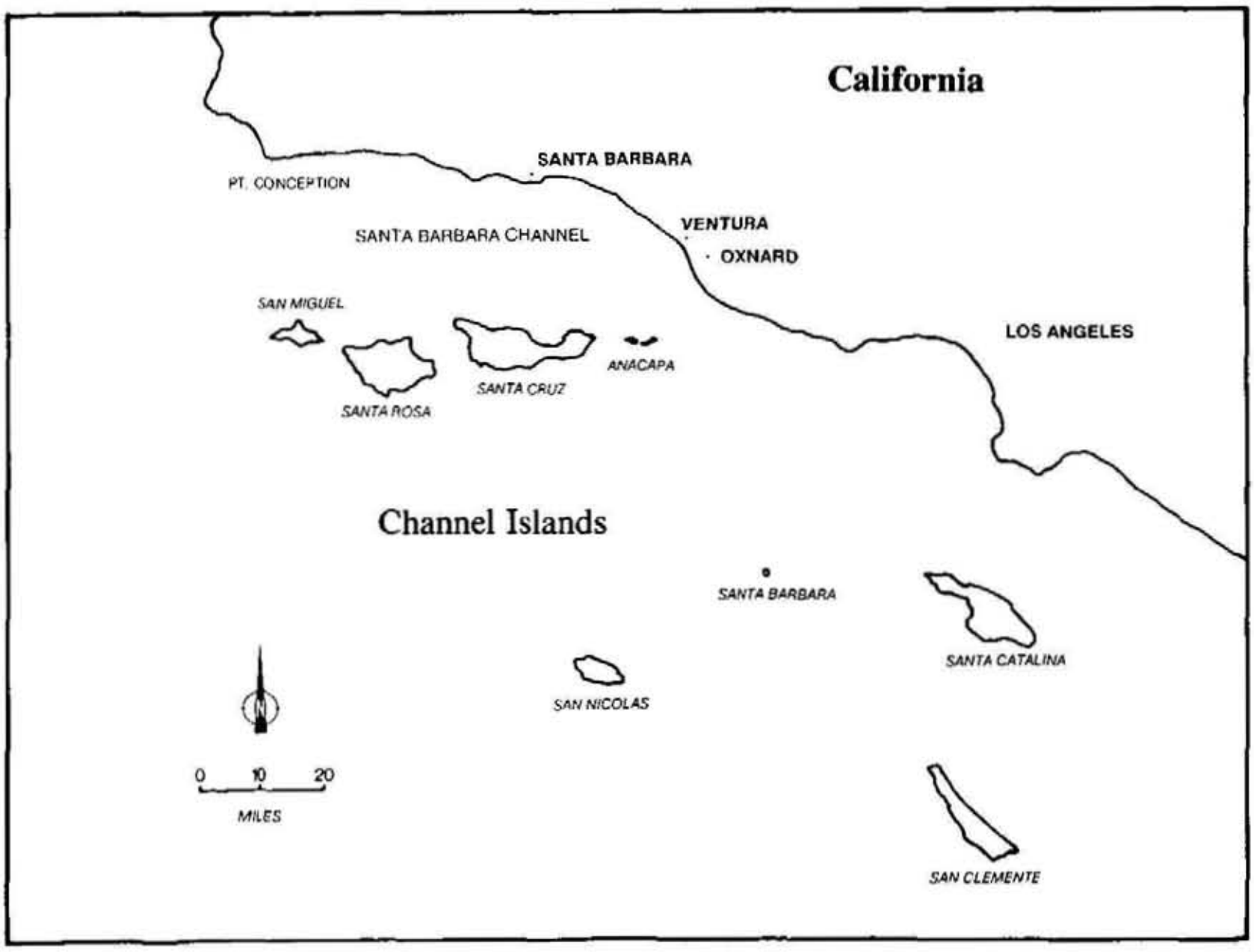


Fig. 1. California's Channel Islands.

an arroyo and mortars buried in arroyo walls at 4-m and 8-m depths. Among the artifacts collected were projectile points, olivella beads, abalone shells with asphaltum, stone rings, fragments of baskets with asphaltum, red stone beads, serpentine beads, a soapstone boat-shaped vessel, and a broken mortar.

When Orr visited Wreck Canyon in the early 1950's, he recorded a site, SRI-154, which was mapped as an open valley floor site in the vicinity of Jones's camp 12. He also noted the presence of a number of rock shelters, some with midden. He made surface observations, commented on Jones's excavations, and collected a radiocarbon sample from a shell lens buried 11 m below the top of an arroyo wall. One additional site identified by Orr in Wreck Canyon was SRI-139, a coastal shell midden located on a marine terrace at the mouth of the canyon on the west side.

Even though no specific date for Orr's radiocarbon sample has been presented, he estimated occupation of Wreck Canyon at between 7,000 and 5,000 years B.P. (Orr 1968). The rock shelter burials excavated by Jones, however, are placed in an occupation during the latter half of the Middle Period, or around A.D. 500, according to Chester King's Santa Barbara Channel chronology (Glassow et al. 1983).

Wreck Canyon, Santa Rosa Island

Wreck Canyon, in the southeast sector of the island (Fig. 2), trends toward the southeast, with steep walls at headward, opening out to level valley floor expanses. The canyon then narrows about a mile from the coast to open again as marine terraces above the water's edge. Geological formations in the canyon include Tertiary sandstones and shales—such as the Rincon Shale, Vaqueros Sandstone, Sespe Formation, Cozy Dell, and South Point Sandstone—within the canyon and Pleistocene terrace sands and gravel along the coast (Weaver 1969).

A permanent stream has cut several steep arroyo walls. Vegetation in the canyon consists of coastal sage scrub and grassland species, which have been greatly affected by grazing of introduced cattle and foraging pigs, elk, and deer. Sea mammals, present around the island today, were much more abundant during prehistoric times. The only endemic terrestrial mammals inhabiting the island currently are the Island fox (*Urocyon littoralis santarosae*), the Santa Rosa Island mouse (*Peromyscus maniculatus santarosae*), and the Santa Rosa Island skunk (*Spilogale gracilis amphialus*).

Survey Project

The archaeological reconnaissance and resurvey of Wreck Canyon began in December 1988, with most field work for the volunteer-based project taking place in September 1989 and March 1990. The National Park Service provided

transportation and housing. Two limitations were imposed by the Park Service on the activities: no ground disturbance and no surface collection.

Nearly 4 km^2 were covered on foot in 5-m transects from the mouth to the head of Wreck Canyon and along both main tributary (or east and west) branches as well as up prominent side drainages. The survey focused on those locales on the valley floor and canyon walls that seemed to have the most potential for archaeological sites, considering degree angle of slope and presence of rock shelters. Several prominent ridges at headward were also included in the survey (Fig. 3). Sites were pinpointed on 1:12,000 color aerial prints and plotted on 7.5-min U.S. Geological Survey (USGS) topographic maps, from which UTM coordinates were established. All rock shelters were investigated and were accessible by easy to moderate scrambling. In one instance, there appeared to be a possible hand and foothold trail etched into a sandstone face, making prehistoric entry easier to a shelter in the west branch of Wreck Canyon. An effort was made to identify possible quarry locations within the canyon, but none were noted. An attempt was also made to locate a sea cave at the mouth of the canyon mentioned by Orr (Halliday 1962) on the chance that it might contain aboriginal material, but no sea caves were found near Wreck Canyon.

Thirty-two new sites were recorded, increasing the number for Wreck Canyon to 34 (Fig. 3). The majority of the sites (79%) were associated with a single rock shelter or a rock shelter complex. Only 6 of the 34 were located on flat valley fill and 1 on a marine terrace at the coast. Average site area was 1,107 m^2. Midden extended downslope in front of shelter sites because of

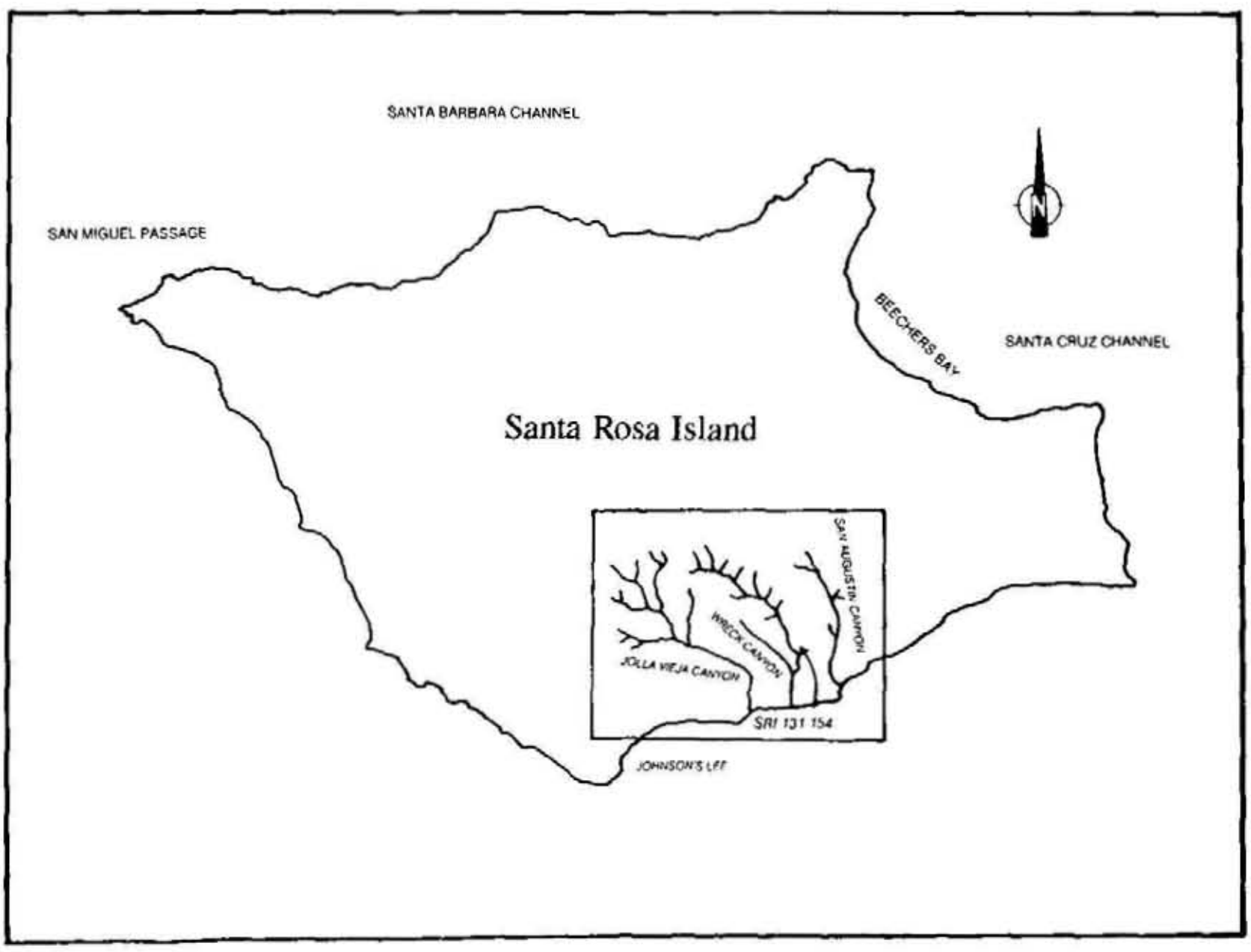


Fig. 2. Santa Rosa Island, showing the location of Wreck Canyon.

gravity and erosional factors. The total area of rock shelter sites, therefore, may be exaggerated. Elevations for shelter sites ranged from 117 to 200 m above sea level.

The average maximum dimensions of the recorded rock shelters were 2 m high by 6 m wide at the dripline and 9 m from the dripline to the rear. These dimensions may be unrepresentative of the actual dimensions of the rock shelters during prehistoric use, as the matrix (sandstone or shale) is relatively soft and constantly being eroded by wind and water, resulting in chambers now larger than when originally occupied or cavities that are now partially collapsed. It is also possible that a number of the shelters collected downwashing sediments,

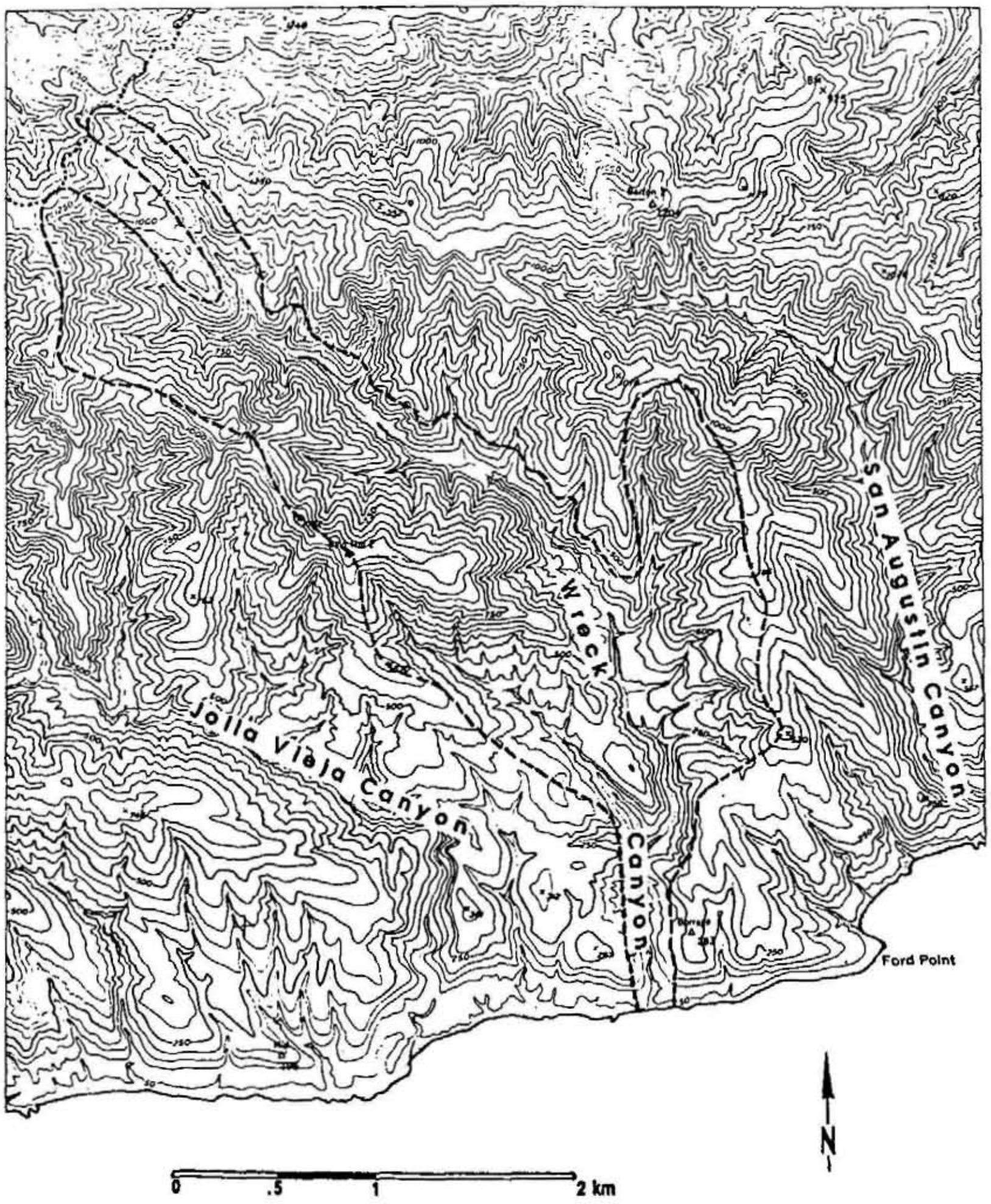


Fig. 3. A portion of Santa Rosa Island south quadrangle map showing Wreck Canyon archaeological site survey area.

an ongoing occurence, and that such infilling could have reduced the shelter floor space and capped any aboriginal material present.

Typical of a rock shelter-type site is SRI 88-8 (Fig. 4), an eroded cavity in Vaqueros Sandstone approximately 4 km from the mouth of the canyon in the east wall of the main drainage. Nearly 9 m long at the dripline, 3 m high, and 5 m deep, this shelter was the only one of several nearby erosional features that contained midden material. The cultural deposit extends downslope in front of the shelter, roughly between two small drainages, 49 m long by 22 m wide, for a total area of 1,078 m^2. Surface midden density was low within the shelter itself, probably due to recent animal disturbance (a feral pig wallow was present at the back of the shelter) and sediment infilling. The midden was characterized by shellfish such as mussel, abalone, chiton, and limpet as well as the greatest number of whole and fragmentary pieces of olivella noted to date in any Wreck Canyon site. Also found within this shelter was the only potentially time-diagnostic artifact reported during the survey, a fragment of a fire-altered chert microdrill used in bead manufacture. The microdrill's overall shape is triangular and shows both Late and Middle Period characteristics with a bit of dorsal scar and retouch (J. Arnold, University of California, Los Angeles, personal communication), a Type "B" from Arnold's chronology (Arnold 1987). Additional flaked stone found both inside the shelter and downslope, where the midden density was more moderate, included chert and quartz flakes, a chert core, and

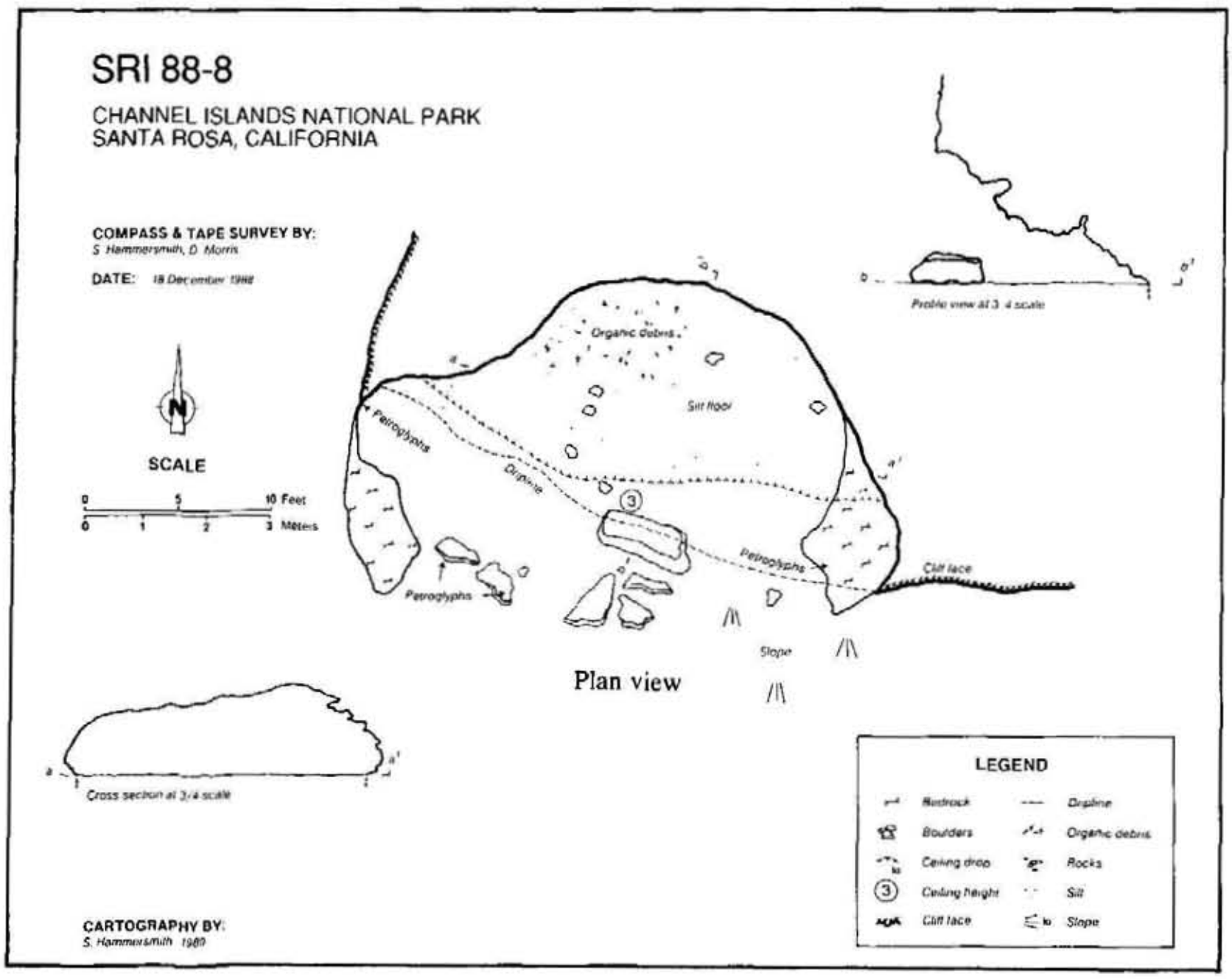


Fig. 4. Wreck Canyon rock shelter site, SRI 88-8.

bifacially retouched flake tools. Rock art was another feature noted for SRI 88-8: simple, incised linear petroglyph elements in two panels at the shelter dripline and on two boulders just outside the entrance.

The exposed Vaqueros Sandstone formation, with differential erosion creating habitable rock shelters, provided the most predictable locations for potential sites. This proved true in Wreck Canyon where 15 of the 32 new sites recorded were in Vaqueros Sandstone. It was also verified in San Augustin Canyon immediately to the east where four rock shelters with associated midden were located in an exposed outcrop of Vaqueros Sandstone during a half-day side trip. The survey crew made every effort to identify all rock shelter sites in Wreck Canyon. A number of potential shelter sites had to be dismissed as sterile, however, possibly as a result of ceiling collapse or sediment infilling that may have capped any midden material present. An attempt was also made to record the shelters previously excavated by Jones and noted by Orr. With reasonable certainty, those shelters have been identified although no evidence of burials or Jones's trenches remained for observation.

A stratified systematic sampling scheme was developed to establish a rough index of diversity for materials on the midden surface or talus slope as a way of assessing food remains versus nonfood remains. Two zones were determined in seven selected sites, inside and outside the rock shelter dripline. A 0.5% area in the center of each zone was established with 1-m^2 grids marked in 10-cm increments. The contents of each sample area were tabulated. Not surprisingly, shellfish proved to be the most common element among food remains. Numerical rankings soon proved to be untenable, however, because of the fragmentary condition of the shells due to cattle trampling. Mussel, black and red abalone, barnacle, chiton, and limpet appeared most often, and occasionally whole olivella and olivella detritus were observed. Other food remains included unidentified mammal bone and crab.

Nearly all the sites recorded were characterized by moderate density shell midden containing flaked lithics and ground stone tools. High density midden was occasionally observed in some sections, particularly when viewed in cross section. Knowledge of the depth of site deposits was limited by the surface survey methods of the project. Occasional glimpses of recurring occupation occurred at the juncture of eroding arroyo walls, however, revealing midden depth from 6 cm in one instance to over 1 m in another (SRI 90-3).

Nonfood elements noted in the sample survey included debitage and whole flaked tools and cores as well as ground stone tools. Chert and basalt were predominant materials utilized, and bifacially retouched flakes and manos were the most common end products. Several whole pestles were observed outside the sample survey area in a site in the west branch of the canyon in an extensive shelter complex. The site also contained a bedrock mortar, the only one noted so far on the island. In addition, house depressions were noted at one open valley floor site (SRI 90-3) at the head of the west branch of Wreck Canyon.

Rock art—in the form of simple, nonrepresentational pictograph (painted dot) and petroglyph (pecked rectilineal) elements—was present in three of the

shelter sites. The art ranged from a single element to multipanel, multielement clusters.

Discussion

The number of new sites located in Wreck Canyon is not surprising, given the limited number of sites located by Orr. What is noteworthy, however, is the number of the rock shelter sites and the potential for them islandwide. In an evaluation of the Santa Rosa Island archaeological site record (Glassow et al. 1983), Glassow suggested that Orr had focused on recording only relatively large sites with dimensions equivalent to 125–150 m diameter. These were much larger than the site averages for the neighboring islands.

Glassow suggested that if Santa Rosa Island site dimensions and density were similar to that of Santa Cruz Island, Santa Rosa Island could contain approximately 2,800 sites. If similar to San Miguel, the number would be closer to 3,300. It seemed that Orr's work was aimed at identifying larger village-size sites with cemeteries to the exclusion of the smaller, low-density sites.

The Wreck Canyon survey results show that small sites, in particular small rock shelters, were indeed left unrecorded and that these sites are abundant. With 34 sites identified within the 4 km^2 covered during the survey, a very rough estimate of potential sites based on these limited data can be made for the island's 215-km^2 total: 1,844 sites, or 8 sites/km^2.

The number and type of sites located in the Wreck Canyon survey imply that rock shelter-bearing exposures of Vaqueros Sandstone provided habitable locations for aboriginal populations, considering environmental context such as those near fresh water sources and coastal intertidal areas. These exposures should be examined elsewhere on the island for prehistoric sites. Other formations on the island are known to contain rock shelters and should be examined in further surveys as well.

Another implication from the survey data regards use of rock shelter sites on Santa Rosa Island. Like those in the neighboring mainland Santa Monica Mountains (Dillon and Boxt 1989), the sites seem to have served many different functions. Shelters in Wreck Canyon provided protection from wind and summer heat. Examination of the classes of cultural features, artifacts, and remains indicates that they were also used as cemeteries, habitation sites, and lithic or bead manufacturing workshops. The presence of rock art suggests use as ritual sites. They may have been seasonally or temporarily occupied and linked to environmental variables that affected food supply. They may also have been satellite specialized function camps related to the larger valley sites. The sites may certainly have changed function over time.

Valley floor sites, fewer in number than the shelter sites encountered during the survey, were certainly an important part of the canyon's settlement system. The flat, valley floor site at the head of the west branch was the only site containing house depressions, implying occupation for extended periods. Whereas this site was well inland, it was still within comfortable walking distance to the

intertidal resources (about 45 min one way) and situated near freshwater seeps and tributary streams. The one environmental advantage that may have been the key to desirability of a valley floor site—and may apply to other inland sites as well—was climate. The greater the distance from the coast, the less the effect of persistent coastal winds, providing a more moderate microclimate.

Since chronological information is limited for the Wreck Canyon rock shelters and nonexistent for valley floor sites, additional investigation is warranted. As noted by Jones from his excavations in 1901, however, shelter ceiling rock fall, sand fill, and heavy sandstone blocks have interrupted stratigraphy and fragmented artifacts. At the very least, the materials that Jones excavated, although of poor provenience, should be studied and compared to the recent survey data.

Regional research goals that attempt to define prehistoric subsistence-settlement patterns must depend on identifying the full complement of site types to gain understanding from intersite relations (Talmadge et al. 1977; Glassow 1985; Yatsko 1989; R. E. Parr and M. Q. Sutton, Los Angeles, unpublished paper). It cannot be assumed that the Wreck Canyon survey project data are representative of Santa Rosa Island's site types as a whole. Because sites within a limited number of physiographic zones were recorded, the survey results do indicate that at least one class of sites, rock shelters, occurs with significantly higher density than originally estimated. This information will influence future settlement pattern studies and should affect management decisions regarding visitor access and use on the island. Surely a much more complex settlement system is indicated for Santa Rosa than had previously been supposed.

Acknowledgments

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Vegetation and Climate of Death Valley National Monument and the Adjacent Mojave and Great Basin Deserts, California and Nevada

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Abstract. The vegetation and climate of Death Valley National Monument and the surrounding area are described in this paper along with elevational trends in precipitation, temperature, potential evapotranspiration, and plant cover. Death Valley National Monument lies in the northeastern Mojave Desert of California and southwestern Nevada. The elevational range from −86 to 3,368 m is one of the steepest gradients in any park unit in the contiguous 48 states. As a result, the unit is bioclimatologically complex and contains within it a broad range of climates ranging from arid to subhumid. The interaction between precipitation and evapotranspiration along elevational gradients determines an arid–humid boundary, which in this region is about 3,100 m. Broad generalizations about the effects of climate on patterns of vegetation within and adjacent to the monument can be made. However, discrete plant assemblages corresponding to specific climatic types cannot be identified.

Key words: Mojave Desert, Great Basin, vegetation, climate, plant ecology, Death Valley.

Study Site

Death Valley National Monument is a 108,351-ha National Park Service unit situated in the northern Mojave Desert of California and Nevada (Fig. 1). The northern Mojave Desert and adjacent southwestern Great Basin Desert compose a region of great geological and botanical interest. Extensive topographic relief and edaphic diversity make this region one of the most important centers of plant endemism in California (Stebbins and Major 1965; Raven and Axelrod 1976). In Death Valley, the steep gradients of elevation and salinity (Hunt 1966; Rowlands 1993) help create a complex physical and biological environment. The gradient from Badwater, at −86 m, to the top of Telescope Peak, at 3,368 m, is one of the steepest in the United States. This constitutes a vertical rise of approximately 3.4 km over a horizontal distance of 23 km.

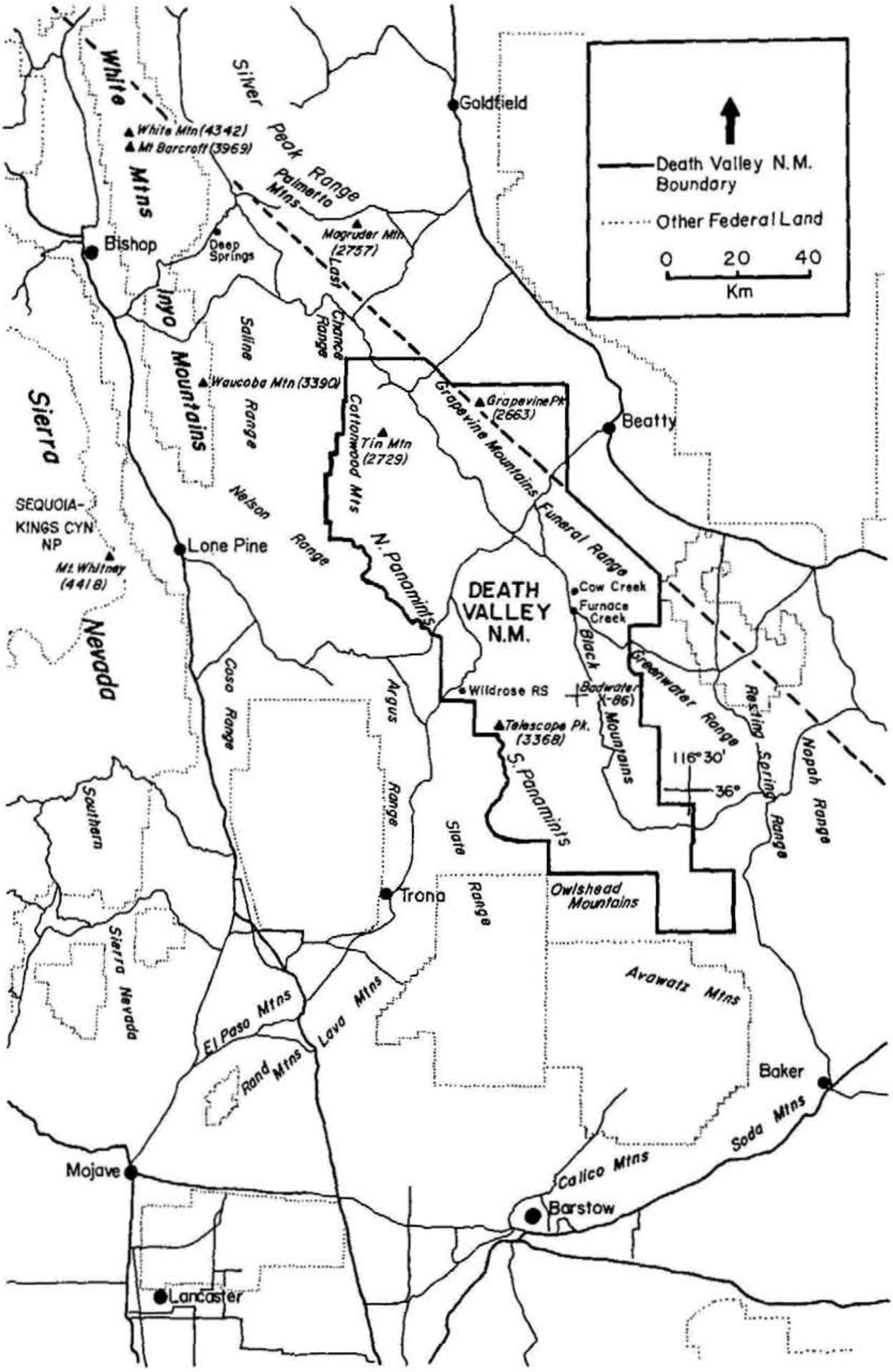


Fig. 1. Regional map of the northern Mojave and southwestern Great Basin deserts of California and Nevada with Death Valley National Monument. (Some southern Nevada landmarks such as the Spring Mountains, Sheep Range, and Desert National Wildlife Refuge [formerly the Desert Game Range] are mentioned in the text but are not included here.)

Climate

The northern Mojave and southwestern Great Basin are basically rain-shadow deserts. However, both also exhibit climatic characteristics associated with continentality: severe conditions of winter cold and great annual ranges of temperatures. This is especially true of the southern Great Basin. Furthermore, the climate of the northern Mojave exhibits some subtropical properties such as mild winters (at low elevations), great summer heat, and summer convectional rainfall (Logan 1968; Johnson 1976; Rowlands 1978; Rowlands et al. 1982; Lathrop and Rowlands 1983).

Huning (1978) has reviewed climatic characteristics of the California deserts, including the Mojave Desert. Rowlands (1993) has done likewise but also focused on bioclimatology and the effects of climate on vegetation patterns throughout the California deserts.

Vegetation

Vegetation of the region has been summarized by Rowlands (1988). Vegetation types range from pickleweed (*Allenrolfea occidentalis*) dominated halophytic assemblages at the bottom to subalpine woodland with limber pine (*Pinus flexilis*) and bristlecone pine (*P. aristata* var. *longaeva*) at the top of the elevational gradient. In between are desertholly saltbush (*Atriplex hymenelytra*), creosotebush (*Larrea tridentata*), bursage (*Ambrosia dumosa*), shadscale (*Atriplex confertifolia*), blackbrush (*Coleogyne ramosissima*), spiny hopsage (*Grayia spinosa*), Nevada ephedra (*Ephedra nevadensis*), spiny menodora (*Menodora spinescens*), sagebrush (*Artemisia tridentata*), pinyon (*Pinus monophylla*), and juniper (*Juniperus osteosperma*). Desertholly–creosotebush assemblages on the lower fans integrate with creosotebush–bursage on the upper fans. Shadscale occupies the middle elevation, followed by a series of mixed scrub assemblages of blackbrush, spiny hopsage, Nevada ephedra, and spiny menodora (not necessarily in elevational sequence). Middle elevation vegetation merges into sagebrush scrub and pinyon–juniper at the upper elevations below the subalpine woodland.

In the southern end of nearby Saline Valley (adjacent to and west of northern Death Valley), Randall (1972) examined the climatic, edaphic, and topographic controls of vegetation distribution. Among these were elevation, steepness of slope and slope aspect, and incident solar radiation. He correlated these with changes in vegetation along the complex elevation–moisture gradient. He found no tendency for the composition of the vegetation to vary discretely with respect to environmental gradients. Further, he found no evidence of any interspecific interactions of the types that could lead to discontinuous variation in the vegetation. Finally, he found no evidence that the environmental tolerance limits for different species might coincide to promote abrupt changes in the composition of the vegetation.

Although it is still useful to break the continuum down into units for the basis of discussion, Randall (1972) makes some important points that directly conflict with the interpretations of Kurzius (1981), Schramm (1982), Peterson (1984), and Annable (1985), who classified their vegetation data taken from four Death Valley mountain ranges into vegetation zones consisting of discrete plant associations. An association is a plant community of definite floristic composition with uniform physiognomy and growing in uniform habitat conditions (Shimwell 1971).

Within the region of interest, I will (1) examine the relations between elevation and the three climatic gradients (precipitation, temperature, and potential evapotranspiration; Thornthwaite 1948; Thornthwaite and Mather 1957); (2) describe the extent of present-day horizontal and vertical variation in these climatic elements; (3) examine how this variation affects regional vegetation patterns; and (4) determine whether or not discrete plant assemblages or vegetation zones should be defined in the Death Valley region as opposed to a complex of interdigitating plant assemblages.

Methods

Data Sources

Climate

Data sources for climate included U.S. Weather Bureau/National Oceanographic and Atmospheric Administration (NOAA) raw and summarized climatic data (U.S. Weather Bureau 1952, 1958, 1964, and 1956–1987). Unfortunately, the desert areas of rural California and adjacent Nevada are sparsely occupied by weather stations. Data were available for only three weather stations in Death Valley: Cow Creek, Greenland Ranch (now renamed Furnace Creek), and Wildrose Ranger Station. Only the latter two still operate, whereas historical data are available for Cow Creek. Data from 10 additional stations in either the adjacent Mojave Desert or southern Great Basin Desert were also incorporated to depict the area's climate.

To obtain usable data from the 13 stations of interest, I could not restrict the data set to those stations having identical lengths or periods of record. The only criteria for admittance of a station into the data set were that it (1) occur within the study area (Fig. 1); (2) have at least 10 years of record; and (3), with the exception of Hidden Forest Camp, Nevada, collect observations on both temperature and precipitation (Table). Definitions of climatic terms used in this paper (e.g., arid, semiarid, subhumid), as well as a discussion of their derivations, can be found in the review by Hare (1973).

Vegetation

Kurzius (1981), Schramm (1982), Peterson (1984), and Annable (1985) provided raw vegetation data from the Grapevine, Black, Cottonwood, and Funeral mountains (respectively), Death Valley National Monument. Clokey

Table. Summary of climatic data from 13 meteorological stations located in the northern Mojave Desert and the southern Great Basin Desert of California and Nevada.[a]

Station	Elevation (m)	Mean annual ppt(mm)	Coefficient of variation	Summer ppt (as % of annual)	Mean temperatures (° C)		
					January minimum	July maximum	Annual
Greenland Ranch (Death Valley)	−51	41.4	0.69	18.4	3.1	46.6	24.4
Cow Creek (Death Valley)	−38	49.5	0.69	17.4	4.9	46.7	25.1
Trona	517	82	0.69	8.4	−0.6	41.3	18.9
Desert Game Range, Nevada	890	103.9	0.47	27.1	−1.5	38.3	16.8
Beatty, Nevada	1,010	118	0.5	14.7	−2.4	37.5	15.3
Sarcobatus, Nevada	1,225	89.9	0.49	40	−6.5	36.8	13.5
Wildrose Ranger Station[b]	1,250	185.2	0.52	19.8	−1.6	35.1	14.5
Bishop	1,252	157.5	0.38	4.7	−6.2	34.9	13.4
Deep Springs	1,593	131.3	0.43	12.8	−10.1	33.4	11.3
Goldfield, Nevada[c]	1,733	127.8	0.61	23.3	−6.8	32	10.5
Hidden Forest Camp, Nevada[d]	2,377	319.5	0.24	32.8	—	—	—
White Mountains 1[b]	3,094	358.1	0.3	27	−13.4	19	1
White Mountains 2[b]	3,801	496	0.4	21	−30	17	−3

[a]Data from Hidden Forest Camp, in the Sheep Mountains of Nevada, were not used in subsequent regression analyses since this station only collected precipitation data.
[b]Data for these stations were obtained from the U.S. Weather Bureau (National Oceanographic and Atmospheric Administration [NOAA]) Annual Summaries 1961–1987 over the years of record for the station. Data for all other stations were obtained from U.S. Weather Bureau (1964) and were based on the years of record. At least 10 years of records were required for any station to be admitted into the data set.
[c]Data based on U.S. Weather Bureau Climatic Summary of the United States—Supplement for 1931 through 1952 (U.S. Weather Bureau 1952).
[d]Data based on U.S. Weather Bureau summaries of precipitation from storage gages (U.S. Weather Bureau 1958).

(1951), Lloyd and Mitchell (1973), and DeDecker (1984) were consulted to confirm or explain elevational ranges of the region's primary plant species. Other vegetation information was gleaned from Randall (1972), Rowlands (1978, 1988, 1993), and Rowlands et al. (1982).

Analytic Methods

Climate

Potential evapotranspiration (PotE) was calculated using the Thornthwaite temperature dependent model (Thornthwaite 1948; Thornthwaite and Mather 1957). The method of Thornthwaite (1948) empirically reduced PotE to a function of temperature and day length. Potential evapotranspiration was calculated either from tables provided in Thornthwaite and Mather (1957) or by using a Quattro Pro V.3 spreadsheet.

Bailey (1981) proposed a similar model and criticized the Thornthwaite model on the basis that the latter underestimates PotE as estimated by the Penman and Penman–Montieth Model (Penman 1956; Montieth 1965). For an example, see figure 8.2 in Gay (1981). Comparison of PotE values derived by the author with those derived by Bailey's approach, however, indicates that Bailey's approach underestimates PotE relative to Thornthwaite's. The former approach was abandoned because it did not seem to offer any advantages.

Criticisms notwithstanding (Bailey 1981), the Thornthwaite model remains the only widely used predictor of PotE based on temperature alone. Other models based on radiation or temperature–radiation combinations (Sellers 1965; Barry 1969; Gay 1981; Yitayew 1990) may more closely approach empirical results. Those models are of limited usefulness, however, due to lack of long-term monitoring stations with proper equipment to record the necessary data. Yitayew (1990), in calculating reference PotE for the State of Arizona using the Blaney–Criddle model (Blaney and Criddle 1962), had to extensively interpolate humidity and solar radiation values using mapped isolines. In extremely arid areas, PotE does underestimate evapotranspiration (Sellers 1965; Barry 1969; Gay 1981). As a climatic index used to compare the relative aridity among different sites, however, PotE is greatly used and accepted (Sellers 1965; Mather and Yoshioka 1968; Etherington 1975; Major 1977).

Vegetation

Site vegetation-cover and elevational data presented in previous studies were reanalyzed. Kurzius (1981) studied the vegetation of the Grapevine Mountains, Death Valley National Monument. Randall (1972) examined the vegetation of southern Saline Valley (about 65 km southwest of the Grapevine Mountains). Rowlands (1978) surveyed Joshua-tree (*Yucca brevifolia*) communities throughout the Mojave Desert. The relation between total vegetation cover and elevation within the study areas was investigated. Cover data were employed as a dependent variable in linear regression analyses with elevation as the independent

variable. Cover data, originally reported as a percentage, were transformed (Neter and Wasserman 1974; Ott 1988) using the arcsine transformation where Y′ is transformed cover and Y is the original observation in a fraction from 0.00 to 1.00.

Results and Discussion

Precipitation and Precipitation Patterns

Mean annual precipitation (ppt) derived from data collected by weather stations within the northern Mojave and southern Great Basin deserts was generally less than 200 mm per year. At the highest elevations in the desert mountains, precipitation exceeded 350 mm per year (Table). Much of the latter was in the form of snow, which at the White Mountains stations averaged 2,720 mm and 3,876 mm, respectively, between 1956 and 1960 (U.S. Weather Bureau 1964; Rowlands 1993). The relative amounts of summer (June–September) precipitation in the region ranged between 5 and 40% of the annual total; the percentage generally increases from west to east.

Mean annual precipitation lapses predictably with elevation in the northern Mojave and southwestern Great Basin desert region (Fig. 2). Over the observed elevational range, mean annual precipitation increases with elevation according to the formula $Y = 0.111X + 10.736$ ($r^2 = 0.894$; $SE_{x\text{-coef.}} = 0.0121$; $SE_{y\text{-est}} = 45.650$; $n = 12$; Y = precipitation in mm; X = elevation in m).

In arid and semiarid environments, the variability of yearly precipitation as measured by the coefficient of variation (C.V.) is a more meaningful bioclimatological statistic. Plants and animals have become adapted to the extremes of climate as a means of biologically responding to the unpredictability. Mean annual rainfall is useful mainly as an indication of differences in relative dryness among localities. Even with the possible statistical drawbacks of this measure in arid regions, the coefficient of variation does give some relative information regarding precipitation variability (Huning 1978).

The C.V. within the region of interest decreases with increasing elevation although the points are scattered. The two Death Valley stations have the most variable precipitation regimes — according to Huning (1978), the most variable in the entire California Desert (Table; Fig. 3). The coefficient of variation for Goldfield seems high, considering its elevation. This station is located in the lee of the Sierra Nevada, the White Mountains, and the Silver Peak Range. The deep rain shadow may account for the relatively high variability. The lowest values for the coefficient of variation were observed at Hidden Forest Camp. This location, although lower in elevation than the two White Mountains stations, receives a relatively greater proportion of its annual rainfall during summer. This may explain the higher relative predictability of annual precipitation.

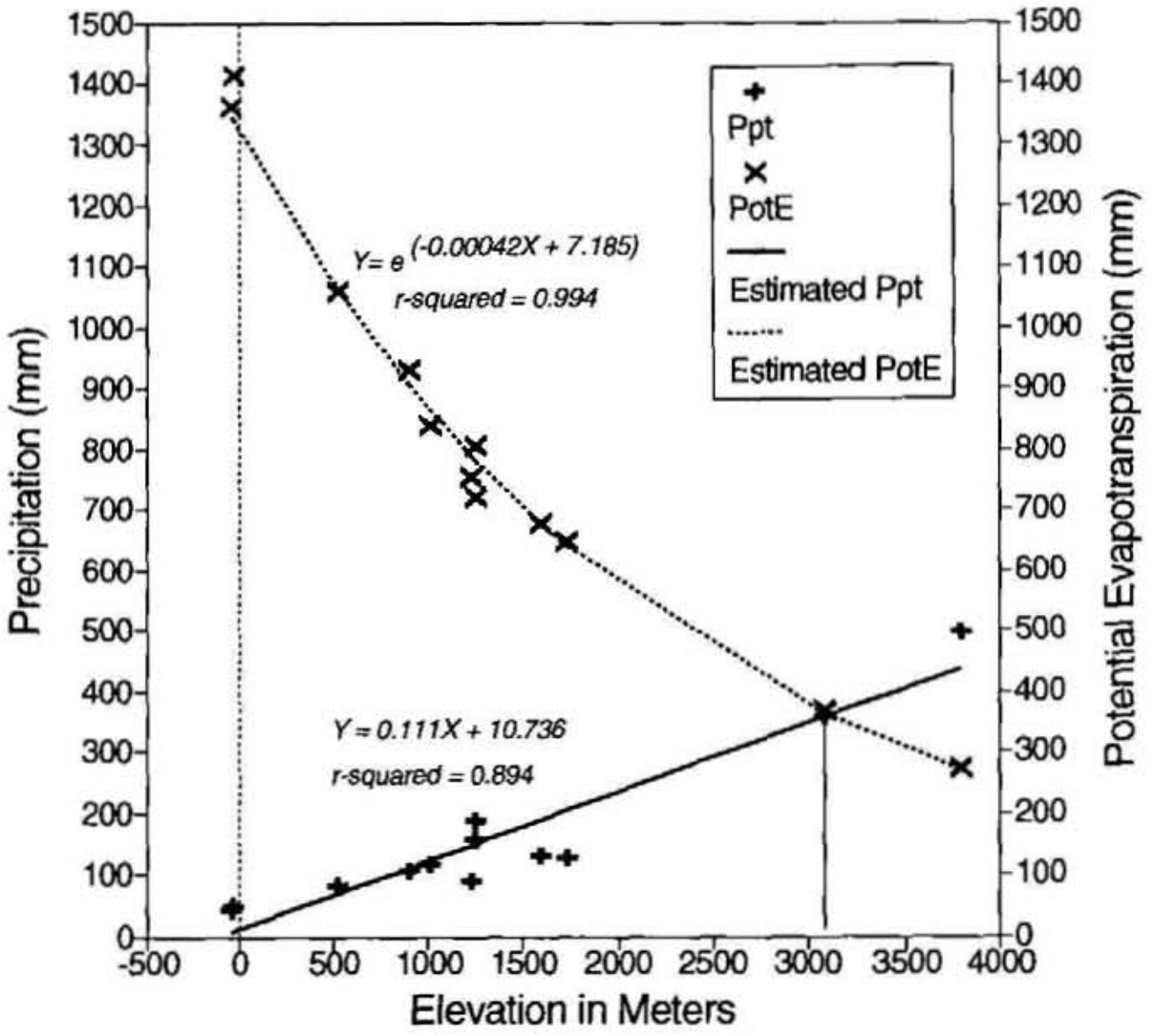


Fig. 2. Relation between mean annual precipitation and potential evapotranspiration (calculated according to the Thornthwaite 1948 model) within the northern Mojave and southwestern Great Basin deserts. (The arid–humid boundary is predicted to occur at 3,100 m.)

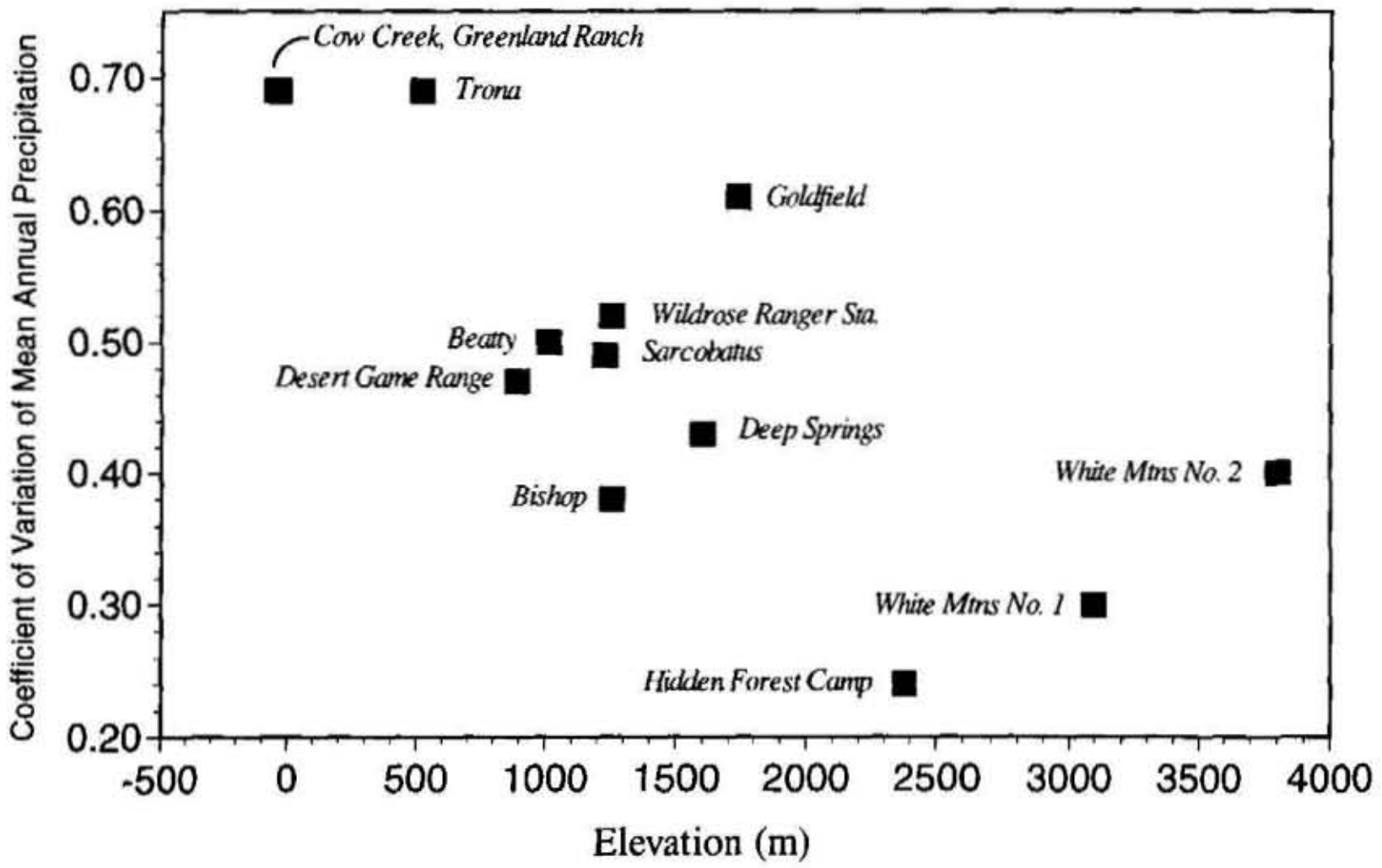


Fig. 3. Scatterplot of coefficients of variation (C.V.) for annual precipitation reported for the stations in the Table.

Potential Evapotranspiration

Potential evapotranspiration, like temperature, lapses with elevation; but, unlike temperature, the PotE lapse rate seems to be defined by an exponential function. A curvilinear fit is logical because a linear model could result in negative values of PotE at high elevations and the Thornthwaite PotE is based on a cubic function of mean monthly temperatures that decrease with elevation. The model takes the form $Y = e^{(-0.00042X + 7.185)}$ ($r^2 = 0.994$; $SE_{x\text{-coef.}} = 1.03E\text{-}05$; $SE_{y\text{-est}} = 0.0388$; $n = 12$; Y = PotE in mm; X = elevation in m). The fitted curve is displayed in Fig. 2. The intersection of the PotE and ppt lapse rates determines a theoretical arid–humid boundary, which in this instance occurs at approximately 3,100 m. However, even above the arid–humid boundary, PotE may exceed precipitation during the hottest and driest part of summer. These observations are consistent with Major (1977), whose estimates of the elevation of the arid–humid boundary in the eastern Mojave were also derived from the Thornthwaite model. Perhaps not coincidentally, limber pine and bristlecone pine, which define desert subalpine woodland, are most abundant between 2,900 and 3,355 m in the White Mountains (Lloyd and Mitchell 1973) and between 3,140 and 3,370 m in the Panamint Range (Vasek and Thorne 1977). The exceptions are shaded drainages where trees have been found as low as 2,200 m (Vasek and Thorne 1977). Refer to Clokey (1951), Bailey (1970), Lloyd and Mitchell (1973), Griffin and Critchfield (1972), Vasek and Thorne (1977), and DeDecker (1984) for additional information on elevational ranges of these tree species.

Temperature

Temperatures are extreme in the Death Valley region of the Mojave Desert. Mean minimum January temperatures vary between 4.9° C on the floor of Death Valley and −29.7° C at the White Mountains station 2 (Table) at an elevation of 3,801 m (Fig. 4). Similarly, mean July maxima range between 46.7 and 17.4° C for these two sites, respectively. Absolute extremes for Death Valley are −9.2 and 56.6° C.

Over the observed elevational range, the mean January minimum temperature (° C) lapses according to the regression equation $Y = -0.008X + 4.448$ ($r^2 = 0.901$; $SE_{x\text{-coef.}} = 0.0008$; $SE_{y\text{-est}} = 3.015$; $n = 12$; Y = temperature in degrees C; X = elevation in m). Likewise, the July mean maximum lapses according to the regression equation $Y = -0.008X + 45.701$ ($r^2 = 0.988$; $SE_{x\text{-coef.}} = 0.0003$; $SE_{y\text{-est}} = 1.051$; $n = 12$). January temperature lapse rates have a lower r^2 (coefficient of determination) than July temperature lapse rates if elevation is the only independent variable; localized cold air inversions are probably responsible for this (Rowlands 1978, 1993). During cold air inversions, marked differences in temperature may occur over elevational increments as small as 1.5 m (Beatley 1974, 1975). Temperatures on surrounding slopes may be several degrees higher than in the basin bottoms. For example, data from Greenland Ranch (now Furnace Creek, near the basin bottom) indicate a mean

January minimum almost 2° C lower than Cow Creek (situated about 13 m higher on an alluvial fan 6.5 km north). The local distribution of vegetation may be affected by the temperature inversions that habitually form within the numerous closed basins of the northern Mojave–southern Great Basin. This has been described in great detail by Beatley (1974, 1975, 1976).

Mean annual temperature follows a similar pattern to mean July maxima and mean January minima: $Y = -0.007X + 23.114$ ($r^2 = 0.988$; $SE_{x\text{-coef.}} = 0.0002$; $SE_{y\text{-est}} = 0.913$; $n = 12$).

Relations Between Climatic Elements and Vegetation

Cover increases concomitantly with precipitation (Fig. 5). No direct correlation between the precipitation lapse rate and increase in total vegetation cover is claimed because the vegetation sites do not directly correspond with the meteorological stations. However, a comparison of the relations between both elevation and precipitation and elevation and cover is instructive. Because of the close correspondence between elevation and precipitation, it is felt that the former is a good surrogate for the latter.

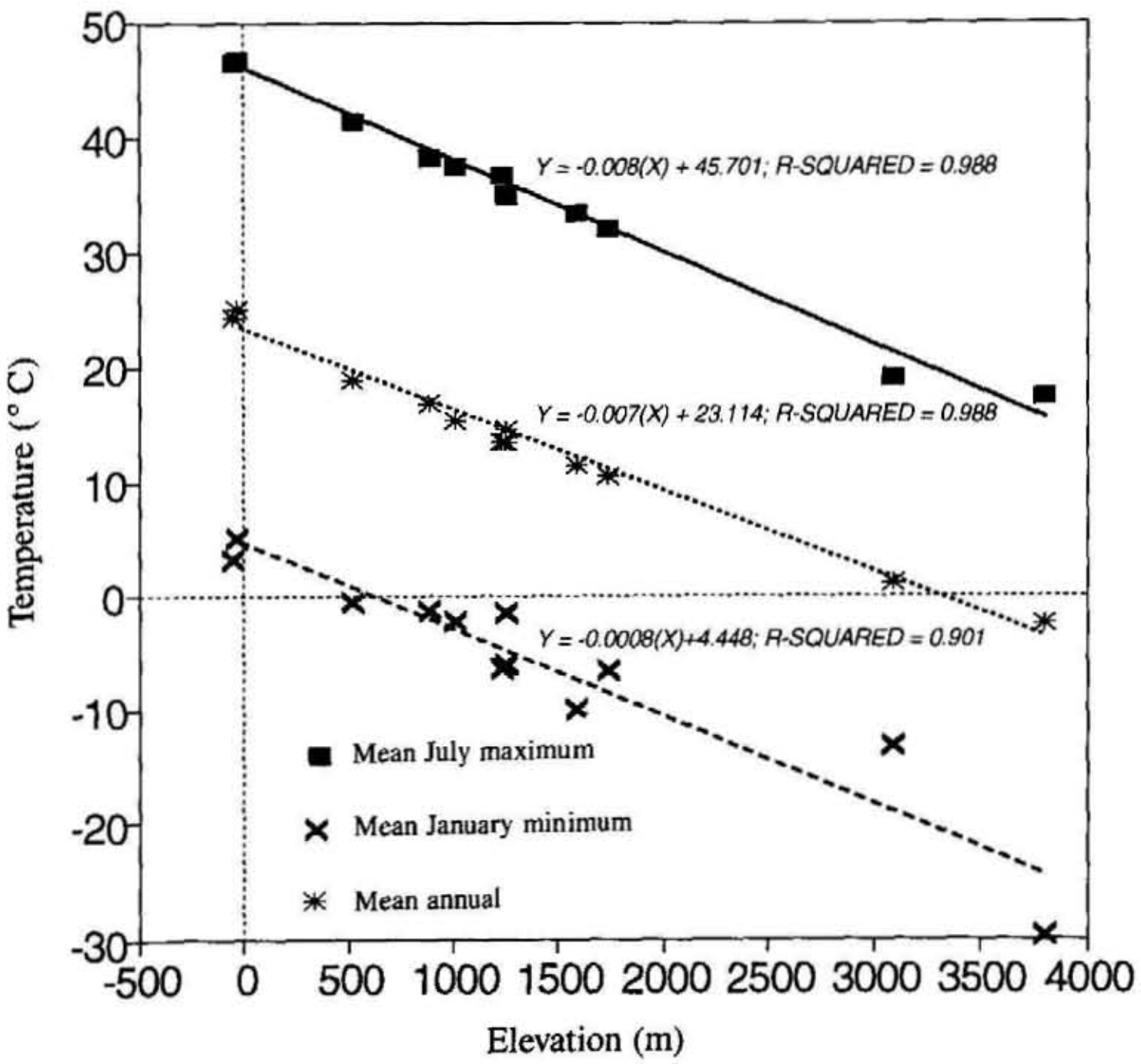


Fig. 4. Relation between mean annual, mean January minimum and mean July maximum temperatures, and elevation within the northern Mojave and southwestern Great Basin deserts.

Linear regression analysis of the Kurzius (1981) Grapevine Mountains data revealed that total perennial vegetation cover increased linearly over the observed elevational range: $Y = 0.01075X + 7.313$ ($r^2 = 0.734$; $SE_{x\text{-coef.}} = 0.0007$; $SE_{y\text{-est}} = 4.2873$; $n = 81$; Y = arcsine of the square root of the total percent ground cover; X = elevation in m).

Similar treatment of the Saline Valley data by Randall (1972) yields a similar increase in cover with elevation except that the slope of the linear regression is somewhat steeper: $Y = 0.01680X - 2.5639$ ($r^2 = 0.848$; $SE_{x\text{-coef.}} = 0.00107$; $SE_{y\text{-est}} = 2.4554$; $n = 46$). The Grapevine Mountains, farther to the east and in the rainshadow of the Cottonwood and Last Chance range, seem to be drier than the regional data would indicate. Both equations are similar to the estimate derived from Rowlands's (1978) data ($Y = 0.01410X + 8.4159$; $r^2 = 0.565$; $SE_{x\text{-coef.}} = 0.0029$; $SE_{y\text{-est}} = 4.4735$; $n = 20$).

Elevational Ranges of Occurrence of Characteristic Species

Although localized gradients (e.g., salinity [Hunt 1966] and calcium–magnesium content of surface outcrops [Stebbins and Major 1965; Raven and Axelrod 1976]) are very important within a regional setting, cover of perennial plant species varied continuously along the elevational gradient in the northern Mojave Desert. Kurzius's (1981) data, subject to reanalysis and presentation in

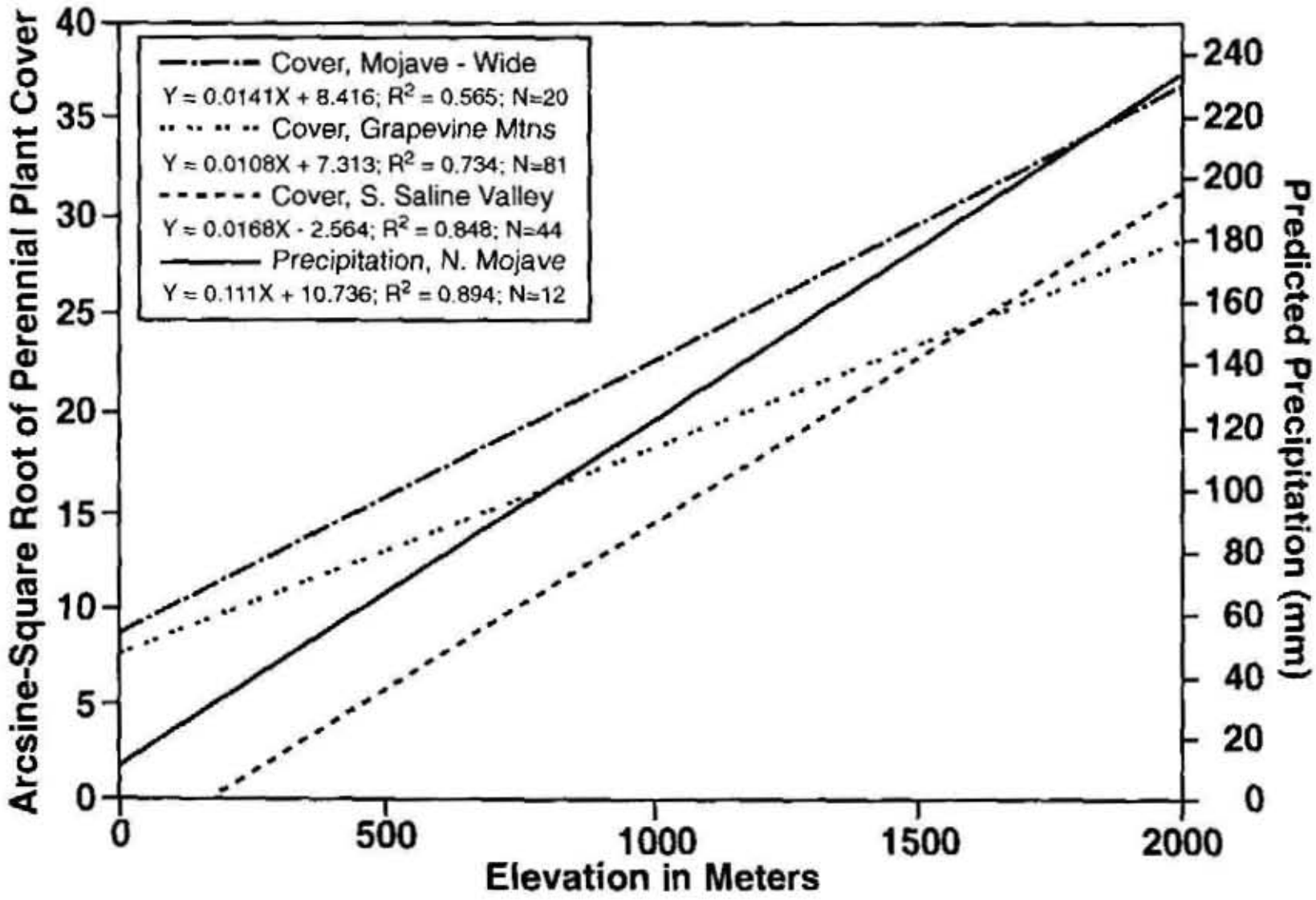


Fig. 5. Comparison of three estimations of increase in total cover of persistent perennial plant species with elevation and the precipitation lapse rate. (Percent cover values have been transformed according to the arcsine—square root method.)

the form of a spindle graph (Fig. 6), shows the overlapping, continuous nature of the distribution of the more important, characteristic perennial plant species with elevation.

The ranges of occurrence of characteristic perennial plant species were plotted relative to elevation and the Thornthwaite model for PotE (Fig. 7). In plotting, the relations between elevation and PotE (Fig. 2) were used, as well as the quantitative vegetation data in Randall (1972), Lloyd and Mitchell (1973), and Kurzius (1981). Clokey (1951), Bailey (1970), Vasek and Thorne (1977), and DeDecker (1984) were used for cross-checking. The overlapping nature of the ranges of tolerance with respect to these metrics is apparent. There also seems to be a tendency of species occupying the lower portions of the elevation–moisture gradient to have broader ranges of tolerance to estimated PotE (i.e., thermal) regimes than those species at the top of the gradient (e.g., compare *Larrea tridentata* to *Pinus monophylla*). An exception seems to be *Artemisia tridentata*, which even overlaps (albeit slightly) with *Larrea* at or

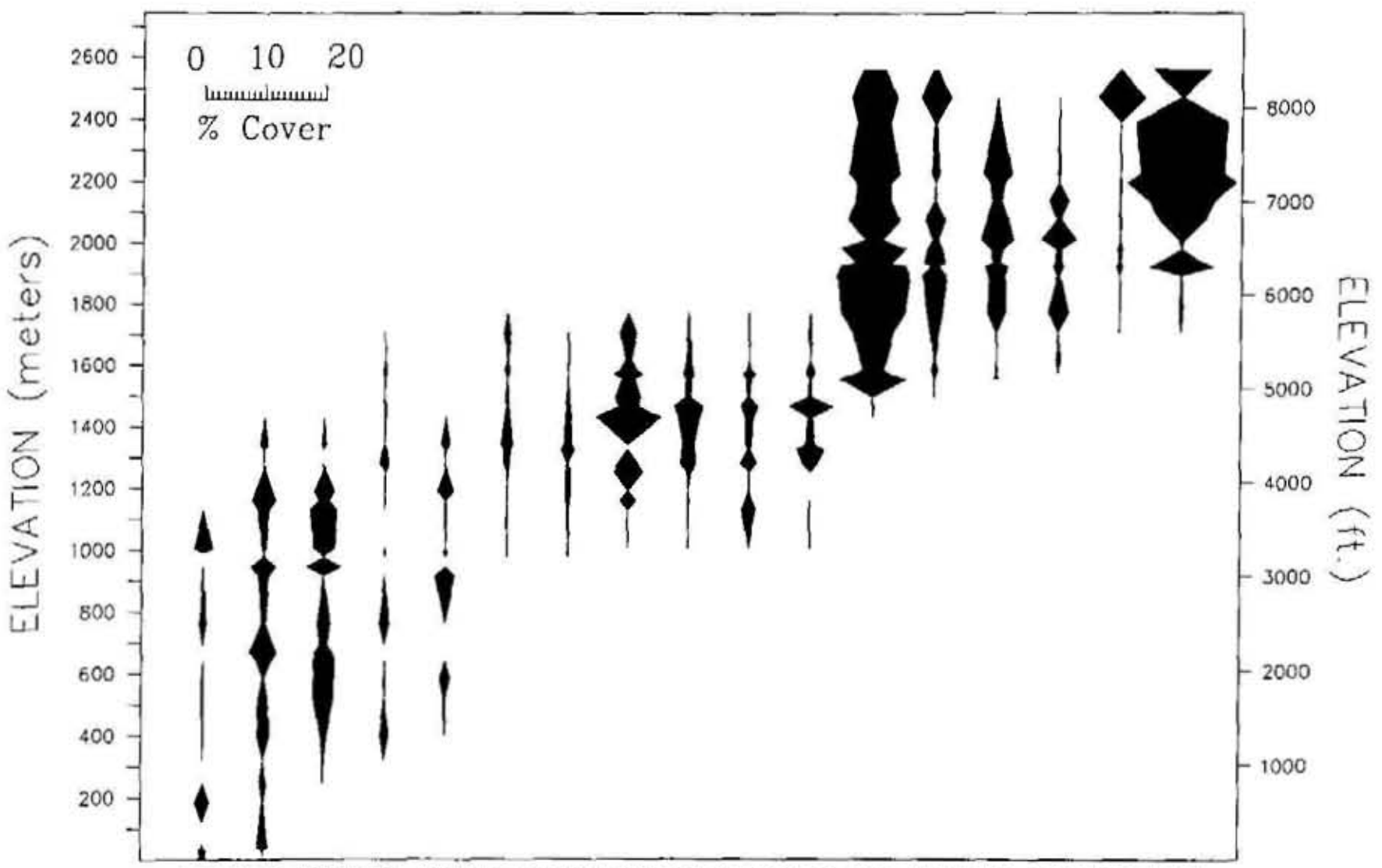


Fig. 6. Spindle graph showing elevation and the change in cover of the more important persistent, perennial plant species in the Grapevine Mountains of Death Valley National Monument. (Constructed after reanalysis of raw data reported in appendixes in Kurzius 1981.) ATHY = *Atriplex hymenelytra*; LATR = *Larrea tridentata*; AMDU = *Ambrosia dumosa*; HYSA = *Hymenoclea salsola*; ATCO = *Atriplex confertifolia;*, ERFA = *Eriogonum fasciculatum*; LYAN = *Lycium andersonii*; MESP = *Menodora spinescens*; EPNE = *Ephedra nevadensis*; GRSP = *Grayia spinosa*; ERCO = *Ericameria (Haploppapus) cooperi*; ARTR = *Artemisia tridentata*; CHVI = *Chrysothamnus viscidiflorus*; PUGL = *Purshia glandulosa*; EPVI = *Ephedra viridis*; ERMI = *Eriogonum microthecum*; PIMO = *Pinus monophylla*.

around a PotE value of 700 mm/year. This is slightly different from observations of Mather and Yoshioka (1968), who stated that a PotE value of 800 mm/year separates creosotebush from sagebrush. However, the latter based their discrimination on latitudinal variation in PotE and used the Kuchler (1964) vegetation map as a source of information on vegetation rather than quantitative data collected along an elevational gradient.

Mixed-scrub in Fig. 7 refers to a collection of perennial shrub species such as Anderson wolfberry (*Lycium andersonii*), California buckwheat (*Eriogonum fasciculatum*), Cooper goldenbush (*Ericameria cooperi*), Nevada ephedra (*Ephedra nevadensis*), and spiny menodora (*Menodora spinescens*). These species tend to have highly coincidental elevational ranges (contrary to Randall 1972) but, with the exception of spiny menodora, rarely show any strong quantitative dominance in this plant assemblage (Fig. 6). It would be tempting to classify this grouping as a discrete community type (i.e., mixed scrub or mixed shrub), as has been done by Kurzius (1981), Peterson (1984), Annable (1985), and others. However, the strong overlap of this midelevation assemblage with woodland and big sagebrush components above it, as well as Mojave desert-scrub components below, argues against the classification.

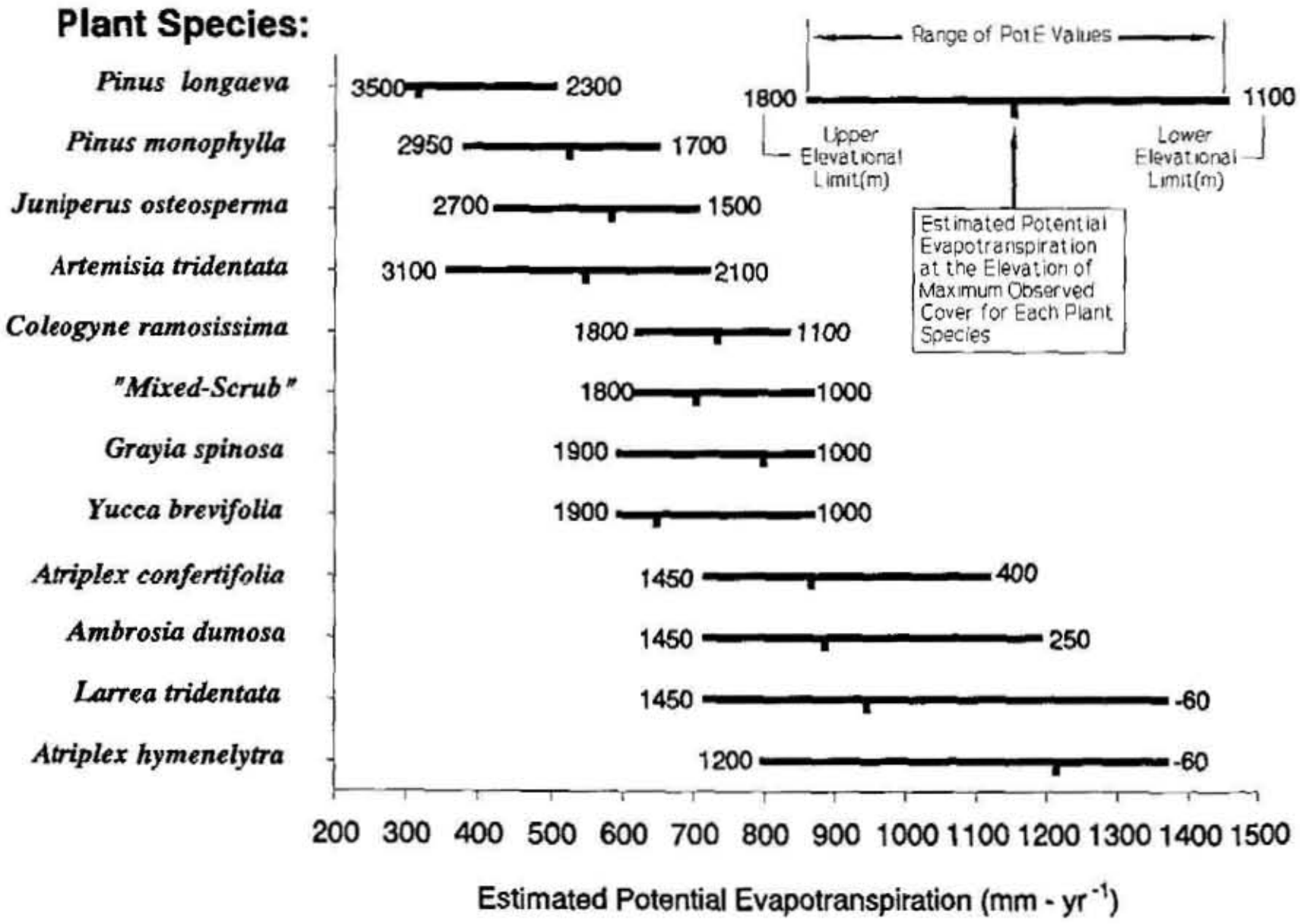


Fig. 7. Ranges of occurrence of some characteristic, community-defining shrubs and trees of the northern Mojave and southern Great Basin desert region with respect to potential evapotranspiration in millimeters per year. (The upper and lower elevational limits [*numbers* at the ends of the PotE range bars] for each species are given as a convenience. The relation between elevation and PotE is not linear. Refer to Fig. 2 for a more accurate representation.)

Conclusions

We can infer from regional elevational trends in climatic elements that the climates of Death Valley National Monument range continuously from the hot, arid, vegetationally barren salt flats and desertholly-dominated lower alluvial fans on the valley floor to the colder, subhumid subalpine zone at the highest elevations of the Panamint Range. Although microclimatic factors may be important, elevation is probably the single most important variable controlling mean annual precipitation, temperature, and potential evapotranspiration within the region.

The arid–humid boundary (sensu Major 1977) is estimated to occur at or around 3,100 m in this region of the desert. The subhumid zone is highly restricted in the Panamint Range because the area of the mountain mass above 3,100 m is quite small (around 0.2% of the total area). Thus, both the extent and diversity of woodland and forest plant assemblages is limited. Limber pine and bristlecone pine associations are found only on a few isolated peaks and ridges in the Panamints, where it is the only woodland type in the range other than pinyon–juniper. Thus, practically every climatic type found within the California desert can be identified within Death Valley National Monument alone, but the far greater portion of the monument is arid and semiarid. The vegetation reflects this in the dominance of the landscape by Mojave and Great Basin desertscrub in basins and on alluvial fans and by Great Basin conifer woodland (as defined in Brown 1982) on upland sites above 1,800 m.

Between the arid and subhumid ends of the spectrum, the vegetation of Death Valley seems to be distributed continuously along a complex elevation–moisture gradient. This is the situation elsewhere in the Southwest (Whittaker 1975; Whittaker and Niering 1975) as well as within the region (Randall 1972). Along with changes in vegetation composition vertically, cover increases monotonically with elevation and moisture, at least over the range of elevation observed. Horizontal gradients of vegetation compositional change can be observed, but generally in response to salinity and groundwater availability. Nevertheless, it is valuable to break up this continuum into discrete vegetation types such as those delimited by Rowlands (1988) and Coonan et al. (1990). This was done in order to facilitate communication among researchers and resource managers and to establish vegetation management units (VMU's) for the purposes of prescribed fire management and other applications where vegetation mapping is essential. Otherwise, vegetation of Death Valley National Monument and the surrounding desert is a complex of interdigitating plant species components.

The response of vegetation to climate is both direct and indirect (e.g., through effects on soils development). Analysis of climatic parameters may reveal differences that seem to be related to different vegetation formation-classes: geographically widespread communities of similar physiognomy and life form and even formations — a group of communities in a single region of similar physiognomy (Shimwell 1971). Climate by itself, however, will not be adequate to provide explanations for differences in vegetation at the association

level (Mather and Yoshioka 1968). This is certainly the situation in Death Valley. Vegetation formations (Mojave desertscrub, Great Basin desertscrub, Great Basin conifer woodland, etc.; i.e., *Regional Formations* or *Biomes* of Brown 1982) sort out well along the elevational gradient. Plant associations are not easily delineated with respect to climatic factors alone, however, as indicated by the presence of the mixed-scrub type discussed above. Climate is simply one factor in a multivariate array of physical and biological parameters that affect vegetation (Major 1951, 1977).

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Preliminary Results From a Demographic Study of Spotted Owls in Sequoia and Kings Canyon National Parks, 1990–1991

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Abstract. In a study area of approximately 343 km^2 in Sequoia and Kings Canyon national parks, 54 adult and subadult and 21 fledgling California spotted owls (*Strix occidentalis occidentalis*) were located in 1990 (crude density = 0.157 owls/km^2). Comparable numbers in 1991 were 60 adults and subadults and 1 fledgling (crude density = 0.175 owls/km^2). Thirteen of 22 pairs counted in 1990 had young, and 1 of 23 pairs counted in 1991 had young. The reproduction rate (the proportion of pairs examined for reproduction that fledged young) was 0.88 in 1990 and 0.08 in 1991; the combined turnover rate for 1990 and 1991 was 19.5%.

Key words: Sequoia, Kings Canyon, spotted owl, *Strix occidentalis occidentalis*, density, demographic, nesting, reproduction.

This report summarizes key activities of a demographic study of the California spotted owl (*Strix occidentalis occidentalis*) in the protected forests of Sequoia and Kings Canyon national parks in 1990 and 1991. Results will be compared with a companion study of spotted owl demographics in a neighboring managed national forest. Standard methods and objectives were adapted to complement existing information and to standardize data collection between this study site and other demographic study sites in the Sierra Nevada. Objectives were to

1. estimate density of spotted owls and occupancy status of owl territories in a designated study area,
2. estimate age-specific vital rates (reproduction, mortality),
3. assess site fidelity among individual spotted owls,
4. estimate turnover rates (replacement of birds between years of the study), and
5. measure the quantity and distribution of habitats within the study area.

Study Area

The study area is in the southern Sierra Nevada within Sequoia and Kings Canyon national parks, approximately 80 km from Fresno, California (Figure). The study location covers 343 km^2 and has three distinct habitat zones. The oak–woodland type, at the lowest elevations (610–1,220 m) encompasses 83 km^2; the canopy is dominated by digger pine (*Pinus sabiniana*), blue oak (*Quercus douglasii*), and live oak (*Q. wislizenii*). Various foothill chaparral species are abundant in large, uniform blocks on southwest-facing slopes. The mixed-conifer type (1,220–2,439 m) occupies 230 km^2. Conifer tree species within stands include sugar pine (*P. lambertiana*), ponderosa pine (*P. ponderosa*), Jeffrey pine (*P. jeffreyi*), white fir (*Abies concolor*), California red fir (*A. magnifica*), incense-cedar (*Calocedrus decurrens*), and black oak (*Q. kelloggii*). Large stands of giant sequoia (*Sequoiadendron giganteum*) are scattered throughout the entire zone. Some logging took place in this zone in the late 1800's and early 1900's, but generally all forest types are currently in mature or old-growth stages. The high-elevation coniferous type (2,440–2,743 m) covers



Figure. Location of study area in Sequoia and Kings Canyon national parks, California.

29 km^2. This zone is dominated by western white pine (*P. monticola*), lodgepole pine (*P. contorta*), and California red fir.

Methods

We attempted to locate, capture, and color band all spotted owls within the study area during a survey period from 1 March to 30 September each year. Birds were located by nighttime and daytime calling surveys using vocal imitations of spotted owls to elicit responses. Surveys included point, leapfrog road, walking-cruise, and walk-in (Forsman 1983). We tried to survey all parts of a given site until an owl responded or, if no owls were detected, until six complete surveys were accomplished. Visits were spaced at least 4 days apart with a goal of four nighttime and two daytime visits. One completed survey was defined as covering an entire delineated site for at least 10 min of calling. At historic locations, we began a survey route at the calling point nearest the center of activity or nest tree. No site within the study area was prejudged to be without owls, regardless of vegetation type, slope, aspect, or elevation.

We attempted to determine pair, nesting, and reproduction status on all spotted owls detected within the study area. Pair status required one or more of the following on two or more occasions at least 1 week apart:

1. a male and female seen or heard less than 400 m from each other;
2. a male observed taking a mouse to a female, or a female confirmed (heard or seen) on a nest;
3. one or both adults seen with young; and
4. a previously marked pair of owls seen in their historic roost area.

Single status was established by the presence or response of a single owl in a site on three or more occasions within the nesting and fledgling periods (1 March–31 August), with no response by an owl of the opposite sex after six complete visits. Unknown status was established by a response of a male or female that did not qualify for pair or single status.

Nesting status was established between 1 March and 1 June if one or more of the following criteria were determined:

1. a female detected on the nest, either member of a pair carried prey to the nest, or a combination of these observed two or more times at least 1 week apart (if this activity was observed after 1 May, a single observation was sufficient);
2. a female possessed a brood patch when examined between mid-April and mid-June; or
3. young detected in the presence of one or both adults.

Nonnesting status was established between 1 March and 1 June if one or more of the following were determined:

1. a female was observed roosting for extended periods (> 0.5 h) on at least two visits between 1 April and 1 June (visits were spaced so the first and last visits were at least 3 weeks apart to ensure that the observation period was sufficient to witness a late nesting attempt);
2. a female did not possess a brood patch when examined in hand from mid-April to mid-June; or
3. on two or more visits between 1 March and 1 June, four mice were offered to one or both members of a pair and one or both took at least two mice but did not deliver them to a nest.

If nesting status was not determined before 1 June and young were not detected, the owls were classified as unknown nesting status. If repeated visits and offering of prey to a pair initially classified as nesting and one or both of the pair ate or cached the prey, sat with the prey, or refused to take the prey, the nesting attempt was reclassified as failed. In addition, if the nest was known to have been destroyed or disturbed and the adults abandoned the nest, the nesting was classified as failed.

Reproduction success was determined by returning to the nest site as the young left the nest, usually in late May to mid-June. We made two or more visits to each nest site to find and count the fledged young, timing our visits so the young were observed as soon as possible after leaving the nest. We offered mice to one or both adults on all visits to the nest site. The sight of an adult with prey usually stimulated the young to beg, revealing their location and number. At least one follow-up visit was made 3–10 days after the young were first seen because it was possible to miss some owlets on the first visit. Data obtained before 15 July were used to determine the minimum reproduction rate. If we did not meet the above criteria, we classified the production of young as unknown.

To detect turnover events, owls marked with color bands were observed carefully to determine their unique color combinations. Three general situations were noted:

1. the presence of previously marked owls was confirmed by direct observation (no turnover event);
2. a turnover event was established by
   a. replacement by another owl of the same sex at a site with no observation of the previously marked bird,
   b. observation of a marked owl that had moved to a different site,
   c. recovery of the carcass of an owl or other confirmation of death, or
   d. absence of a marked owl after six complete surveys in 2 consecutive years;
3. any instance not meeting either criterion 1 or 2 was classified as undetermined.

We used capture techniques similar to those described by Forsman (1983). All captured owls were fitted with a U.S. Fish and Wildlife Service locking aluminum leg band on the right tarsometatarsus and a plastic, color-coded band with a separate color tab on the left tarsometatarsus.

The sex of adult and subadult birds was determined from the pitch of calls and general behavior as described by Forsman et al. (1984). Owls were categorized by plumage characteristics into juvenile (<1 year old), subadult (1–2 years old), and adult (>2 years old; Forsman 1981). Crude densities were determined by dividing the number of adults and subadults or pairs by the total study area.

Results

Surveys

We surveyed approximately 71% of the study area in 1990 and 90% in 1991. Owl behavior and lack of time hampered the recalling of areas and prevented or delayed meeting protocol requirements on a few sites. A problem encountered both years was the reluctance of owls to take mice or rats, even on the first encounter. This problem did not limit our ability to determine nesting. It did, however, require extra visits to sites where owls had not responded to bait, thus reducing the time we could spend surveying for new owls. The lack of roads and trails in much of the study area also hampered coverage of some sites. The noise from rivers and streams affected the survey in some calling sites until late summer. We were able to overcome most of these obstacles by increasing crew size and prolonging work hours.

Detection and Capture

We located 75 owls in 1990—54 adults and subadults and 21 juveniles—and we confirmed 22 pairs and 7 males and 3 females of unknown status. In 1991 we located 61 owls—60 adults and subadults and 1 juvenile—and confirmed 23 pairs. Five pairs were detected but not confirmed to protocol standards. One female and one male were confirmed as singles in 1991, and two birds were of unknown status (Table 1). Thirty adults and subadults were positively identified in 1990, of which 15 were banded in 1988 or 1989 (Roberts 1990) and 15 in 1990. Twenty-nine adults and subadults were positively identified in 1991, of which 18 were banded in previous years and 11 in 1991. We captured and banded 15 juveniles in 1990 and one in 1991. No banded juveniles were relocated after dispersal.

Density

Crude density estimates for adults and subadults were 0.157 owls/km^2 in 1990 and 0.175/km^2 in 1991. Crude density for the high-elevation coniferous type was 0.034 owls/km^2 in both 1990 and 1991. We found only two birds above 2,438 m—a female detected once in 1990 at 2,652 m and an owl of unknown sex at 2,865 m in 1991. Crude density for the oak–woodland type was 0.108 owls/km^2 in 1990 and 0.145 owls/km^2 in 1991. The difference between years reflects the increased survey effort in 1991, when we were able to document six

Table 1. Spotted owl (*Strix occidentalis occidentalis*) detections, status, and capture for 1990–1991 in Sequoia and Kings Canyon national parks study area.

	Detections			Confirmed		Unconfirmed		Captured and banded	
Year	Total detections	Adult and subadults	Juveniles	Pairs	Singles	Pairs	Singles	Adult and subadults	Juveniles
1990	75	54	21	22	—[a]	2	6	15	15
1991	61	60	1	23	2	5	2	11	1
Total[b]			22					26	16

[a]Data not available.
[b]Number of new birds, not previously detected or captured and banded.

pairs, but in 1990 we documented only four pairs (not all were confirmed to protocol standards). The mixed-conifer type had the highest density of birds in both years, with 0.191 owls/km^2 in 1990 and 0.204 owls/km^2 in 1991.

Mortalities

In the 2 years of study, we documented three mortalities of chicks or young fledglings. Remains of one juvenile were found near a suspected nest site in 1990. We believe it died before fledging; the pair successfully fledged at least one young that year. Two juveniles in 1991 disappeared from a nest cavity before fledging, with no trace of predation around or near the nest site.

Turnover Events

Two turnovers were observed in 1990—one female and one male were replaced from 17 identified birds (12%). In 1991, four turnovers were recorded—three females and one male were replaced among 22 identified birds (18%). The only case of replacement by another banded bird was in 1991, when the male was replaced by a neighboring banded male. In addition, two females were replaced sometime in the 1990 or 1991 season (we could not determine the year). The combined turnover rate for the 2 years, including these latter two females, was 19.5%. The combined rate for females was 27.3% and for males was 10.5%.

Reproduction and Nesting Attempts

Thirteen of 22 pairs were found with juveniles in 1990. Eight of these pairs fledged at least two young, and five fledged at least one, equating to a mean productivity rate of 1.61 young per successful female. The nesting status of most pairs not found with juveniles was unknown in 1990, mainly because of our late start in surveying that year. We were able to determine reproduction status for eight pairs, seven of which fledged young. In 1991, nesting status was determined for 11 pairs, 2 of which nested (18%). Reproduction status was determined for 12 pairs, 11 of which were nonreproductive, and one produced a single young. The reproduction rate, or the proportion of pairs examined for reproduction that fledged young, was 0.88 in 1990 and 0.08 in 1991.

Discussion

Although we are only in the early data-gathering stages of this demographic study of spotted owls in Sequoia and Kings Canyon national parks, several interesting parallels with previously reported studies are emerging. Densities of spotted owls in the study area are similar to those previously reported for the California spotted owl (Table 2). We found a reduced occurrence of owls above 2,134 m, which has also been reported by Roberts et al. (1988), Neal et al. (1989), Roberts (1990), and Verner et al. (1990). One possible explanation for the lower

Table 2. Crude densities of spotted owls (*Strix occidentalis occidentalis*) and owl pairs in the Sequoia and Kings Canyon national parks study area and densities reported from other studies on the California spotted owl, 1986–1991.

Owls[a]	Owl pairs[a]	Location[b]	Year[c]	Reference
0.157	0.064	Sequoia–Kings Canyon NP	1990	Present study
0.175	0.067	Sequoia–Kings Canyon NP	1991	Present study
0.170	0.090	Sequoia–Kings Canyon NP	1989	Robert (1990)
0.090	0.080	Central Sierra Nevada	1986	Bias and Gutiérrez (1988)
0.130	0.070	Central Sierra Nevada	1987	Bias and Gutiérrez (1988)
0.090	0.080	Central Sierra Nevada	1988	Lutz and Gutiérrez (1989)[d]
0.206	0.074	Sierra NF	1990	Verner et al. (1990)
0.200	0.120	Yosemite NP	1988	Roberts et al. (1988)
0.110	—[e]	Big Bear	1987	La Haye and Gutiérrez (1988)
0.160	—[e]	Mount San Jacinto	1988	Gutiérrez and Pritchard (1989)
0.650	—[e]	Palomar Mountain	1988	Gutiérrez and Pritchard (1989)

[a]Numbers per km^2.
[b]NP = national park; NF = national forest.
[c]Includes years of present study, 1990–91, and other reported studies, 1986–90.
[d]D. W. Lutz and R. J. Gutiérrez, California Department of Fish and Game, Sacramento, unpublished report.
[e]Data not available.

densities at these elevations is fragmentation of habitat by rock outcroppings and forest types changing from a mixture of conifer species to mono-types of California red fir and lodgepole pine. Another possible, but not necessarily independent, explanation may be lower prey densities at higher elevations. Further study is needed to determine the effect of elevation on owl presence.

Roberts et al. (1988) and Roberts (1990) reported reduced owl densities below 1,295 m and 1,066 m, respectively, but Verner et al. (1990) reported owl densities equal or higher in oak woodlands than in coniferous forests in a demographic study 24.1 km north of the Sequoia study site. Verner et al. (1990) also reported use of oak woodland sites year-round and documented breeding and reproduction as low as 350 m elevation. In most areas with riparian habitat or dense-canopied oak woodlands, we found pairs of owls, yet our crude densities of owls in the oak woodland type were still slightly lower than in the mixed-conifer type.

Productivity for the Sequoia study site in 1990 was similar to that reported for California spotted owls by M. A. Bias and R. J. Gutiérrez (California Department of Fish and Game, Sacramento, unpublished report), LaHaye and Gutiérrez (1988), and Roberts (1990), who reported productivity of 1.50–1.67, 1.33, and 1.25–1.50 young per successful female, respectively. Fecundity estimates for the Sequoia study site were higher in 1990 than the 0.67 reported in 1988 and the 0.31 in 1989 (Roberts 1990), but the 1991 fecundity rate in the Sequoia study area was exceptionally low. Part, if not all, of this low fecundity rate may be explained by record precipitation that fell in the study site during March, just as the birds were beginning to nest.

Turnover rates for 1990 and 1991 were higher than the 0.08 reported by M. A. Bias and R. J. Gutiérrez (California Department of Fish and Game, Sacramento, unpublished report) for the Eldorado National Forest. The higher incidence of turnover among females than males that we observed agrees with the findings of Gutiérrez and Pritchard (1989) on Mount San Jacinto.

It is important to remember that all data reported here were collected during a drought that has persisted for the last 5 years. This condition may have affected reproduction ranges, turnover rates, and densities. Other biases may exist because data collection in 1990 began late in the breeding season. Furthermore, we encountered several owls that did not respond when presented with bait, thus potentially limiting our ability to meet protocol for determining nesting and reproduction at those sites. We believe, however, that there is enough flexibility in the protocol that status can be determined by increasing visits to those sites.

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A Research Program for Predicting the Effects of Climatic Change on the Sierra Nevada

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Abstract. California's Sierra Nevada faces possible losses of biotic diversity and changes in ecosystem structure and function from anticipated global climatic change. A research program (funded largely by the National Park Service) was initiated to understand and predict the effects of climatic change on the Sierra Nevada. The Sierran national parks (Yosemite, Sequoia, and Kings Canyon) form the core study areas of this program.

The Sierran global change program proposes to address three broad questions: What changes in the structure, composition, and dynamics of forests are likely to occur as a result of anticipated climatic change? For as many species of plants and animals as possible (not just forest trees), what are the likely changes in distribution and the potential vulnerabilities of species to regional extinction? and What hydrologic changes are likely to occur? The first two questions recognize the role of the Sierra Nevada in the preservation of native ecosystems and biotic diversity; the third question recognizes the vital role of Sierran watersheds in supplying water to much of California.

The Sierran global change program has initiated an integrated package of projects addressing the first goal — understanding and predicting forest change. These projects fall into three groups. The first is modern studies, largely designed to adjust parameters in (and sometimes to test) predictive models. The second is paleoecological studies, largely designed to test (and sometimes to adjust parameters in) predictive models. The third group is predictive studies, designed to integrate the results of the modern studies and paleoecological studies into models capable of projecting changes in forest pattern under different climatic scenarios. Assessing possible management strategies for adapting to climatic change is included in the third group.

Key words: Global change, climatic change, Sierra Nevada, coniferous forest, forest dynamics, forest modeling, paleoecology.

California, like most of the world, is vulnerable to the potential consequences of the global increase in atmospheric greenhouse (heat-trapping) gases. Though available projections are crude, climatic models suggest that California and the Sierra Nevada may experience significant changes in temperature and the timing and amount of precipitation, leading to fundamental changes in climatic regime (Knox 1989; Westman and Malanson 1992). Anticipated climatic changes are expected to alter (sometimes profoundly) the structure and

function of biotic communities in most ecosystems (e.g., Pastor and Post 1988; Melillo et al. 1990; Overpeck et al. 1990; Schindler et al. 1990; Clark 1991; Peters and Lovejoy 1992). Such regional manifestations of a broader global change threaten some of the very values that California's national parks and other protected areas were established to preserve (Peters and Darling 1985; Wein et al. 1990; Parsons 1991).

As part of a larger federal program to determine the effects of global change in the United States (Committee on Earth Sciences 1989), the National Park Service (NPS or Park Service) has developed an interdisciplinary research program to understand and predict the potential effects of climatic change on selected natural ecosystems (Anonymous 1990; Parsons 1991). Park areas are using this program as a springboard to take a regional perspective on scientific and management issues, to better understand factors controlling regional ecosystem structure and function, and to develop state-of-the-art models for predicting the consequences of different climatic and management scenarios. These efforts will provide some of the basic information needed to evaluate management strategies for adaptation to climatic change, such as evaluating options for saving species from regional extinction.

The Sierra Nevada of California was one of the first areas selected for NPS global change research funding. This paper introduces the study area, then briefly outlines the logic and methods aimed at achieving the three broad goals of the Sierran Global Change Program: predicting changes in forest structure, composition, and dynamics; predicting species' vulnerabilities to regional extinction; and predicting hydrologic change. Presently, a package of complementary studies addressing the first of these goals has been initiated. These forest studies are organized around modern studies, paleoecological studies, and predictive studies. The final section of this paper describes the studies and their integration as a package capable of improving our understanding and prediction of the effects of changing climates on Sierran forests.

Study Area

With Yosemite, Sequoia, and Kings Canyon national parks as the core study areas, the full Sierran study region encompasses adjacent federal, state, and private lands and stretches from north of Yosemite to the southern end of the range, from the San Joaquin Valley in the west to the Owens Valley in the east (Fig. 1). The outstanding feature of the study area is its extreme elevational gradient and corresponding range of climate and vegetation types. Elevation climbs from near sea level to 4,418 m in less than 100 km horizontal distance—the most extreme elevational gradient in temperate North America. A steep temperature gradient—from warm Mediterranean to cold alpine—parallels the elevational gradient. The temperature gradient, in turn, is overlain by a broad gradient of decreasing precipitation from west to east (Stephenson 1988). Dominant plant formations (and their associated fauna) are ordered more or less according to elevation and include hardwood woodland, chaparral shrubland,

montane coniferous forest, subalpine coniferous forest, and alpine tundra (Rundel et al. 1977; Vankat 1982).

The range of climates encountered in the study area offers outstanding opportunities for determining the likely effects of climatic change on biota. For example, seedling survival under different moisture or temperature regimes can be determined by planting seedlings in common gardens at similar elevations along the west-east precipitation gradient or at different elevations along the temperature gradient (part of our Forest Demography project; see below). Additionally, the effects of climate on the distribution of major plant life forms can be determined at three distinct physiognomic ecotones (woodland–shrub, shrub–forest, and forest–tundra).

The Sierra Nevada is richly endowed with paleoecological records that can provide important insights into future changes through reconstructions of past changes in climate, disturbance regimes, and vegetation. The Sierra Nevada and



Fig. 1. The approximate location of the Sierran global change study area (*shaded*) and the core national parks (Yosemite and Sequoia–Kings Canyon; *dark*) in California.

vicinity are unique worldwide in having at least three tree species from which multimillennial tree-ring chronologies can be derived: *Pinus balfouriana* (Scuderi 1987a, 1987b; Graumlich 1990), *P. longaeva* (in the White Mountains 50 km northeast of the Sierran crest; Schulman 1958; Ferguson 1969; LaMarche 1974), and *Sequoiadendron giganteum* (Douglass 1919, 1928; Hughes and Brown 1992). Detailed climatic reconstructions are also possible from dozens of additional, well-replicated tree-ring chronologies from within a 500-km radius of the Sierra Nevada (e.g., Holmes et al. 1986). Multimillennial fire chronologies, cross-dated to the exact year, have been extracted from *Sequoiadendron* tree rings, demonstrating a link between climate and fire frequency and size (Swetnam et al. 1990; Swetnam 1992). Significant changes in Sierran vegetation through the Holocene and portions of the Pleistocene have been documented by pollen and macrofossil records from sediment cores and woodrat middens (Cole 1983; Davis et al. 1985; Anderson 1990). The study area also has a substantial history of scientific research, which will provide a strong foundation for research on the effects of climatic change (e.g., Rundel et al. 1977; Parsons and King 1980; Parsons and Haggerty 1986; Parsons et al. 1990).

Research Goals and General Methods

Predicting Changes in Forest Structure, Composition, and Dynamics

We will focus a large portion of our global change research efforts on forest trees because

1. any change in forest structure is likely to have major effects on hydrology, wildlife habitat, and the microhabitats of herbs and shrubs;
2. predicting changes in the large carbon pools stored in forests is essential for understanding biogenic feedbacks to global change;
3. the recreational and economic importance of forests also makes them a target of global change research by the U.S. Forest Service, allowing potential pooling of resources and dividing research responsibilities; and
4. predicting forest changes allows us to assess threats to some of the other values for which most Sierran lands are managed, including aesthetics and biotic diversity.

The biological, hydrological, and climatological importance of climatically-induced forest change are discussed in greater detail by Graham et al. (1990).

We will carry out an integrated package of forest studies to improve our understanding of the controls of forest dynamics and to formulate and test predictive models. The predictive models will be designed to reflect both the direct effects of climate (through its influence on tree physiology, growth, demography, and life history) and the indirect effects of climate (through its

influence on disturbance regimes, mainly fire; Kercher and Axelrod 1984; Pastor and Post 1988; Keane et al. 1990; Overpeck et al. 1990). The models therefore will provide a means for evaluating the interacting effects of changing climatic and disturbance regimes on Sierran forests, including the possible use of fire as a management tool to lessen or slow the effects of climatic change. A more detailed description of the research program aimed at understanding and predicting forest change appears later.

Predicting Changes in Habitat Distributions and the Vulnerability of Species to Regional Extinction

The forest studies just described will be aimed at a detailed understanding of the effects of climatic change on a handful of tree species. We will use a much broader (and necessarily coarser) approach to evaluate the vulnerability of as many other Sierran species as possible (both plant and animal) to regional extinction. Species will be classified according to their vulnerability to extinction from complete loss of habitat in the Sierra Nevada or rapid geographic shifts in habitat that outstrip the species' abilities to disperse or complete their life cycles. The classification will be carried out in four steps.

First, a geographic information system (GIS), using inputs of soils maps, vegetation maps, and mountain climate models (such as MT-CLIM; Running et al. 1987; Hungerford et al. 1989), will be used to model the present distribution of local habitats for portions of the Sierra Nevada. (Local habitat is defined by soil type and local climate for plants and soil type, local climate, and vegetation type for animals.) Second, the habitat needs of individual species will be determined by correlating modern species distributions with local habitats. The species distributions will be determined from an extensive geo-referenced library of wildlife observations and an expanding network of over 1,000 biotic inventory plots (Stephenson 1988; Graber et al. 1993; P. E. Moore and J. W. van Wagtendonk, Yosemite National Park, California, unpublished data). Third, the GIS will be used to predict the future distributions of local habitats under a range of climatic scenarios. Finally, knowledge of species dispersal and life history traits (gained from literature review and selected field studies) will be coupled with the predicted changes in habitat distributions to classify species according to their vulnerabilities to regional extinction. The classes will be

1. high probability of extinction, regardless of management actions (species whose habitats are predicted to disappear entirely from the Sierra Nevada);
2. high probability of extinction unless management actions are taken (species whose habitats are predicted still to exist in the Sierra Nevada but that are judged to be incapable of following the predicted habitat shifts due to dispersal or life history problems); and
3. low probability of extinction (species whose habitats are predicted still to exist in the Sierra Nevada and that are judged to be capable of following the predicted habitat shifts).

This approach is simplistic in that the present distributional limits of some species may be a conservative estimate of potential limits, reflecting chance and biotic interactions more than environmental tolerances. For plants, this approach also ignores the complicating effects of increased water use efficiency that result from increased atmospheric CO_2 (e.g., Leverenz and Lev 1987; Davis 1989; Bazzaz 1990; Mooney et al. 1991). However, the results should provide managers and policymakers with a rough estimate of the potential loss of diversity from the Sierra Nevada and a ranking of individual species for more detailed study.

Predicting Hydrologic Changes

Change in Sierran hydrology is of immense importance not only for its influence on regional biota and ecosystem function but also for its influence on people throughout California. A substantial proportion of the water for residential, agricultural, and industrial use in the state comes from Sierran watersheds. Thus, a major goal of this program is to estimate likely changes in the timing and quantity of outflows from Sierran watersheds under different climatic scenarios.

Appropriate models, such as the U.S. Geological Survey's (USGS) Precipitation-Runoff Modeling System (PRMS), will be used to estimate local water balances on homogeneous subunits within individual watersheds. The outflows from individual subunits will then be summed to estimate basinwide outflows under different climatic scenarios. The USGS already is taking this approach in the American, Carson, and Truckee watersheds of the north-central Sierra Nevada (A. Jeton, U.S. Geological Survey, Carson City, Nevada, personal communication). Other models will be pursued in cooperation with National Aeronautics and Space Administration's Earth Observing System (EOS) program, which has targeted the central and southern Sierra Nevada for monitoring and predicting snow dynamics (J. Dozier, University of California, Santa Barbara, personal communication).

Implementation

Collaborators in the Sierran global change program are currently initiating the package of linked studies aimed at understanding and predicting forest changes. Full implementation, as well as initiation of the other two packages of studies (predicting species vulnerabilities to extinction and predicting hydrologic change), will depend on the availability of new funds.

Most of the initial forest research and modeling efforts will focus on the white fir forest—sometimes called mixed conifer forest or white fir–mixed conifer forest (Rundel et al. 1977; Barbour 1988)—found from about 1,800 to 2,300 m elevation on the west slope of the Sierra (see Rundel et al. 1977 and Stephenson 1988 for descriptions). This forest type—home of the famous giant sequoias—is easily accessible, contains the vast majority of permanent forest

plots available for study, and is by far the most extensively studied for fire history (Kilgore and Taylor 1979; Swetnam et al. 1990; Swetnam 1992), fire ecology (Kilgore 1973; Harvey et al. 1980; van Wagtendonk 1985), paleoecology (Davis et al. 1985; Anderson 1990), and general forest ecology (Rundel et al. 1977; Harvey et al. 1980; Barbour 1988). Less intensive research will also be carried out in forest types above and below the white fir forest.

To reach our goal of understanding and predicting forest change, we have identified a series of linked projects organized around three time periods: modern studies, paleoecological studies, and predictive studies. The modern studies are designed to improve our understanding of how climate and disturbance shape Sierran forests, provide parameters for the predictive models, provide independent tests of the predictive models in some cases, and detect early changes, thereby providing a further check (along with paleoecological and other modern studies) for model validation. The paleoecological studies are designed to improve our understanding of how Sierran forests respond to long-term changes in climate and disturbance (e.g., Davis 1989) and to provide independent data to test the predictive models. Finally, the predictive studies are designed to integrate information gained from the modern studies and paleoecological studies into models capable of projecting changes under different climatic scenarios and assessing possible management strategies for adapting to climatic change.

The relation among the individual projects is shown in Fig. 2. Each project is described briefly below. Most projects address several relevant global change issues; however, space limits us to emphasizing those aspects of the projects that collectively link them as a logical unit.

Modern Studies

M. Finney and N. Stephenson (NPS) and R. Kern and N. Christensen (Duke University) will carry out the Forest Demography project. Demographic data (those that seek to explain changes in the numbers of individuals in populations) are indispensable to understanding forest dynamics and predicting future changes (e.g., Harper 1977; Shugart 1984). This project will draw heavily on data (much of them already collected) from a network of 153 existing permanent forest plots in which tens of thousands of seedlings and trees have been individually monitored for up to 25 years. For the major midelevation tree species of the Sierra Nevada (Table), the project will

1. determine the environmental controls of seedling germination, establishment, growth, and survival under natural conditions and experimentally manipulated CO_2 and moisture regimes;
2. determine size-specific death rates of saplings and mature trees relative to recent climatic and fire history; and
3. use forest age structure and long-term climatic and fire history (see Paleoecological Studies, below) to determine the importance of rare (century-scale) events in shaping forest pattern.

In addition to improving our basic understanding of the forces controlling forest pattern, the project will provide inputs to the Forest Dynamics model (below). This project has been partially funded by the NPS Global Change Program.

The Conifer Physiology project, to be carried out by N. Grulke (U.S. Forest Service), is designed to reflect the fact that more than just changes in temperature and precipitation will determine the future structure and composition of forests. Increasing concentrations of atmospheric CO_2, by affecting tree

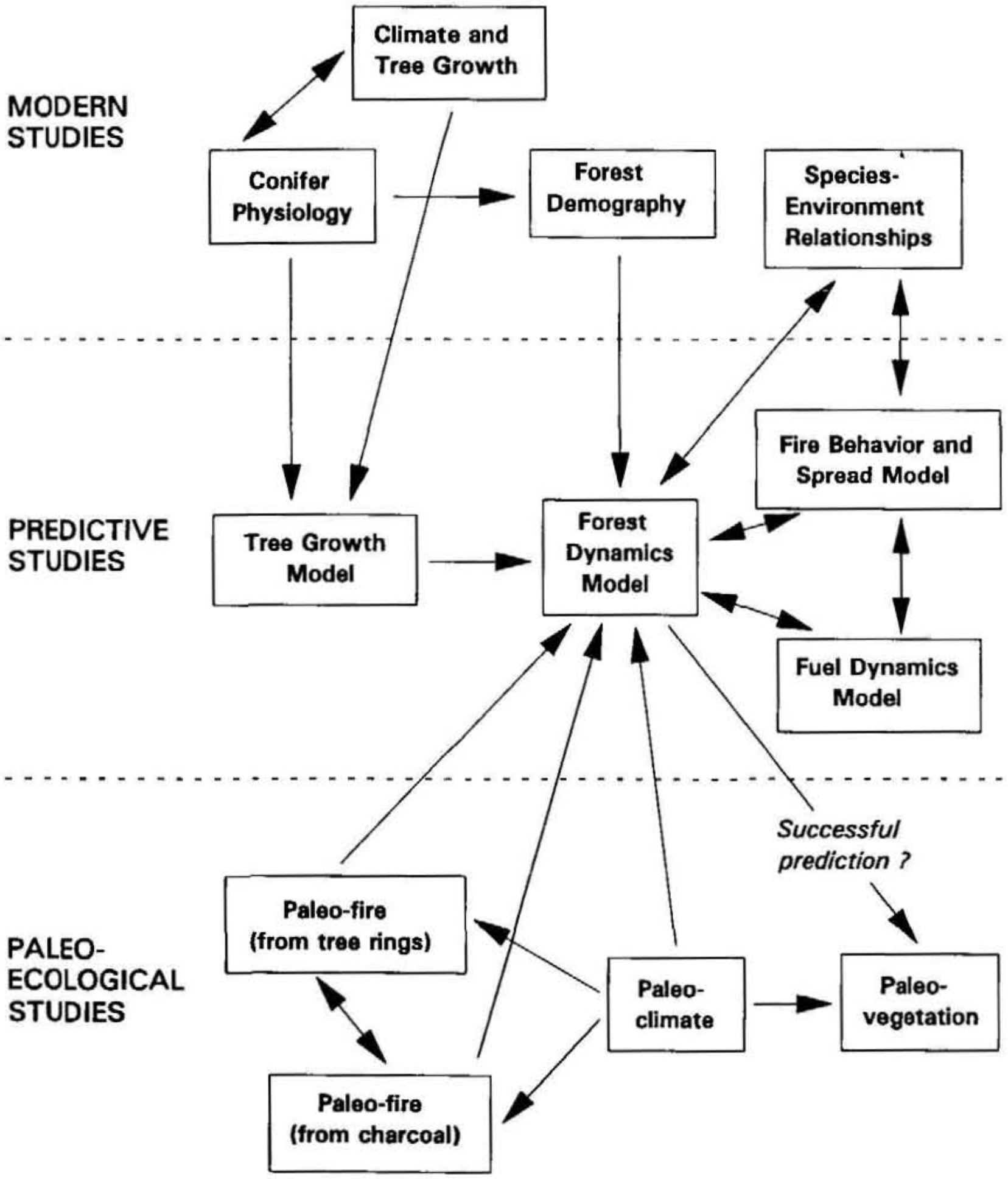


Fig. 2. The relation among studies aimed at understanding and predicting changes in forest structure, composition, and dynamics — the first package of studies to be initiated in the Sierran global change program. *Boxes* represent the individual projects discussed in the text; *arrows* represent some of the major linkages. Model outputs are discussed under Synthesis and the individual project descriptions in the text.

use efficiency, are likely to have profound influence on the distribution of forest species (Leverenz and Lev 1987; Davis 1989; Bazzaz 1990). This project will gather fundamental data on the seasonal carbon, water, and nitrogen budgets of five of the major midelevation tree species of the Sierra Nevada (*Abies concolor*, *Pinus jeffreyi*, *P. lambertiana*, *P. ponderosa*, and *Sequoiadendron giganteum*), including experimental manipulations to determine the interacting effects of temperature, soil moisture, and atmospheric CO_2. Together with the Climate and Tree Growth project and Tree Growth model (below), these data will form the basis for predicting individual species' growth responses to changing climate and CO_2. This project has been partially funded by the U.S. Forest Service and the NPS Global Change Program.

The Climate and Tree Growth project, carried out by L. Graumlich (University of Arizona), is critical because realistic models of climate–growth relations are needed to adapt gap-phase forest simulation models to predicting changes in forest structure and composition resulting from climatic change (Graumlich 1989; Cook and Cole 1991). Complementing the Conifer Physiology project (above), this project will develop a network of tree-ring data for the major midelevation tree species of the Sierra Nevada (Table). Ring widths from the lower, middle, and upper portions of each species' elevational range will be correlated with historical temperature and precipitation records and knowledge of the seasonal carbon budgets of the species. The resulting climate-growth response functions will improve our understanding of climatic controls of species distributions and, coupled with the physiological studies, will supply parameters for the Tree Growth model (below). This project has been fully funded by the NPS Global Change Program.

The Species–Environment Relationships project will be carried out by D. Graber, J. van Wagtendonk (NPS), F. Davis (University of California, Santa Barbara), and C. Jett (Soil Conservation Service). An important test of the

Table. Major midelevation tree species of the central and southern Sierra Nevada.[a]

Scientific name	Common name
Abies concolor	White fir
Abies magnifica	California red fir
Calocedrus decurrens	Incense-cedar
Pinus jeffreyi	Jeffrey pine
Pinus lambertiana	Sugar pine
Pinus ponderosa	Ponderosa pine
Pseudotsuga menziesii	Douglas-fir
Sequoiadendron giganteum	Giant sequoia
Quercus kelloggii	California black oak

[a] These species are the primary focus of research directed at predicting changes in forest structure, composition, and dynamimcs.

Forest Dynamics model will be to determine the accuracy with which it can recreate the modern distribution of forest types across the landscape, given the inputs of slope steepness, slope aspect, elevation, and soil type. The GIS databases of the Sierran national parks presently have most of the information needed to carry out such a test except soil maps and accurate vegetation maps. This project will use Order-4-resolution soil surveys and remotely-sensed digital imagery combined with extensive field reconnaissance to develop GIS-based soil and land-cover maps of Yosemite, Sequoia, and Kings Canyon national parks. In addition to helping test the forest modeling efforts, these same data will be central to modeling fuel distributions, fire behavior, and fire spread across landscapes (see Predictive Studies, below) and to the proposed studies aimed at predicting species vulnerabilities to regional extinction. This project is currently unfunded.

Paleoecological Studies

The Paleoclimate study, led by L. Graumlich and M. Hughes (University of Arizona), will use tree-ring chronologies from western juniper (*Juniperus occidentalis*), foxtail pine (*P. balfouriana*), and giant sequoia to develop multi-millennial reconstructions of late Holocene climatic variation in the Sierra Nevada (Graumlich 1990; Hughes and Brown 1992). These reconstructions will be put to two main uses. First, because community structure and composition may be greatly affected by the indirect effects of climatic change on disturbance regimes (e.g., Overpeck et al. 1990), the paleoclimatic reconstructions will be used with paleo-fire reconstructions (below) to elucidate the link between climate and fire regime in the fire-prone ecosystems of the Sierra Nevada. Second, the paleoclimatic reconstructions will be used to drive the fire behavior and forest dynamics models to test their ability to recreate observed changes in past fire regimes and vegetation composition. This project is fully funded by the NPS Global Change Program.

The Paleo-fire (from tree rings) study will be coordinated by T. Swetnam (University of Arizona). It will prove useful to elucidate the link between past changes in climate and past changes in fire regimes, given that the most profound effects of climatic change on forest structure and composition may be indirect, through changes in disturbance regimes (e.g., Overpeck et al. 1990). Fire scars within giant sequoia tree-rings can provide a rich and detailed history of hundreds of fires over the last 1,500 years or more and have already revealed links between climate, fire frequency, and fire size (Swetnam et al. 1990; Swetnam 1992). The present study will extend existing fire reconstructions even further back in time by targeting research in areas containing exceptionally old sequoia wood and will extend reconstructions into other forest types beyond the sequoia groves. The results will allow determination of the long-term degree of synchrony of fire years in widely dispersed sites and in different forest types and, thus, the relative importance of large-scale climatic forcing of fire regimes (e.g., Swetnam and Betancourt 1990). Results will also be used with the paleoclimatic reconstructions to drive the Forest Dynamics model, testing the

forest model's ability to recreate observed changes in past vegetation composition. This project is fully funded by the NPS Global Change Program.

The Paleo-fire (from charcoal sediments) study will be conducted by R. S. Anderson (Northern Arizona University). Reconstructions of past fire regimes from tree-rings in the Sierra Nevada are limited to the last few thousand years. This project, in contrast, will test the potential for using charcoal from sediment cores to extend reconstructions over the entire Holocene. Using thin-section techniques (Clark 1988), the abundance of different size classes of charcoal particles will be determined every 1–2 mm throughout the length of sediment cores from sequoia groves in which millennial-length fire chronologies have been developed from tree rings. Charcoal sediment has roughly decadal resolution for fires in the Sierra Nevada (R. S. Anderson, Northern Arizona University, Flagstaff, personal communication). After calibrating the charcoal record to the tree-ring record, the charcoal record will be used to extend fire regime reconstructions over the last 11,000 years — the age of the oldest cores yet obtained in sequoia groves. These longer reconstructions will serve a role in model testing similar to that of the shorter reconstructions from tree rings. This project is partially funded by the NPS Global Change Program.

Anderson will also coordinate the Paleovegetation study. Reconstructions of past vegetation change provide insights into how communities dissociate and reassociate in the face of climatic change and provide some of the only data capable of testing models designed to predict future vegetation change (e.g., Solomon et al. 1981; Prentice and Solomon 1990). Sierran studies have already demonstrated pronounced changes in midelevation forest composition over the Holocene (Davis et al. 1985; Anderson 1990), including the past existence of forest types that have no modern analogs (R. S. Anderson, Northern Arizona University, Flagstaff, personal communication). This study will determine species-specific changes in forest composition from macrofossils and pollen taken from sediment cores in local catchments (cf. Dunwiddie 1986) and from woodrat middens (Cole 1983), targeting specific elevational and time-series gaps in the Sierran paleovegetation record. The data will be used to test the ability of the Forest Dynamics model to recreate observed changes in past forest composition. This project is currently unfunded.

Predictive Studies

Successful modeling of forest change will depend heavily on realistic modeling of fire frequency and behavior, which in turn will depend in part on realistic modeling of fuel dynamics. The Fuel Dynamics model, under development for the past several years by J. van Wagtendonk (NPS), is aimed at refining the fuel dynamics component of the FYRCYCL model (van Wagtendonk 1985) for use in conjunction with fire and vegetation dynamics models. Accumulation rates for litter and coarse woody debris are being determined for several middle-elevation forest types of different structures, compositions, and ages. Further data collection will fill gaps in the data (such as the relative lack of data from

sequoia groves) and refine estimates of year-to-year variation in fuel accumulation. This project is funded by the NPS.

The Fire Behavior and Spread model will be developed by M. Finney (NPS), in conjunction with C. Bevins (Systems for Environmental Management) and P. Andrews (U.S. Forest Service). The greatest effects of climatic change on forests may be indirect, through changing disturbance regimes (Overpeck et al. 1990). This project will complete development of a fire model (FARSITE) and link it with models of fuel and vegetation dynamics to predict changes in fire behavior and spread resulting from changing climate, forest structure, and fuel characteristics. The model, based on rapid and efficient elliptical spread algorithms (Richards 1989), will be designed for GIS applications, using local climate, slope steepness, and fuel characteristics to model fire characteristics. Trial runs of an early version of the model have shown good agreement with actual fires in the Sierran conifer zone. This project is jointly funded by the U.S. Forest Service and the NPS.

D. Weinstein, R. Yanai, and R. Beloin (Boyce Thompson Institute, Cornell University) will develop the Tree Growth model. At present, gap-phase forest succession models base estimates of annual tree growth on broad correlations between geographical species distributions and temperature and precipitation gradients (Shugart 1984). A problem with this approach is that modern species limits reflect only realized growth in the presence of competitors and therefore may substantially misidentify the climatic optima and potential range limits of species (Weinstein et al. 1991b). More realistic growth estimates can be obtained from physiologically driven models of tree growth, such as TREGRO (Weinstein and Beloin 1990; Weinstein et al. 1991a). This project is aimed, in part, at using results from the Conifer Physiology and Climate and Tree Growth projects to provide TREGRO with growth parameters for the major mid-elevation Sierran tree species. TREGRO will be linked with the Forest Dynamics model to provide realistic estimates of growth in response to climate and other stressors (such as air pollution). The Electric Power Research Institute has funded this project.

The Forest Dynamics model, ZELIG, is being developed by D. Urban (Colorado State University, Fort Collins). The model will integrate much of the information derived from the projects discussed above into a model capable of projecting changes in forest structure, composition, and dynamics under different climatic and management scenarios. ZELIG is a gap model, simulating demographics on a tree-by-tree basis (Urban 1990). Application of the model in the Sierra Nevada will add the Sierra Nevada to a network of sites throughout the United States—most of them members of the National Science Foundation's Long-Term Ecological Research (LTER) network—in which ZELIG or related models are used as a framework for cross-site comparison of the links between climate, disturbance, vegetation pattern, and ecosystem processes. Some of the specific applications to which we will apply the Sierran version of ZELIG are discussed briefly below. The NPS Global Change Program has funded this project.

Synthesis

While each of the twelve projects listed above addresses relevant global change issues individually, we have chosen to emphasize how they are linked as a logical unit leading to prediction. Ultimately, we will use the modern studies and paleoecological studies in conjunction with the predictive studies to explore, among others, the following five questions:

First, what factors most strongly influence the present distribution, species composition, structure, and dynamics of Sierran forests? We cannot predict change until we understand the controls of forest pattern. We will compare and contrast model outputs (under present conditions) with results of the Modern Studies, particularly the Forest Demography and Species–Environment Relationships projects (being careful that the comparison data are independent of the parameterization data).

Second, what changes in forest pattern might occur under a range of different climatic change scenarios, assuming the fire regime is allowed to change unhindered in response to climate? The effects of climate cannot be addressed independently of disturbance. Model projections will be compared and contrasted with reconstructions of Holocene climate, fire, and vegetation changes derived from the Paleoecological Studies.

Third, what changes in forest pattern might occur under different climatic change scenarios, assuming a range of different fire regimes imposed by managers? Model projections will be used to explore the possible use of fire as a management tool for slowing or minimizing climatically-induced forest change, including evaluation of what kinds of prescribed fire programs might lessen the possibility of sudden, catastrophic conversion of forest types by wildfire.

Fourth, under changing climatic and fire regimes, will Sierran forests act as net sources or net sinks of carbon? Projections from the Forest Dynamics model will be compared especially with results of the Conifer Physiology, Climate and Tree Growth, and Tree Growth model projects, taking care that the comparison data are independent of parameterization data.

Finally, what changes in hydrology might result from changes in forest structure, composition, and water use efficiency? Results of the Conifer Physiology project, Forest Dynamics model, and Tree Growth model will be integrated to predict the effects of changing tree water use efficiency and forest structure and composition on site water balances. These results will provide important inputs into our proposed future research on hydrologic change.

The final synthesis of project results, addressing the above questions and others, should yield the information needed to assess the possible consequences of climatic change on Sierran forests, and possible management strategies for adaptation.

Acknowledgments

Many people contributed to the ideas presented here, particularly the researchers listed under the individual projects in the text. We thank C. Bevins, P. Comanor, M. Finney, D. Graber, N. Grulke, M. Hughes, R. Kern, T. Swetnam, D. Urban, J. van Wagtendonk, S. Veirs, D. Weinstein, R. Yanai, and two anonymous reviewers for useful comments on the manuscript.

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Evaluating Human Effects on Vegetation: An Example From the Sierran Foothills

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Abstract. Assessing the historical effects of humans on vegetation in national parks often is hampered by the lack of site-specific information on paleoecology and cultural land use history (i.e., protohistoric and European settlement periods). Land managers must often rely on modern scientific studies on ecology and succession to evaluate past and present human effects. I discuss the advantages and disadvantages of approaches commonly used in assessing vegetation change. I also present one interpretation of the best available information on the influence of humans on vegetation in the low elevation foothills of Sequoia National Park in the southern Sierra Nevada.

During their occupation from approximately A.D. 1000 to 1865, the native American Indians may have altered vegetation characteristics (i.e., successional seres, etc.) locally with the use of fire and horticulture. Recent studies, however, on soils and fire ecology in chamise (*Adenostoma fasciculatum*) chaparral and blue oak (*Quercus douglasii*) woodland suggest Indians probably didn't alter plant community boundaries at the landscape level. Between about 1870 and 1910, ranchers greatly changed the southern Sierra Nevada by intensive grazing of cattle and sheep, introduction of exotic plants, and use of fire. Today, over 90% of the biomass of understory species in the blue oak woodland is that of European annual grasses. Park establishment in 1890 and the accompanying fire suppression policy resulted in the creation of vast, homogeneous areas of high-biomass stands of chamise chaparral. Park managers have been unsuccessful in mitigating the influence of current inhabitants who continue to affect the landscape with arson and atypically large wildfires, continued fire suppression, continued spread of exotic species, and air pollution.

Key words: Chaparral, oak woodland, land use history, Native Americans, European settlers, national parks.

Investigations of human influences on vegetation require information on the general ecology of the site and cultural history of human use of the plant

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community in question (Cooper 1960). Often historical information is incomplete, is of poor resolution, and is qualitative rather than quantitative (Cooper 1960; Pyne 1982; Forman and Russell 1983; Noss 1985). Still, effective land management requires us to synthesize the available data, provide an interim evaluation of the cultural geography of the community, devise a management scheme, and design and carry out research to address glaring information gaps.

Managers in Sequoia National Park, California, are required by the Organic Act of 1916 to "conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such a manner and by such a means as will leave them unimpaired for future generations (16 USC 1)." This can be interpreted as including, in part, maintaining a natural fire regime and mitigating effects of modern humans (i.e., exotic species invasions, fire suppression, grazing, air pollution, development).

Managers need information on the ecology of the plant community and an accurate characterization of human use before and after park designation before a management strategy can be designed to comply with the above goals (Vankat and Major 1978). Interim management decisions must be based on the best available information because ecological and human use information will likely be incomplete (Graber 1985).

Despite the lack of physical evidence, complete ethnohistory, and long-term fire history data, authors have often claimed Native Americans (Indians) have played a major role in influencing vegetation patterns (Lewis 1973; Pyne 1982). For example, Reynolds (1959) suggested "lightning was not the most significant or effective ignition agent operating in the central Sierra Nevada during aboriginal times." Elsasser (1962) and Vankat (1977) state the Western Mono burning practices "must have played an important role in producing ecological patterns in the Sequoia National Park region." And Parsons (1981) declared "both [Indians and lightning] played an important role in determining the vegetation patterns in the foothill zone." A reevaluation of these claims is necessary after more than a decade of additional research including studies on soils (Huntington and Akeson 1987), anthropology (Wickstrom 1987, 1988), chaparral ecology (Parsons et al. 1981; Stohlgren et al. 1984, 1989; Rundel 1986), and oak woodland ecology (McClaran 1986; Parsons and Stohlgren 1989; Mensing 1992).

I investigated the cultural plant geography of one location in the foothills of Sequoia National Park to draw attention to the human influences, past and present, on chamise chaparral and blue oak woodland in the area (now called the Hospital Rock area). Specific objectives were to

1. evaluate the advantages and disadvantages of approaches commonly used in assessing vegetation change;
2. review the findings of recent studies on chamise chaparral and blue oak woodland ecology and human use;
3. evaluate the relative effects of Indians, early settlers, and modern humans on the landscape (particularly with respect to fire); and
4. develop a framework for managing chaparral and woodland resources within the guidelines of National Park Service policy.

Study Area

Hospital Rock is beside the Middle Fork of the Kaweah River in Sequoia National Park (900 m elevation; Fig. 1). The foothill vegetation, primarily chamise (*Adenostoma fasciculatum*) chaparral and blue oak (*Quercus douglasii*) woodland, ranges between 460 m and 1,830 m in elevation on generally steep, narrow canyons (Parsons 1981; Fig. 2).

Chamise is the dominant shrub species in many summer-drought Mediterranean ecosystems that characterize California (Mooney and Dunn 1970; Parsons 1981). Throughout central and southern California and in much of the study area, chamise occurs in more than 70% of chaparral stands (Hanes 1977; Rundel 1986). Growing in both pure and mixed stands, chamise is adapted to

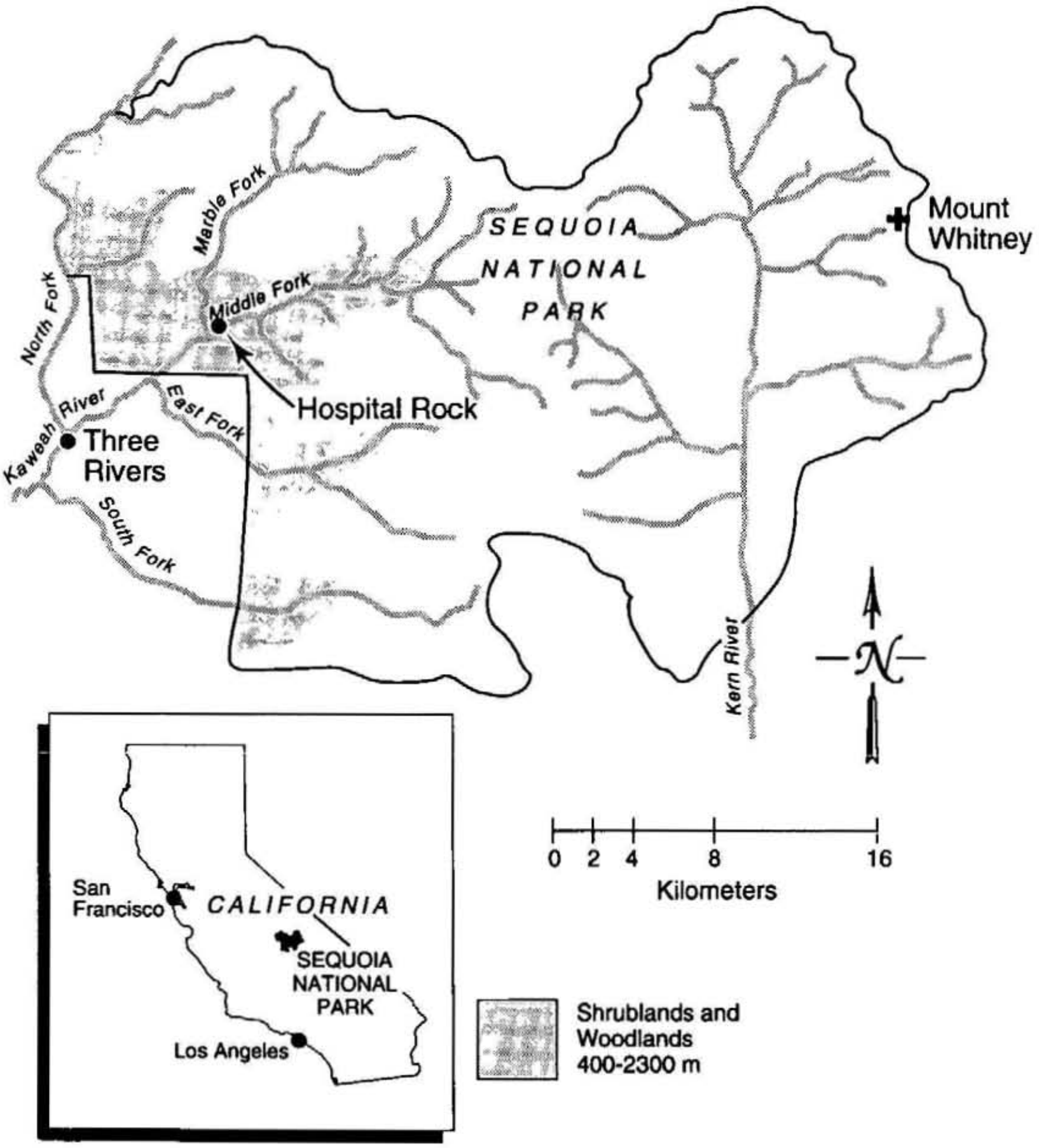


Fig. 1. Location of the study area and the distribution of vegetation within Sequoia National Park, California. Adapted from Vankat (1977; used with permission of J. Vankat).



Fig. 2. Photographs of typical blue oak woodland (*top*) and chamise chaparral vegetation (*bottom*) in the foothills of Sequoia National Park.

rapid regrowth after fire by resprouting from a burl and facultative seeding (Laude et al. 1961; Hanes 1977; Radosevich et al. 1977).

The oak woodland community type combines California's annual grassland with isolated evergreen or cold-deciduous trees. This vegetation type is located usually between valley grassland or shrub and montane forests. A typical example is the blue oak woodland in the foothills of the west slope of the Sierra Nevada (McClaran 1986). In this study area and throughout California, the native annual and perennial grasses have been almost entirely replaced by exotic European and Asian annual grass including *Avena fatua*, *Festuca* sp., and *Bromus* sp. (Bartolome et al. 1986).

The study area has a Mediterranean-type climate with hot, dry summers and cool, moist winters. Annual precipitation averages between 65 cm in the lower elevations and 90 cm in the upper elevations (Parsons 1981).

Approaches Commonly Used in Assessing Vegetation Change

Approaches commonly used to evaluate vegetation change and human influences to vegetation include paleoecology (e.g., pollen cores, pack rat middens), land use history (e.g., ethnohistory, historical accounts and photographs), and ecological studies (e.g., observations, experimental field studies, models). Each has general advantages and disadvantages and site-specific considerations for application (Table).

Paleoecology

Paleoecological investigations can provide information on past pollen assemblages and general trends and rates of climatically-induced vegetation change. This is important information from which to assess long-term, human-influenced rates of vegetation change (Anderson and Carpenter 1991). This information, however, tends to be regional in scope (some pollen can be airborne for several kilometers) and of low temporal resolution (i.e., based on only a few carbon dates over long periods). In addition, past and present pollen rain may not be proportional to species composition (percent cover or biomass). For example, modern pollen rain of *Quercus* was 16.5 and *Pinus* 3.0 times greater than their vegetation cover values in giant sequoia (*Sequoiadendron giganteum*) groves in Yosemite and Sequoia national parks (Anderson 1990). Other plants (e.g., *Chrysolepis sempervirons*, 50 times and *Cornus nuttallii*, 100 times) had less pollen than vegetation cover values would indicate. Thus, inferences about past vegetation assemblages based solely on pollen stratigraphy are problematic because the accuracy of past vegetation assemblages depends on the constancy of pollen source area, pollen degradation rates, and the relation of pollen deposition to percent vegetation cover, biomass, and dominance.

Detailed information on land use practices is needed to understand fully human–resource interactions (e.g., resource procurement systems, landscape

Table. Advantages and disadvantages of selected approaches to evaluating vegetation changes and effects of humans.

Approach	Advantages	Disadvantages	This study area
Paleoecology			
Pollen cores, packrat middens, and plant phytolyths	• can detect long-term changes in regional pollen assemblages (i.e., the presence or absence of species)	• for many species, there can be a poor correlation between plant abundance (i.e., cover or basal area) and pollen rain	• pollen catchments (wet meadows, lakes, and natural ponds) are extremely rare in this area
	• macrofossils (in cores and middens) can indicate local vegetation assemblages over time.	• it is difficult or impossible to determine past community structure (relative species composition, dominance) based on pollen assemblages expressed as a percentage of total pollen	• packrat midden sites (deep caves) also are rare in this area
	• charcoal presence can indicate fluctuations in fire occurrence	• rare species, poor pollen dispersers or species with rapidly degrading pollen can go undetected	• phytolyths could be used to determine the spatial extent of native perennial grasses prior to the invasion of European alien annual grasses
	• pollen assemblages (usually expressed as a percentage of total pollen) can be "aged" or carbon-dated to produce a record of vegetation change through time	• events outside the study area (floods,	

Table. *Continued.*

Approach	*Advantages*	*Disadvantages*	*This study area*
	• phytolyths can be used to differentiate some orders or families of grasses; or to differentiate between annual and perennial life forms	erosion, high winds) can influence pollen catchment • provide little information on the relative influence of the complex mechanisms influencing observed vegetation change	
Land use history Ethnohistory (cultural anthropology)	• can determine preferences for certain plant species • can indicate resource-procurement systems (horticultural techniques, destructive land use, use of water diversions, etc.) • can demonstrate the use of fire in manipulating landscapes	• reliance on contact-time observations (and later interviews) may not represent past land use practices (i.e., of earlier peoples and cultures) • little, if any, information can be obtained on the spatial extent of past land use practices, or on the intensity and frequency of past land use practices (such as	• ethnohistory of Indians in the area is very scant • ethnohistory was not systematically collected until about the 1920's or 1930's • lack of old trees as fire-scare material makes it difficult or impossible to verify historical accounts

Table. *Continued.*

Approach	Advantages	Disadvantages	This study area
	• can provide insights on human-caused species invasions and extinctions	fire, water diversions, agriculture, hunting and gathering pressures on plant and animal populations, etc.) • there is difficulty in determining the relative importance of non-human-caused and human-caused perturbations on the landscape over time	
Post-settlement historical account (and old photographs)	• can provide written detailed descriptions of settled areas and local land use practices • photographs can provide detailed qualitative information on community type and openness	• historical accounts can be exaggerated • some historic photographs can't be precisely relocated • accounts are usually spatially clustered very near settlements. Little is written about more remote landscapes (perhaps the majority of the landscapes)	• written accounts with detailed vegetation descriptions are few • photographs of the area are fairly recent (late 1890's) and show little change in vegetation boundaries

Table. *Continued.*

Approach	Advantages	Disadvantages	This study area
		• species composition can rarely be gained from historic photos • settled areas (those with better accounts) may be atypical in landscape features, disturbance history, and subsequent land use history, compared to remote areas	
Ecological studies Observations and experimental studies	• can gather detailed observations of natural history, wildlife behavior, community structure, etc. • can develop a detailed understanding of current rates of vegetation change • can develop a better understanding of the role of disturbance	• community structure (species composition, relative dominance, etc.), and thus, the response of a given community to disturbance can be different in modern compared to past times • experimental disturbances (e.g., prescribed fires) may not be similar in	• studies have been extremely helpful in describing current plant communities, species composition and biomass, responses of select vegetation types (or species) to fire and drought, and the autecology of the dominant species • long-term plots

Table. *Continued.*

Approach	Advantages	Disadvantages	This study area
	in present-day communities • can begin to develop a better understanding of the relative importance of complex mechanisms influencing vegetation change	frequency, intensity and duration (or spatial extent) to natural disturbances in the past • many experimental studies are conducted in small areas (i.e., only a fraction of the landscape) and may not be typical of larger-scale processes	have been established to document current rates of vegetation change • many unknowns still exist on the structure and function of these community types and on the ecology of dominant species
Ecological models Back-in-time models	• can aid in planning restoration projects • can show data gaps (i.e., where more information is needed)	• data are rarely of sufficient detail to provide an accurate evaluation of past (or future) community structure and function	• lack of detailed paleoecologic data, landuse history information, and extensive experimental studies prohibit the development of accurate back-in-time or predictive models
Predictive models	• can show data gaps (i.e., where more information is needed • can aid in planning mitigation projects	• models tend to be too simplistic trading off mathematical tractability for biological reality	

manipulation, use of fire). Land use practices such as agriculture, fire, and water diversions can vary in effect depending on their level of use spatially and temporally throughout habitation. Fire effects, for example, vary with intensity, frequency, duration, location, and seasonality; and land use practices vary with changing cultures (Table). Unfortunately, written records are unavailable from the protohistoric period before European and Anglo settlement, and only sketchy information is available from the first half of the European and Anglo occupation (Lewis 1973; Wickstrom 1987). Historical accounts and old photographs, though they may be available, often lack detailed vegetation descriptions.

By default, we are left to assess human influences on vegetation based largely on recent ecological observations, studies, and models (Table). The disadvantages here, too, can be intimidating. Projecting vegetation change back in time or into the future based on study results requires the acceptance of many tenuous assumptions about the fidelity of vegetation communities in space over time and similarities of community responses to past and present disturbance. Sound ecological studies, however, may provide the least-biased information on the persistence of species and communities, resilience of species and communities following disturbance, and biotic and abiotic factors influencing changes in vegetation structure and function. Nevertheless, while such studies are essential for understanding the effects of modern humans on vegetation, they may not provide the information needed to determine long-term trends in vegetation change.

Land Use History

Indians occupied the present Sequoia National Park area from as far back as 6,000–7,000 years ago (Wickstrom 1988) but may not have been permanent residents until A.D. 1000 (Elsasser 1962). It is impossible to assess the relative effects of the transient versus permanent Native Americans. The Western Mono or Monache, who permanently occupied the Kaweah River drainage, were largely a hunting–gathering people, although they may have planted some plants (e.g., tobacco). They were thought to trade acorns and baskets for obsidian (eastern Sierra Nevada) and sea shells (west coast; Elsasser 1962).

Indian population estimates are problematic. As many as 2,000 may have been in the foothills of present-day Sequoia National Park before European contact (Kroeber 1925). In 1858, Hale Tharp, a pioneer and cattleman, found about 600 Indians at Hospital Rock. There were other smaller camps located nearby and in the conifer forests, but these were used only seasonally (Vankat 1977). After European and Anglo settlement outside the western boundary of the present Park, outbreaks of smallpox, measles, and scarlet fever decimated the Indians. By 1865, the Hospital Rock site was abandoned (Elsasser 1962).

Between 1870 and 1910, the Sierra Nevada became summer pasture for cattle and sheep, and shepherds were thought to burn the hills as they retreated to the valley each fall (Vankat 1977). Sequoia and General Grant national parks were established in 1890 and grazing was abandoned in most areas of the parks in 1910.

A fire suppression policy was adopted then, although an effective fire control program didn't begin until about 1930 (Vankat 1977) or perhaps as late as the mid-1950's for the highly flammable foothill vegetation types.

Except for small experimental burns and localized prescribed fires to protect boundary areas, most of the foothill zone of Sequoia National Park remains under full fire suppression (Parsons 1981). The park now receives over a million visitors per year, resulting in occasional wildfires in the foothill areas, often clustered along roads and near campgrounds.

Ecological Studies on Soils and Vegetation

Soils

Vegetation distributions and the resiliency of vegetation to human-caused and natural disturbances may be partially dependent on soils. Soils in the area were recently described as either Ultic Haploxeralfs or an Ultic Haploxerolls–Typic Xerochrepts (Huntington and Akeson 1987). Ultic Haploxeralfs are moderately deep (150 cm), reddish, well leached fine–loamy soils formed from mica schist or granite. The soil supports blue oak woodland (blue oak; European wild oats [*Avena fatua*] and *Bromus* sp.) where the parent material is mica schist but semidense to dense shrub cover (chamise, buck brush [*Ceanothus cuneatus*] and whiteleaf manzanita [*Arctostaphylos viscida*]) with some interior live oak (*Q. wislizenii*), buckeye (*Aesculus californica*), and California laurel (*Umbellularia californica*) where the parent material is mostly granite.

The Ultic Haploxerolls–Typic Xerochrepts association is a shallower soil (55–125 cm), typically on southeast or east slopes, and supports blue oak woodland, canyon live oak (*Q. chrysolepis*), California laurel, buckeye, and some black oak (*Q. kelloggii*) but few shrubs. The parent material here is mostly mica schist, amphibolithic schist, and some quartzite (Huntington and Akeson 1987).

In many areas of the foothill zone of Sequoia National Park, and especially near the Hospital Rock area, major differences between grassland and chaparral soils exist below the subgroup level of classification (G. Huntington, University of California, Davis, personal communication). Within the Ultic Haploxeralfs, course-grained, shallower soils on steeper slopes generally support chaparral. This parent material is mostly granitic rock, and the soils have low water-holding capacity. On less steep slopes, deeper, finer-textured soils of quartz mica schist origin favor grassland development. The hillslope directly behind Hospital Rock containing both types of soil formations demonstrates a strong, edaphically controlled boundary between the blue oak woodland and chamise chaparral communities (G. Huntington, personal communication).

Vegetation

Evaluating the effects of humans on vegetation requires an understanding of how the vegetation resists disturbance, responds to disturbance, and persists despite disturbance. High levels of fuel moisture (plant material water content), for example, may reduce the probability of large spring wildfires in chamise—

resistance. Copious resprouting from a basal burl in chamise provides for rapid recovery of chamise biomass to the preburn state—resilience. Resiliency through time and over space leads to a continued presence on the landscape—persistence.

Early research in the foothill areas of Sequoia National Park (Fig. 1) described fire occurrence and chamise stand characteristics in the chaparral (Rundel and Parsons 1979; Parsons 1981; Stohlgren et al. 1984). These studies provide a quantitative assessment showing that chamise stands are resistant to winter and early spring fires and resilient to late- spring-to-fall fires—matching the natural fire (lightning) frequency.

Additional research on chaparral demography revealed the attributes of chamise chaparral that make it highly resilient to periodic fire. The larger shrubs within a stand have larger basal burls (Rundel et al. 1986), produce more flowers per year (Stohlgren 1985), and resprout more vigorously (Baker et al. 1982; Stohlgren et al. 1984) than smaller shrubs. Large chamise shrubs can maintain their dominance in the postburn stand because large preburn shrubs produce large resprouts that commonly survive a fire (Stohlgren and Rundel 1986; Stohlgren et al. 1989).

Chamise is also prolific. As many as 2.73×10^6 chamise seedlings per hectare may germinate in postburn stands in this area, but these are thought to be out-competed by faster-growing chamise resprouts (Rundel et al. 1986). Mortality of established chamise shrubs following typical summer and fall burns in mature stands is low, averaging 28.7% (Stohlgren 1985). This includes some preburn thinning and fire-caused mortality.

The probability of a shrub surviving a fire is size-dependent. The rate of mortality is low (<20%) but is variable for smaller shrubs and increases sharply for larger size classes. The number of dead individuals observed after fire decreases with size because the size class distribution is heavily weighted toward small individuals. Because over 70% of the shrubs resprout after fire, most individuals are likely to survive several fires once they become established (Stohlgren and Rundel 1986).

Experimental studies revealed that changes in the seasonality of fire significantly affect chamise mortality (Rundel 1982; Rundel et al. 1986). Fires that occur in spring (May–June) or late fall (October–November) under cooler conditions than those that occur during midsummer (i.e., peak lightning season) have different effects. Observed mortality rates for chamise ranged from 40–60% in spring, 20–40% in summer, and 0–20% in fall.

Blue oak ecology and demography are not as well studied as chamise (Baker et al. 1981; McClaran 1986). The widely spaced, cold-deciduous trees are extremely drought resistant with summer predawn xylem sap tensions commonly below 35 bars (Baker et al. 1981). Small and young blue oaks are capable of resprouting after fire. The reproduction of blue oaks, however, may be dependent on many biotic and abiotic factors and is poorly understood (Bartolome et al. 1987; McClaran 1987). McClaran (1986) reported many blue oaks near the study site were 80 to 90 years old and that reproduction since 1910 was nearly nonexistent.

In other oak woodland areas in California, the native annual and perennial grasses have been almost entirely replaced by exotic European and Asian annual grass species (Bartolome et al. 1986). In the study area, the dominant nonnative grasses—*Avena fatua*, *Festuca* sp., and *Bromus* sp.—account for over 90% of the annual aboveground biomass. This understory vegetation recovers quickly after spring or fall burning (Parsons and Stohlgren 1989).

This new information from studies in chamise chaparral and blue oak woodland allows us to assess better the influence of Native Americans, early settlers, and current patterns of use on these ecosystems. The following information provides a current analysis.

Influence of Indians on the Landscape

Despite recent additions to knowledge, precious little is known of the actual effects Native Americans had on foothill vegetation. A recent review of ethnographic and historical literature reported that little is known (and may never be known) about local Native American use of fire (Wickstrom 1987; C. Wickstrom, National Park Service, Sequoia National Park, personal communication). From the little qualitative information that is known, native California Indians reportedly burned a variety of habitats for many different reasons including driving game, clearing meadows, and preparing wild seedbeds and tobacco plots (Lewis 1973). Some groups reported burning to remove brush (i.e., to improve visibility and facilitate travel), as protection against snakes, and to thin forests to allow growth of other vegetation (Lewis 1973). No quantitative data are available (see Wickstrom 1987 for a review).

Recently, even the work of early ethnographers has come under closer scrutiny. Most of the research was done in the 20th century, long after most groups ceased using fire as a tool and long after their culture had been influenced by early Europeans (O'Connell 1974; Timbrook et al. 1982; Wickstrom 1987). Early accounts of aboriginal use of fire by John Muir (1894) are sketchy, but he emphasized the local use of fire rather than widespread burning, which he attributed to shepherds. Muir claimed that Indians "burn off the underbrush in certain localities to facilitate deer hunting."

These general statements provide insights on why native groups burned vegetation. They tell us little of the specific vegetation types, however, or the conditions under which they burned, the size and frequency of burns, or the spatial patterning of burns (or fire escapes). Any evaluation of aboriginal use of fire must consider the relative role of lightning-cause ignitions, the specific reasons where and why Indians may have burned to augment lightning fires, and what the overall effects were on the landscape.

Indians could have altered successional seres on the landscape by altering the frequency or seasonality of fire. Repeated spring fires would have reduced chamise populations due to high burl mortality rates (Stohlgren et al. 1984, 1989). Too short a fire interval would have generally increased chamise mortality (Zedler et al. 1983).

Indian burning (including fire escapes) may not have altered plant community distributions greatly if chamise were resilient to a wide range of fire return intervals. Field studies in Sequoia National Park found that a fire interval of 3 years caused atypically high (>90%) chamise mortality (Rundel 1986). The stand in question was on an ecotone with oak woodland–grassland and was invaded by highly-flammable, exotic, annual grasses (e.g., *Avena fatua*). Whereas the two fires (3 years apart) were both human-caused and influenced by introduced species, similar occurrences may have been rare under natural conditions. Chamise remained the dominant species in most locations in the twice-burned area despite the short fire return interval of only 3 years. High foliage moisture and low percentage of dead material would generally reduce the flammability of stands less than 20 years old.

There is little evidence that long fire intervals increase chamise mortality in this area. In several stands thought to be 60–90 years old or older, fires have resulted in low mortality rates of 0–20% for fall burns and 20–40% in hotter, summer burns. Regrowth in these stands was rapid. Thinning mortality in mature stands averaged only 15% (Stohlgren 1985) and was concentrated in the smaller size class shrubs that could easily be replaced after fire by seedlings. Although stands more than 60 years old have more dead material (Rundel and Parsons 1979) and lower foliage nutrient concentrations (Rundel and Parsons 1980) than younger stands, stand senescence is not reflected in mortality data. This may demonstrate that chamise in this area may be better adapted to a longer fire interval than previously thought (Rundel and Parsons 1979, 1980). The range of fire frequencies that would favor continued dominance of chamise may likely be from less than 20 to 100 or more years (Stohlgren et al. 1989).

Because chamise stands are resilient to a wide range of fire frequencies, it is likely Indians may not have had large scale or long-term effects on shaping chamise chaparral distribution patterns in the Hospital Rock area. As Vankat (1977) points out, "the ecological significance of their (Indian) burning is somewhat unclear, since lightning fires have always been frequent in the dry summer environment of the Sierra Nevada." Furthermore, extensive augmentation of lightning fires (i.e., increasing the fire return interval) would have led to vegetation-type conversions from chaparral to grassland (Bentley 1967; Zedler et al. 1983) and may have negatively affected deer populations that favor young chaparral stands as browse.

On a landscape scale, extensive burning would not concentrate deer or important plant species (e.g., *Chlorogalum* sp. [soap plant] for brushes, *Quercus* sp. for acorns). The use of fire for driving game in extremely mountainous regions may not have been the preferred method if local burns in chaparral areas near camps were successful in baiting in the target species. My interpretation matches descriptions by Muir of Native American use of fire and coincides with the accounts of Hale Tharp (C. Wickstrom, National Park Service, Sequoia National Park, personal communication). Early U.S. Cavalry and Park Superintendent's reports (unpublished reports, Sequoia National Park) confirm the expanses of impenetrable brush in the foothill areas at the turn of the century.

Other factors, beyond Indian (or modern human) control, may act to stabilize vegetation distributions on the landscape for hundreds of years. The recent research on the distribution of soils in the area shows major contrasts (locally) between chaparral and grassland soils (Huntington and Akeson 1987). The chaparral–grassland ecotone immediately upslope from Hospital Rock seems to be a stable, edaphic controlled boundary. Griffen (1988) also suggests that chaparral patches throughout the state are concentrated on less developed, shallower soils than is the woodland. Edaphic controlled boundaries in oak grassland, chaparral, and coastal sage communities were also reported in Santa Barbara County, California (Cole 1980).

If Indians burned the area too frequently for chamise persistence, one might expect to find chaparral soils under the grassland (i.e., evidence of a type conversion). Based on the Huntington and Akeson (1987) soils survey, there is little evidence of extensive type conversions from chaparral to grassland. Furthermore, shrubs do not seem to be invading grassland areas in this area. Prescribed fires in grassland areas adjacent to chamise stands resulted in no shrub seedling establishment (Parsons and Stohlgren 1989). This may, however, be from competition (or other mechanisms) between annual grassland species and chaparral species. Still, the soils data suggest that edaphic (or other biotic and abiotic) factors on this site may be more important than past land uses in determining long-term vegetation distribution patterns. If Indians augmented the natural frequency of fire in the immediate area of Hospital Rock, it was probably not enough to result in type conversions on a large scale. Chamise chaparral continues to dominate on coarse-textured soils, and grasslands dominate on the fine-textured soils of the low elevation foothills of the park. In sum, these observations suggest that Indian practices of burning may have influenced plant successional seres locally. They may not, however, have played as important a role in producing the plant community distribution patterns in the foothill region of Sequoia National Park as earlier authors suggested.

Influence of Early Settlers on the Landscape

In contrast to Indian-caused fires, Muir (1894) describes a 1875 shepherd-caused fire as "a great fire in the Middle and East Forks of the Kaweah River" that "came racing up the steep chaparral-covered slopes of the East Fork canyon." Muir later recognized that lightning was actually the main cause of fire in the Sierra Nevada (Barrett 1935). Muir described the effects of sheep on the montane meadows by writing, "The wild botanic garden is trodden down, the shrubs are stripped of leaves as if devoured by locusts, and the woods are burned," but little was written of the effects on the foothill grasslands or chaparral (Vankat 1977).

Again, it is difficult to evaluate the influences of cattleman and shepherd use of fire on the landscape. They occupied the area in summer and fall for about 40 years. Lack of fuel accumulation casts doubt that they were able to burn the same chaparral or forest area more than a few times. Instead, the greatest effect

on the landscape was in the oak woodland during this era. Intensive grazing, repeated burning, and introduction of exotic European grasses (*Avena fatua* and *Bromus* sp.) almost entirely replaced the native California annual and perennial grasses (Parsons and Stohlgren 1989).

No records exist on the pristine species composition of the grassland understory of the blue oak woodland. The extent to which native perennial grasses have been replaced can only be determined indirectly by analyzing plant phytoliths (Bartolome et al. 1986). Recent research shows European annual grasses continued to dominate native herbs and grasses with or without fire (Parsons and Stohlgren 1989). In terms of species composition, phenology, and plant physiology, the grass and herbaceous understory of the blue oak woodland remains the most human-altered vegetation type in the Sequoia National Park.

Overgrazing by sheep and cattle between 1860 and 1880 has also been suggested as the cause of an increasing density of blue oak. Removing grasses and herbs reduced competition and favored establishment of blue oak (Baker et al. 1981; McClaran 1986; but see Allen-Diaz and Bartolome 1992 and Hall et al. 1992). Long-term changes in blue oak recruitment are difficult to verify without accurate site-specific information on the pristine landscape and without better information on the factors affecting blue oak demography (Bartolome et al. 1987; Borchert et al. 1989; Allen-Diaz and Bartolome 1992). In three blue oak woodland sites in the Tehachapi Mountains of California, Mensing (1992) found blue oak recruitment was

1. fairly continuous during Indian habitation (mean fire-free intervals of 9.6–13.6 years),
2. unusually high in the 1850's during early European settlement (mean fire-free intervals of only 3.3–5.8 years), and
3. virtually completely suppressed since the 1860's despite the presence of recurring fire (mean fire-free intervals of 13.5–20.3 years).

Influence of Current Inhabitants on the Landscape

Since about 1930, people have been responsible for many influences on the landscape, but none is as overtly noticeable as the homogeneous distribution of old, high-biomass stands of chaparral that have resulted from fire suppression (Parsons 1981). Vankat (1977) and Parsons (1981) provide detailed histories of the fire suppression policy in Sequoia National Park that goes back to the early 1900's, but the effective practice of fire suppression probably began about 1933 when members of the Civilian Conservation Corps worked on fire projects. Fire suppression improved considerably in the early 1950's with the use of aerial tankers.

The flammable nature of chaparral fuels (Rundel 1982), however, does not allow easy fire suppression or control. From 1930 to 1981, about 30% of the foothill zone of Sequoia National Park has burned at least once due to lightning

or human-caused fires (Parsons 1981). The larger, unburned areas of the landscape may not represent the mosaic of chaparral stand age classes that would have been present without fire suppression (Minnich 1990). It is possible to restore a more natural mosaic of stand age classes using prescribed burning (Rundel 1982), because chamise stands are resilient to long fire-free intervals (Stohlgren 1985; Stohlgren et al. 1989). Additionally, such burns would allow a replenishment of seed reserves (i.e., fire-ephemeral herbs and grasses) in the soil (Parsons and Stohlgren 1989).

Unfortunately, fire also may facilitate invasion of exotic grasses and herbs. Recent attempts to prescribe burn the exotic annual grassland (blue oak woodland) have not been successful at reducing alien species or increasing native grasses (Parsons and Stohlgren 1989). The vegetation composition of this portion of the landscape may be difficult (and impractical) to restore to a pre-European settlement state until better vegetation restoration techniques become available (i.e., biological control, better native grass planting techniques).

Air pollution (particularly acid rain and increased ozone concentrations) also may be negatively affecting foothill vegetation and soils. Acid deposition may artificially add more than 3 kg/ha/year of nitrogen and 3 kg/ha/year of sulfur to these nutrient-poor systems (Stohlgren and Parsons 1987; Stohlgren et al. 1991). This fertilizer may cause changes in a system that evolved without such inputs. Chaparral soils may be particularly sensitive to sulfate additions (Wyels 1986; Stanko and Fitzgerald 1989). Also, high daily ozone concentrations are known to be hazardous to chaparral seedlings (Stolte 1982; Sequoia National Park, unpublished data). Some studies are under way to determine the long-term effects of air pollution on chaparral vegetation (Parsons and Stohlgren 1986), but this research should be greatly expanded.

Current inhabitants may be responsible for other, more subtle, changes in the foothill landscape. The now-extinct California grizzly bear surely affected vegetation and wildlife. Roads, campgrounds, water diversions, increased invasion and spread of exotic species (plants, animals, and diseases), and recreationists negatively affect natural functioning ecosystems. We have only begun to document these subtle, perhaps chronic, effects.

Conclusions

Chamise chaparral in the foothills area seems to have topographic and edaphically-controlled boundaries similar to other chaparral stands in California (Cole 1980). The available evidence is inconclusive that Indians in Sequoia National Park greatly augmented fire frequencies to affect long-term vegetation distribution patterns on large spatial scales. Chamise stands continue to dominate the southern aspect foothill communities with coarse-grained soils. The combination of demographic traits, resilience to periodic fire, and persistence on many sites suggest chamise chaparral has vegetation inertia. Once established, the vegetation can continue to exist long after conditions suitable

for establishment have disappeared (Cole 1985). Thus, despite temporary or localized increases in fire frequency due to human activity, chamise chaparral distribution may not have been affected radically.

Pristine chaparral vegetation of the foothill zone probably had a similar overall spatial distribution and species composition, but with more of a mosaic pattern of different-aged shrub stands. The homogeneous, mature stands seen today are the result of fire suppression. Such areas should be fragmented with large and small prescribed burns conforming to natural physical boundaries and coinciding with natural occurrences of lightning.

The understory of blue oak woodland remains the most obviously altered vegetation type in the Sierran foothills. The invasion of European annual grasses was almost complete and probably irreversible given today's techniques for controlling annual grass invasions on landscape scales (U.S. Forest Service 1990). It is unknown whether seed dispersal alone or some combination of burning by Indians or early Europeans and intensive sheep and cattle grazing facilitated the invasion of the alien plants. Remnant species of the pristine (pre-European settlement) oak woodland understory can only be found in certain areas or as a temporary sere following fire (Parsons and Stohlgren 1989). Managers and scientists should seek to protect what germ plasm remains of native grasses and herbs and encourage research to prevent further devastation of the native flora.

Human activities will continue to affect these foothill communities by either shortening the fire interval with accidental or arson fires or by elongating the fire cycle with fire suppression. In national parks, where the preservation of naturally functioning ecosystems is a primary objective, management efforts should be careful not to compound these effects by concentrating prescribed burns seasonally (i.e., increased spring fires) or in certain localities (i.e., along roads or ridge tops, or near developed areas). Increased efforts are needed to monitor effects of air pollution and climate change on foothill vegetation and soils.

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Ecology of Mountain Sheep Reintroduced in the Sierra Nevada of California

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Abstract. From March 1986 through September 1991, we evaluated a mountain sheep (*Ovis canadensis californiana*) reintroduction to Lee Vining Canyon, Sierra Nevada, California. Natality, mortality, and habitat suitability were studied. We monitored movements and distribution to learn how reintroduced sheep explore and colonize an unfamiliar location. Data were collected at ewe forage sites to develop a discriminant model for classifying foraging habitat.

Twenty-seven sheep were translocated in March 1986. Eleven were added in March 1988, raising the number introduced to 38. The herd grew to 62 sheep after 6 years, with at least 56 lambs born during the study. Survival to 1 year of age averaged 72%. Most of the increase occurred during the last 2 years when the annual growth rate averaged 24.5%. We confirmed 22 deaths, although the actual mortality was more likely 32 sheep. Mountain lion (*Felis concolor*) predation and severe winter weather caused most of the deaths. The age structure of the herd at the end of the study suggests a potential for rapid population growth.

The herd colonized Lee Vining Canyon in two phases. The first phase was characterized by small home range sizes, failure to disperse from the release site, and limited sexual segregation. During the second phase, behavior was more typical of established herds.

The discriminant model correctly classified ewe foraging sites 72% of the time. Distance to escape terrain, herbaceous cover, and presence of surface water were the most useful parameters for classifying a site. Fecal crude protein levels, in conjunction with natality and survival rates, suggested that the habitat was suitable for reproduction and survival of the herd.

Key words: Mountain sheep, reintroduction, population dynamics, movement patterns, habitat use, nutrition, *Ovis canadensis californiana*.

Mountain sheep (*Ovis canadensis californiana*) were once widely distributed throughout the Sierra Nevada of California. A rapid decline in numbers began about 1850 and continued for the next 3 decades. During that time, many of the Sierra herds were reduced to remnant status. A long period of attrition followed, during which most remnant herds disappeared (Wehausen 1980). The major causes of decline include overhunting (Grinnell and Storer 1924:243), forage competition with domestic sheep (Dixon 1936), and diseases contracted from domestic stock (Jones 1950; Wehausen 1988).

In 1974, Wehausen (1979, 1980) began to assess the status of mountain sheep in the Sierra Nevada. After an extensive literature review and field surveys throughout likely mountain sheep habitat, he concluded that only the Mount Baxter and Mount Williamson herds had survived (Fig. 1). The Mount Williamson herd seemed stable at approximately 30 animals. The Mount Baxter herd, however, contained approximately 220 sheep and had been growing for nearly a decade.

Wehausen (1979) developed a series of management alternatives for Sierra Nevada mountain sheep. Major recommendations were that the Mount Baxter herd provide transplant stock for repopulating historic ranges in the Sierra Nevada and that an interagency advisory panel be established to coordinate management of the herds.

The Sierra Nevada Bighorn Sheep Interagency Advisory Group (SNBSIAG) was formed in 1981 to foster cooperation between federal and state agencies involved with Sierra Nevada mountain sheep management.

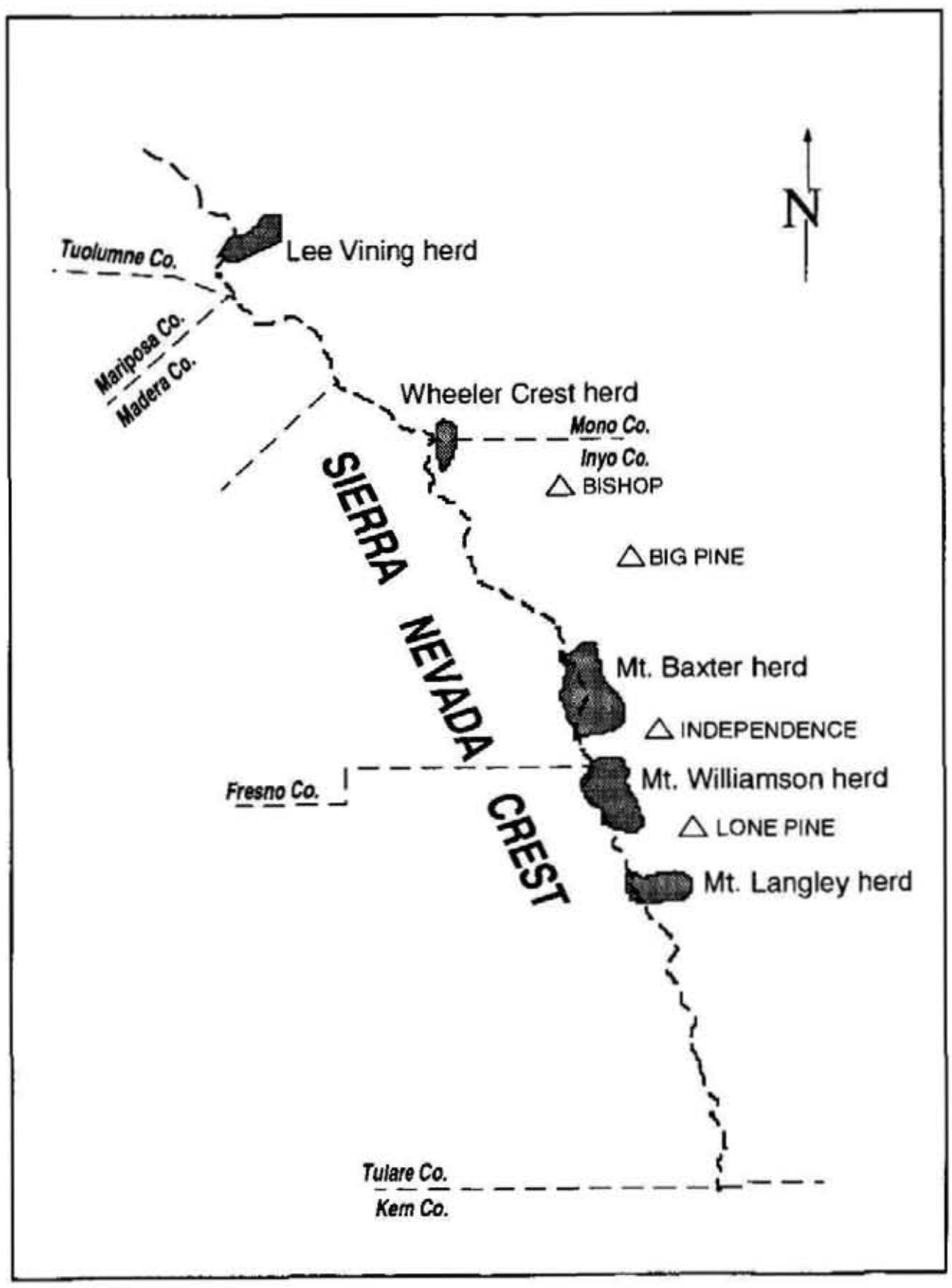


Fig. 1. Distribution of bighorn sheep herds in the Sierra Nevada, California, as of January 1992.

Participants included biologists from the California Department of Fish and Game, National Park Service, U.S. Forest Service, and the Bureau of Land Management. John Wehausen acted as a consultant (Keay et al. 1987).

In 1984, the advisory group issued the Sierra Nevada Bighorn Sheep Recovery and Conservation Plan (Sierra Nevada Bighorn Sheep Interagency Advisory Group 1984). The goal of Sierra Nevada mountain sheep management was to ensure the continued existence of the sheep. This objective was to be achieved by maintaining the health and viability of all existing populations and by promoting the establishment of at least three reintroduced populations that would be large (exceeding 100 animals) and geographically distant from one another (Sierra Nevada Bighorn Sheep Interagency Advisory Group 1984). Lee Vining Canyon, near Yosemite National Park, was identified as the best possible reintroduction site in the northern Sierra Nevada (Wehausen 1979).

History of Mountain Sheep in the Yosemite Region

Mountain sheep historically occupied the Yosemite region (Jones 1950), where they summered along the main crest of the Sierra Nevada (Fig. 2). Most of them disappeared by the early 1880's (Grinnell and Storer 1924). In 1914, Yosemite's mountain sheep were declared extinct (Jones 1950).

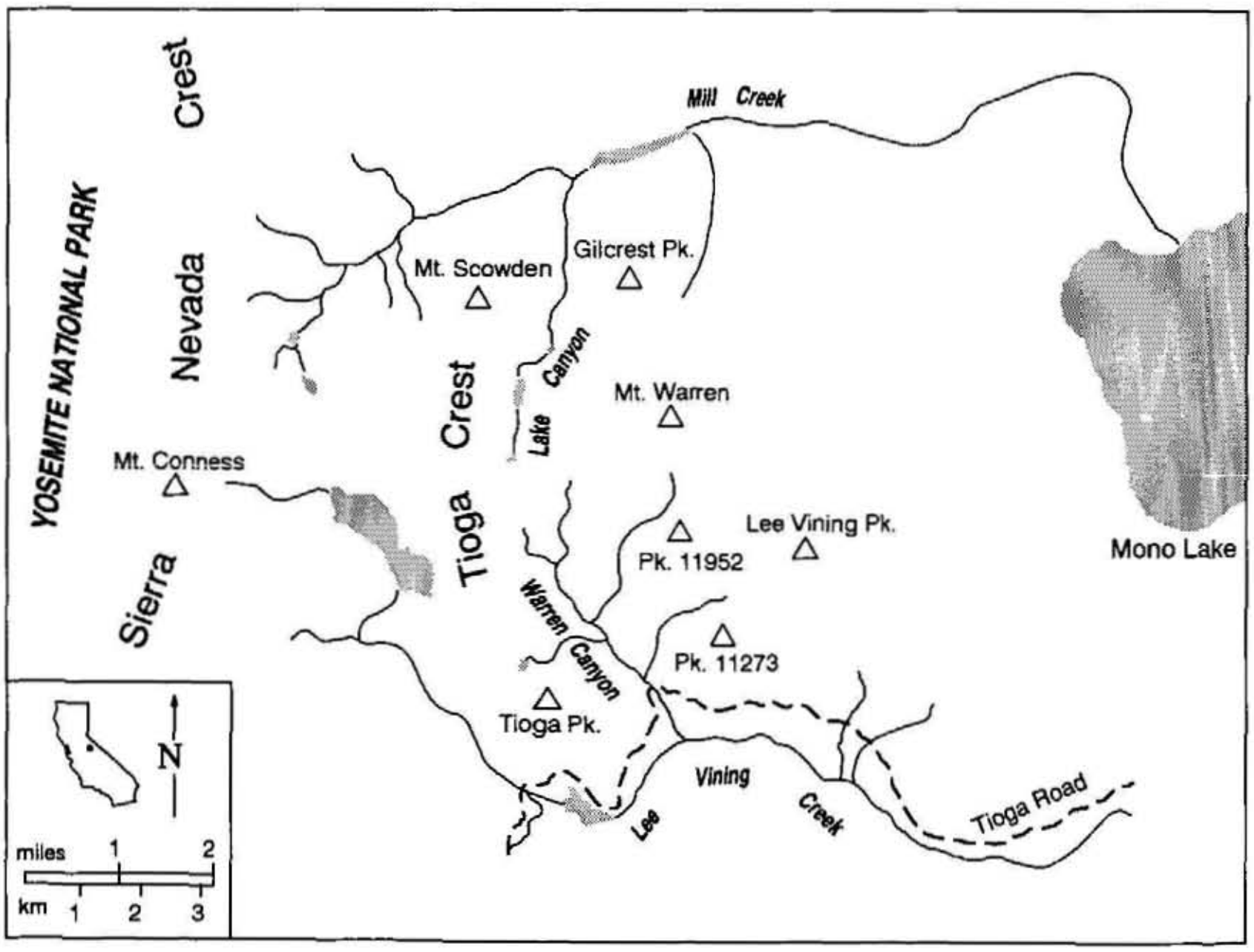


Fig. 2. Map of the Lee Vining Canyon bighorn sheep reintroduction study area showing significant topographic features.

Although the idea of restoring mountain sheep to Yosemite gained early support (Blake 1941, 1949), biologists at the time preferred natural recolonization to reintroduction (Wright et al. 1932; Grinnell 1935). More than 50 years elapsed, however, without mountain sheep recolonizing Yosemite. Spurred by objectives in the recovery and conservation plan (Sierra Nevada Bighorn Sheep Interagency Advisory Group 1984) and recognition that mountain sheep dispersal is limited by their fidelity to traditional ranges (Geist 1971:99), managers began reconsidering reintroduction as an alternative (Keay et al. 1987).

On 5 and 6 March 1986, the California Department of Fish and Game translocated 27 native Sierra Nevada mountain sheep from Mount Baxter to Lee Vining Canyon, just east of Yosemite. The Lee Vining herd was augmented with 11 more sheep from Mount Baxter in March 1988 because the number of adult ewes in Lee Vining Canyon had declined to only five individuals.

The primary objective of our study was to evaluate the reintroduction and identify factors contributing to its success or failure. We planned to monitor population dynamics, identify important components of mountain sheep habitat, assess the suitability of habitat in Lee Vining Canyon, and document how mountain sheep explore and colonize an unfamiliar location.

Study Area

Description

The 46-km^2 study area adjoins the eastern edge of Yosemite National Park along the Sierra Nevada crest. It is bounded on the north by Mill Creek in Lundy Canyon and on the south by Lee Vining Creek (Fig. 2). Elevation ranges from 2,188 m at the eastern end of Lee Vining Canyon to 3,758 m atop Mount Warren. Lands in the study area are managed by the U.S. Forest Service as parts of Inyo National Forest, Hoover Wilderness, and the Harvey Monroe Hall Natural Area.

Fault block uplift and early-to-mid-Pliocene riverine cutting combined to produce the area's complex physiography (Bateman and Wahrhaftig 1966). The landscape was further shaped by at least five glacial sequences (Blackwelder 1931; Sharp and Birman 1963). Substrates on the eastern half of the study area are primarily granitic while those on the west are metasedimentary (Kistler 1966; Bateman et al. 1983). Soils are generally shallow and poorly developed.

Climate

Climate is characterized by cold, wet winters and warm, dry summers. Long periods of clear, sunny weather are broken by storms that are usually short-lived. Mean monthly temperatures range between 1 and 20° C in summer ($\bar{x}$ = 13° C) and 2 and −12° C ($\bar{x}$ = −5° C) during winter. Annual precipitation averages 76 cm and is deposited primarily as snow falling between November and April.

Vegetation

Lower elevations (2,180–2,590 m) used by the Lee Vining herd as winter range are characterized by sagebrush steppe (Young et al. 1977) and pinyon–juniper woodland communities (Munz and Keck 1973; Laudenslayer and Boggs 1988). Summer ranges extend from 3,232 to 3,437 m elevation and consist of subalpine forest and alpine communities (Benson 1977; Major and Taylor 1977).

Methods

Movement and Distribution

We monitored movement and distribution patterns from March 1986 through September 1991 by equipping 36 of the 38 transplanted sheep with radiotelemetry collars. Seasonal movement data were analyzed using the 100% minimum convex polygon method (Hayne 1949). Although the method has shortcomings (Van Winkle 1975; Schoener 1981; Worton 1987), it delineated the extent of movements and allowed comparisons with other studies. When sample sizes were adequate (≥ 80), we also examined location data using the program PDF-XYZ 1.0 (Crabtree 1988) to describe the extent and intensity of space use.

Population Dynamics

We conducted a complete census every 10 days to document reproduction and survival. Motion sensors in the collars alerted us to deaths and enabled us to recover carcasses to determine causes of death.

Habitat

The polygynous mating system of mountain sheep makes ewes the most important reproductive component in sheep populations. Balancing lamb safety and the nutritional demands of lactation forces ewes to be more selective when choosing forage sites (Wehausen 1980). Consequently, we focused on evaluating habitat at sites used by the ewe–juvenile component of the herd.

We conducted fieldwork to evaluate habitat in the summers of 1988 and 1989. We sampled habitat characteristics at 52 forage sites used by ewe–juvenile groups and at 55 randomly selected sites. A forage site was an area, ≤ 40 m in diameter, where a ewe–juvenile band foraged for at least 5 min. We measured elevation, aspect, slope, visibility, distance to escape terrain, vegetative cover, and whether or not water was present at each site.

Visibility was defined as the percentage of each quarter of the compass over which a 90-cm-tall object could be seen from 40 m away (Risenhoover and Bailey 1980). Escape terrain was steep, broken, rocky terrain that would allow sheep to outmaneuver or outdistance predators (Gionfriddo and Krausman 1986). Cover along three line-point transects on each plot was recorded as

absolute vegetative cover by species, litter, or bare ground. At each point covered by vegetation, we measured the height of the tallest plant (in centimeters).

Random sites were areas located within ewe summer range, but where sheep were not observed foraging. Their number and location were determined by stratified random sampling. The number of random sites within each habitat type was based on the proportion of ewe–juvenile forage sites occurring within that habitat. Precise locations were determined from randomly selected 0.1-km Universal Transverse Mercator grid intersections within a composite home range of adult ewes. Sampling protocols for random sites followed those used at forage sites.

We used two-way indicator species analysis (TWINSPAN; Hill 1979) to define the plant communities at forage and random sites. Discriminant analysis was used to identify habitat characteristics that best distinguished between forage and random sites, develop a model describing forage site use by ewe–juvenile groups, and test the model's accuracy (Norusis 1988).

Fecal crude protein (6.25 × nitrogen values) levels were used as indices of diet quality (Wehausen 1980; Leslie and Starkey 1985). We tracked fecal crude protein levels throughout the year by collecting fecal pellets at weekly intervals and analyzing them using the micro-Kjeldahl technique. Results were expressed on a percent-organic matter basis (Seip and Bunnell 1985). We indirectly assessed habitat suitability using rates of reproduction and lamb recruitment.

Results

Movement and Distribution

Distribution patterns during the first year consisted of seasonal movements between summer range on the upper slopes of Peak 11,273 (Fig. 3a) and winter range in lower Lee Vining Canyon (Fig. 3b). Movements rarely extended more than 3 km from the release site, and the boundary between winter and summer ranges was indistinct. Rams associated with ewes throughout the year. Home range sizes averaged 9.5 km^2 for ewes and 15.8 km^2 for rams during the first summer (Table 1). A series of mild storms in September and October produced repeated movements between summer and winter ranges. Movements during this period also included forays to previously unvisited areas. On two occasions, the herd abruptly moved 6 km north to the vicinity of Mount Warren (Fig. 2) but returned to summer range within 2 or 3 days.

Members of the Lee Vining Canyon herd moved to lower elevations following the first major storm in late November 1986. They established their 1987 winter range on the brushy hillsides bordering embankments along Tioga Road (Fig. 4a). A notable exception was the emigration in October 1986 of three ewes and two lambs to Bloody Canyon, 8 km south of Lee Vining Canyon. These sheep established residence in Bloody Canyon and remained isolated from the main herd for the duration of the study.

During the second year, distances between summer and winter ranges increased as some herd members extended movements into new areas. The average female summer range increased ($P < 0.05$) to 22.4 km^2 (Table 1) with the migration of ewes to Gilcrest Peak and Mount Scowden (Fig. 4b). Most rams shifted summer activities to areas along the Sierra Nevada crest in Yosemite National Park (Fig. 2). These changes increased sexual segregation. By late November, most herd members had returned to winter range used the previous year (Fig. 4a).

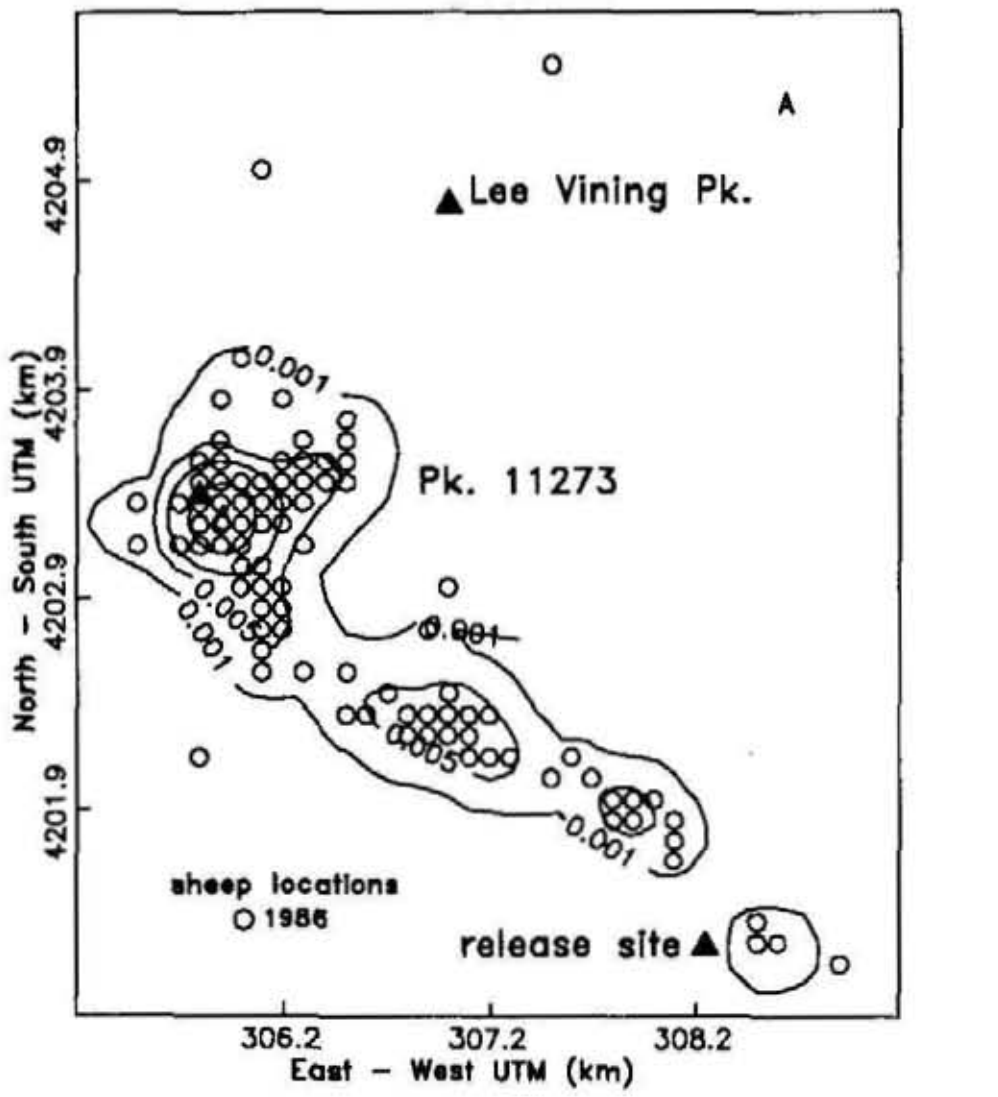


Fig. 3. Summer (*A*) and winter (*B*) home ranges used by bighorn ewe 4411 in 1986 in Lee Vining Canyon, Mono County, California.

Table 1. Estimates of individual home range size (km^2) in the Lee Vining Canyon mountain sheep (*Ovis canadensis californiana*) herd determined using the minimum convex polygon method.

	Winter–Spring						Summer–Fall					
	Ewes			Rams			Ewes			Rams		
Year	$\bar{x}$ area	SD	n	$\bar{x}$ area	SD	n	$\bar{x}$ area	SD	n	$\bar{x}$ area	SD	n
1986	4.2	4.3	12	18.1	22.0	4	9.5[a]	2.9	12	15.8	4.4	5
1987	7.3	0.9	7	11.9	3.8	4	22.4	8.3	6	35.4	5.1	4
1988	18.1	9.1	5	28.0	1.2	4	22.0	3.9	5	23.7	11.4	4
1989	17.4	17.0	5	17.7	7.8	4	18.0	10.2	5	14.7	16.9	3

[a]Denotes significant differences between years at $P < 0.05$ level using Dunn's test (Zar 1984:201).

The general pattern of movements exhibited during the second year remained relatively constant in subsequent years. An exception occurred when a few individuals from the 1986 reintroduction delayed returning to lower elevations until midwinter 1988. This change persisted through the remainder of the study.

Members of the 1988 supplement generally adopted the movement patterns of their predecessors with one significant exception. While most sheep from the 1986 reintroduction descended to lower elevations by mid-March 1988, members of the 1988 supplement remained on the summit (3,509 m) of Tioga Peak (Fig. 2).

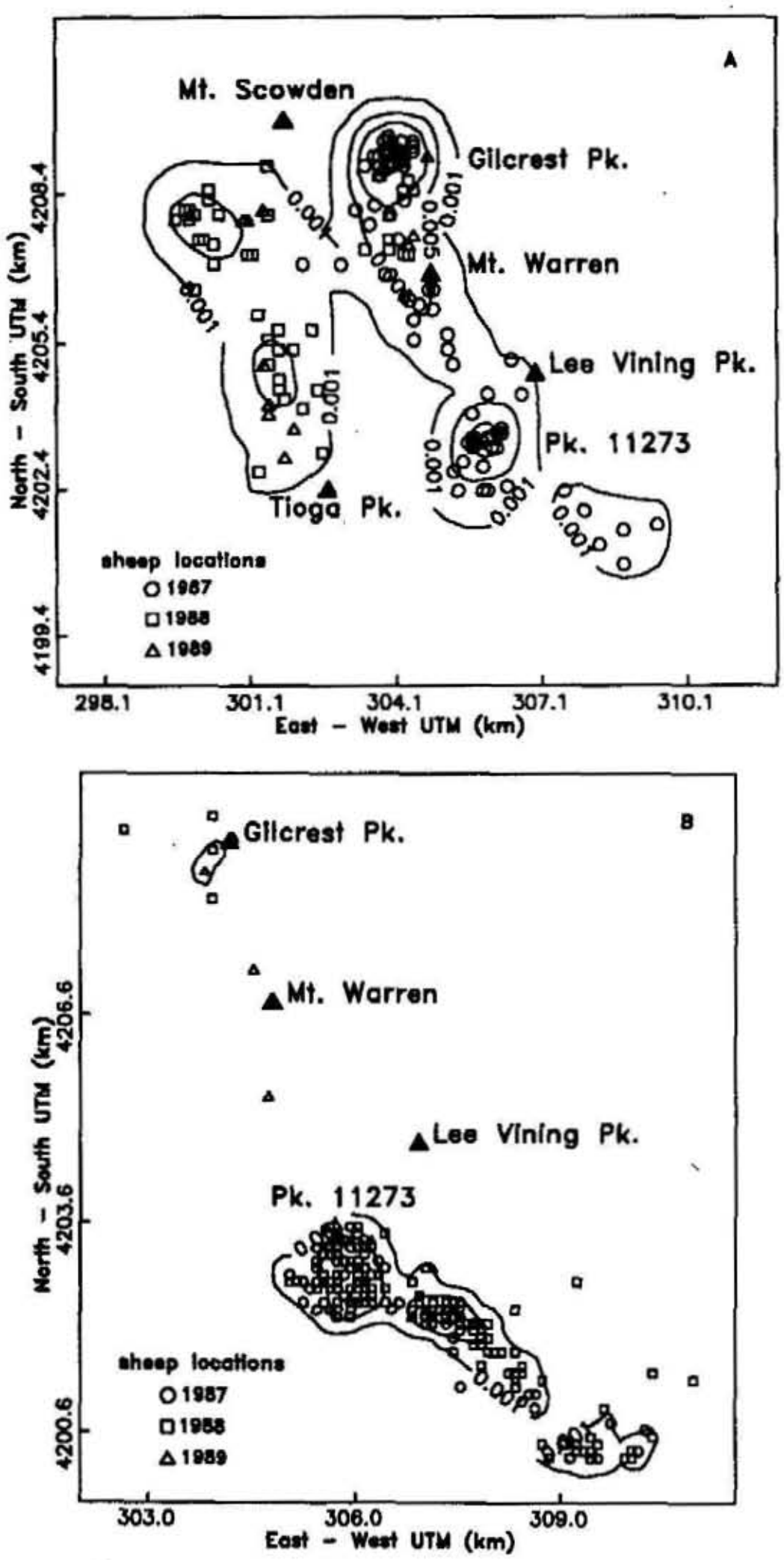


Fig. 4. Winter (*A*) and summer (*B*) home ranges used by bighorn ewe 4411 in 1987, 1988, and 1989 in Lee Vining Canyon, Mono County, California.

Population Dynamics

Natality

A minimum of 56 lambs was born during the study, and the annual ratio of lambs to ewes averaged 65:100 (Table 2). Lamb survival averaged 72% annually for the first 5 years. The mean recruitment rate during that period, expressed as the ratio of yearlings per 100 ewes ($\geq$2 years of age), was 47:100.

Mortality

Twenty-two confirmed deaths and 10 presumed deaths (Table 3) occurred between March 1986 and September 1991. Seven of 22 confirmed deaths occurred within 3 weeks of the 1986 reintroduction and resulted from accidents and exposure (Chow 1991). Ten of the remaining 15 confirmed deaths were from mountain lion (*Felis concolor*) predation. At least seven of nine radio-collared sheep that died were killed by mountain lions. Thus, it is likely that some of the presumed deaths also resulted from mountain lion predation.

Population Size

The Lee Vining Canyon herd increased from 38 sheep (Table 4) to an estimated maximum of 62 sheep in 6 years (Table 5). If the sheep in Bloody Canyon are discounted, and lamb survival in 1990 and 1991 is recalculated using the mean survival rate observed during the first 4 years of the study, estimated herd size is 51 animals. A minimum of 49 sheep was recorded during a census conducted in July 1991. Discrepancies between the minimum number and the totals projected in Table 5 are probably attributable to unconfirmed lamb deaths in 1990 and 1991.

Despite the birth of nine lambs in 1986, the Lee Vining Canyon herd declined from 27 to 20 sheep. The annual growth rate that year was -25.9% (Table 6). Annual growth rates during the next 2 years were only 5.0 and 6.3%, respectively. The 1988 supplement of 11 more sheep from Mount Baxter increased the total herd size to 32. In 1989, the annual growth rate rose to 17.6% and reached 25% in 1990. Because monitoring ended in September 1991, the 24% growth rate for 1991 does not account for probable overwinter mortality, and the actual figure is probably slightly lower.

Habitat

Analysis by TWINSPAN divided vegetation at forage and random sites into seven communities (Fig. 5). The primary dichotomy was between dry and wet sites. Dry site communities fell along an elevation gradient, indicating temperature may be the second most important factor affecting species composition on summer range.

Of the classified forage sites, 43% were located on high, exposed alpine slopes and ridges with sparse cover ($<25\%$) of low perennial herbs and graminoids. Indicator species of this dry *Podistera–Phlox* community included *Podistera nevadensis*, *Phlox covillei*, *Eriogonum ovalifolium*, and *Festuca ovina*. *Astragalus kentrophyta* and *Chrysothamnus parryi monocephalus*

Table 2. Lamb production and recruitment by cohort in the Lee Vining Canyon mountain sheep (*Ovis canadensis californiana*) herd between 1 May 1986 and 6 September 1991.

Year	Number of lambs born	Lee Vining		Overall[a]		
		Lamb:ewe ratio	Yearling:ewe ratio	Lamb:ewe ratio	Surviving to 1 year (%)	*n*
1986	9	75:100		75:100	67	6
1987	5	83:100	67:100	55:100[b]	60	3
1988	8	43:100	50:100	44:100	63	5
1989	9	56:100	25:100	47:100[b]	78	7
1990	13	68:100	37:100	59:100	92	12
1991	12	57:100	57:100	50:100[b]		

[a]Includes ewes in Bloody Canyon.
[b]No rams were present in Bloody Canyon during the previous breeding season.

Table 3. Sources of mortality in the Lee Vining Canyon mountain sheep (*Ovis canadensis californiana*) herd between March 1986 and September 1991.

		Sources of mortality					
Cohort	Initial number	Exposure	Accident	Mountain lion[a] predation	Unknown	Presumed dead	Current number
1986 transplant	27	5	2	6		3	11
1986 lambs	9			1	1	2	5
1987 lambs	5			1	1		3
1988 transplant	11			2	2		7
1988 lambs	8				1	2	5
1989 lambs	9					2	7
1990 lambs	13					1	12
1991 lambs	12						12
Total	94	5	2	10	5	10	62

[a]*Felis concolor*.

commonly occurred as well. Ewe groups used this community throughout summer, once it was free of snow.

A second alpine xeric community, which included 10 (20%) of the forage sites, was characterized by *Ribes cereum*. Mean elevation of the *Ribes* community was 245 m lower than the *Podistera–Phlox* community. The xerophytic species *Leptodactylon pungens* and *Sitanion hystrix* were common in both of these communities.

The *Carex–Juncus* community was used throughout the growing season, but the *Artemisia tridentata–Monardella odoratissima* community received minimal use.

Samples from mesic sites were grouped into three plant communities (Fig. 5). Sheep visited these in mid- to late August in both years. *Trisetum spicatum* and *Trifolium monanthum* were indicators for sites located on, or adjacent to, metasedimentary rock outcrops or cliffs. These were steep, moderately high elevation ($\bar{x}$ = 3,224 m) sites with surface or subsurface water. The other two mesic communities were dominated by sedge (*Carex* sp.) and grass species. Forage sites in these communities were less common but those present were used repeatedly.

Five variables were used in the final discriminant model to explain differences between forage sites (FS) and random sites (RS). They were presence of water (H_2O), herbaceous dicot cover (FORBCOV), distance to escape terrain (ETD), vegetation height (VEGHT), and visibility (VIS). Surface water was present on 19% of forage sites and none of the random sites. Forage sites averaged more than twice as much herbaceous cover ($\bar{x}_{FS}$ = 9.8%; $\bar{x}_{RS}$ = 3.9%), and mean vegetation height was 32% taller than on random sites ($\bar{x}_{FS}$ = 11.0 cm; $\bar{x}_{RS}$ = 8.3 cm). Steep, rocky terrain averaged 68.6 m from forage sites ($\bar{x}_{RS}$ = 150.0 m), and mean visibility on forage sites was 51.4% ($\bar{x}_{RS}$ = 43.1%). The resulting linear discriminant function was

$$\text{Discriminant score} = 1.309(H_2O) + 4.188(\text{FORBCOV}) - 0.097(\text{ETD}) + 0.609(\text{VEGHT}) + 0.984(\text{VIS}) - 2.180.$$

Table 4. Sex and age distribution of mountain sheep (*Ovis canadensis californiana*) reintroduced to Lee Vining Canyon, Mono County, California, in 1986 and 1988.

	Age class										
Sample	L[a]	1	2	3	4	5	6	7	8	9	**Total**
1986											
Male	5	4	1			1				1	12
Female	2		2	4	4		1	2			15
1988											
Male			2				1				3
Female		1	3		1	1	1		1		8
Total	7	5	8	4	5	2	3	2	1	1	38

[a]Lamb.

Table 5. Sex and age distribution of mountain sheep (*Ovis canadensis californiana*) in Lee Vining and Bloody canyons on 1 September 1991.

	Age class														
Sample	L[a]	1	2	3	4	5	6	7	8	9	10	11	12	13	**Total**
Lee Vining Canyon															
Male		3	2	1		3	1	3	1		1				15
Female		3	2	3	3	2	3		1	3	2				22
Unknown	12	6	3												21
Subtotal	12	12	7	4	3	5	4	3	2	3	3				58
Bloody Canyon															
Male				1											1
Female						1					1			1	3
Total	12	12	7	5	3	6	4	3	2	3	4			1	62

[a]Lamb.

Of the 51 sites used by sheep, 36 (70.6%) were correctly classified. Of the 54 randomly placed sites, 40 (74.1%) were assigned accurately (Table 7).

Fecal crude protein values ranged from a high of 41.90% in summer to a low of 4.46% in winter. Monthly mean levels of crude protein plotted annually increased with the onset of new growth in spring, then gradually declined from July to December each year (Fig. 6).

Table 6. Annual natality, mortality, and growth rate in the Lee Vining and Bloody canyon mountain sheep (*Ovis canadensis californiana*) herds between March 1986 and October 1991.

Year	Initial number	Number born	Natality	Number dying	Mortality	Final number	Growth rate
1986	27	9	75.0	16	44.4	20	−25.9
1987	20	5	55.5	4	16.0	21	5.0
1988	32[a]	8	44.4	6	15.0	34	6.3
1989	34	9	47.4	3	7.0	40	17.6
1990	40	13	59.1	3	5.7	50	25.0
1991	50	12	50.0			62	24.0

[a]Includes 11 sheep reintroduced in the 1988 supplement.

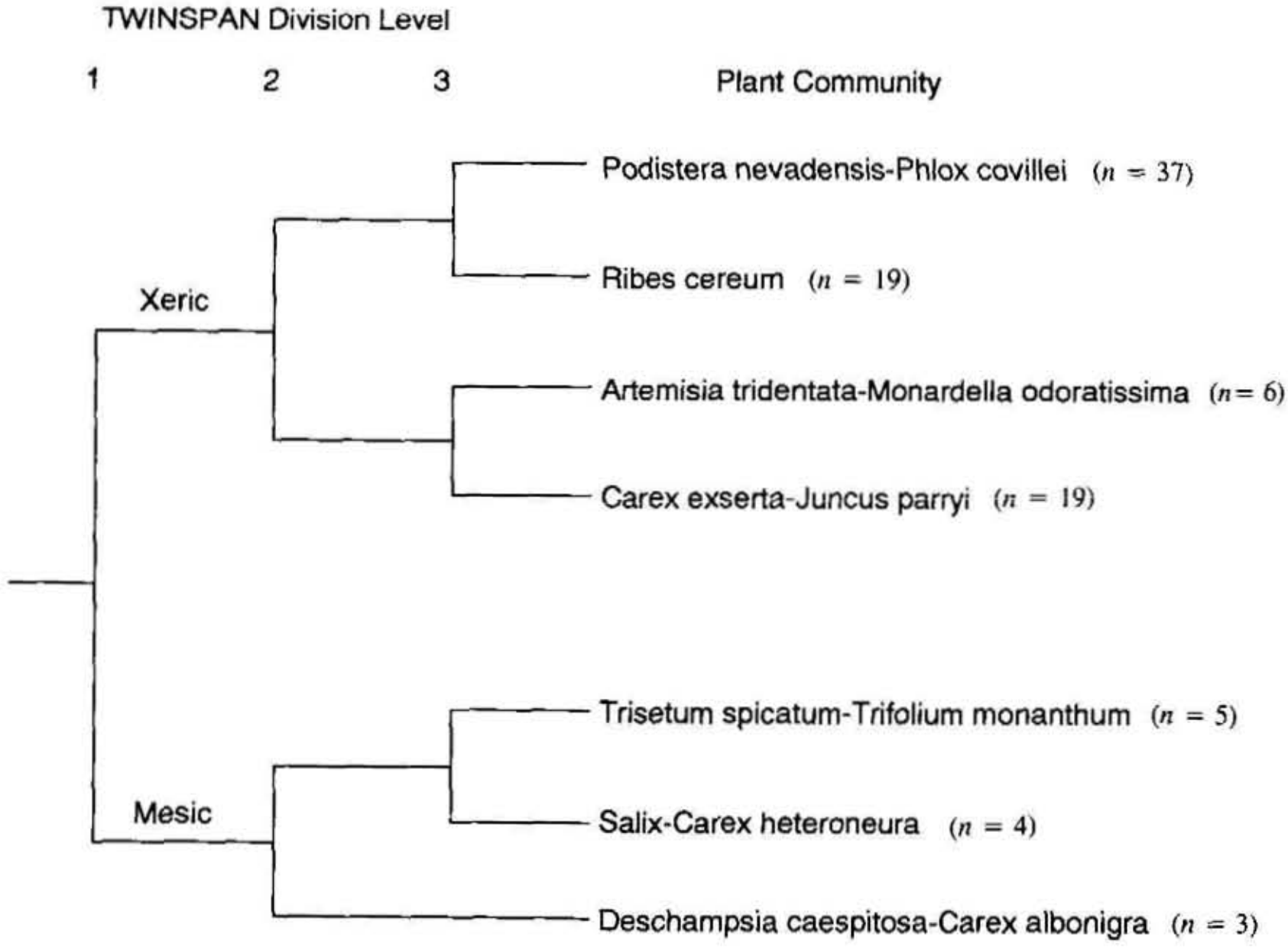


Fig. 5. Plant communities identified by two-way indicator species analysis (TWINSPAN) from mountain sheep summer ranges in Lee Vining Canyon, Mono County, California.

Seasonal means of fecal crude protein were significantly different between seasons in the Lee Vining Canyon herd ($\chi^2 = 147.04$, $P < 0.0001$). Spring and summer values were similar but were significantly higher than fall and winter values in all years. There were no differences in seasonal fecal protein levels from year to year.

Discussion

Movement and Distribution Patterns

The Lee Vining Canyon herd colonized their new location in two stages. The two-stage process seems typical of reintroduced mountain sheep and has

Table 7. Number of sites classified as forage sites or as randomly located sites by discriminant analysis for mountain sheep (*Ovis canadensis californiana*) ewes in Lee Vining Canyon, summer 1988 and 1989.

		Predicted group membership	
Sampled group	*n*	Random	Forage
Random	54	40 (74.1%)	14 (25.9%)
Forage	51	15 (29.4%)	36 (70.6%)

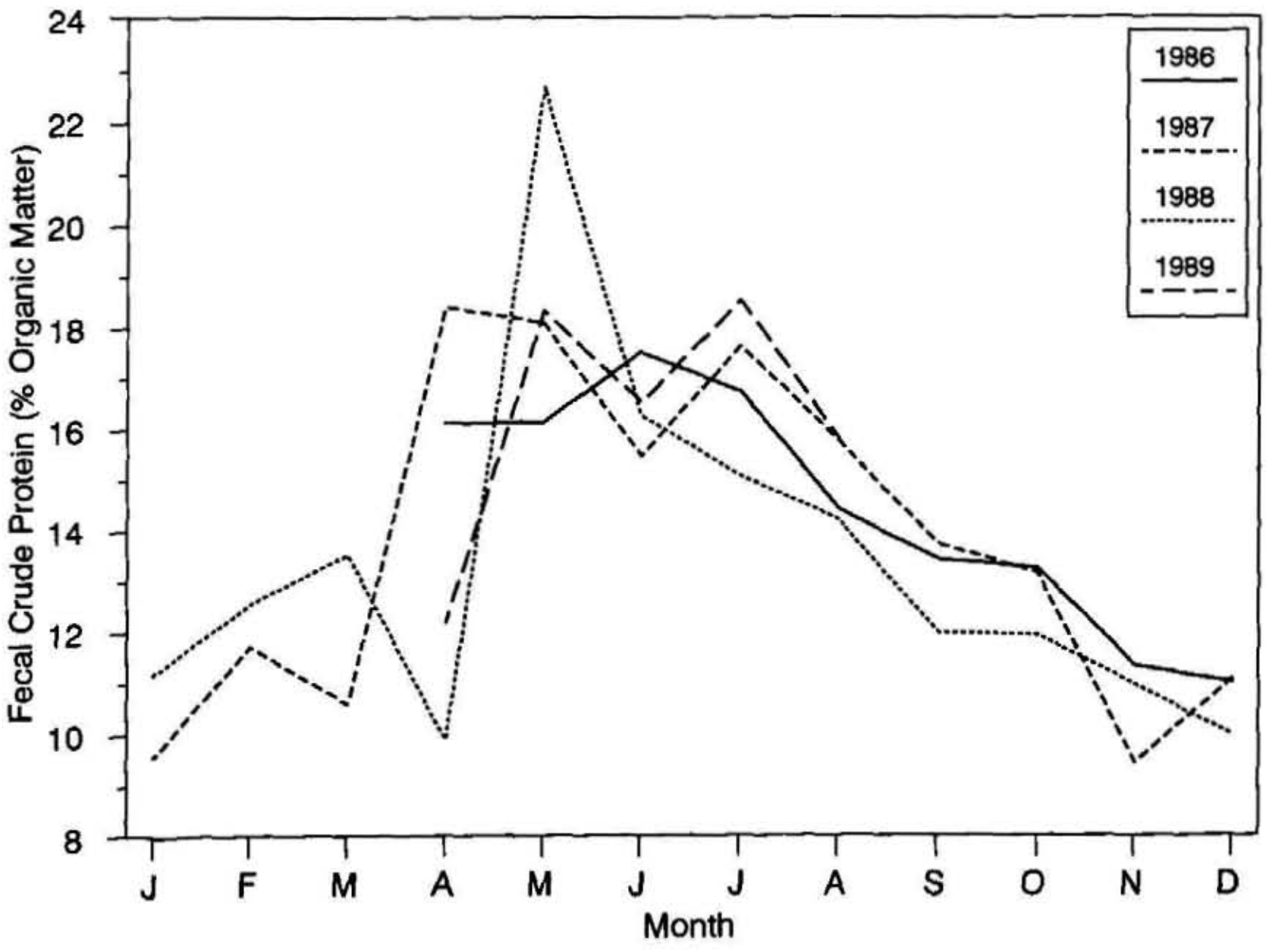


Fig. 6. Mean monthly percent fecal crude protein by year for mountain sheep at Lee Vining Canyon, Mono County, California, 1986–89.

been observed in the Rocky Mountain (Kopec 1982), desert (Elenowitz 1983; Shaw 1986; Berbach 1987), and California (Andaloro and Ramey 1981; Hanson 1984) subspecies.

The first stage commenced with the initial reintroduction and extended through the summer of 1986. This stage was characterized by small home range sizes ($\bar{x}_{ewes} = 9.5$ km^2; $\bar{x}_{rams} = 15.8$ km^2) and the absence of long-distance (>5 km) migration between seasonal ranges. The move to winter range in late November 1986 marked the beginning of the second stage. During the second stage, the sheep began migrating long distances between summer and winter ranges and developed distribution patterns retained in subsequent years.

The herd's restricted movements during the first year contrasted sharply with patterns of long distance migration seen in native mountain sheep herds (Murie 1940; Packard 1946; Geist 1971) and observed by Wehausen (1980) at Mount Baxter. Failure to segregate by sex was also atypical of native herds (Blood 1963; Geist 1971).

Migration enables mountain sheep to remain in a zone of active plant growth where forage species are at peak nutritional content (Geist 1971; Hebert 1973; Wehausen 1980). Hebert (1973) studied captive mountain sheep and found a strong correlation between altitudinal migration and body condition. Thus, the transition from sedentary to migratory status may be important for a reintroduction to succeed.

Geist (1971) suggested that movement and distribution patterns in native mountain sheep herds are determined by tradition. Traditions arise when younger sheep follow older sheep, learn the location of resources, and subsequently maintain fidelity to those sites.

Geist (1971) surveyed agencies conducting mountain sheep reintroductions in western North America and found that transplanted sheep frequently remain near the release site and fail to expand into new areas. He attributed the sedentary nature of reintroduced herds to the absence of existing traditions in their new location. He proposed that, in the absence of tradition, range extensions were possible where habitat is continuous and visibility unobscured by forest. The absence of trees on the high elevation summer range and the Lee Vining Canyon herd's establishment of migration routes through areas lacking trees support this idea.

Differences in snow depth between years offers an alternate explanation for the shift from sedentary to migratory status. In 1986, snowfall was nearly twice the annual average. This was followed by 5 consecutive years of drought. Most snow melted before sheep moved to summer ranges and did not impede movements. In 1986, however, movements may have been indirectly influenced by snow banks that persisted throughout the year.

Plant growth in the Sierra Nevada is generally limited by available moisture (Major 1977). Winter snowpack has a major influence on the length of the growing season by providing water to plants during dry summer months (Billings and Bliss 1959). Persistent snow banks at higher elevations in 1986 may have allowed the herd to obtain adequate forage in one location while drought conditions in subsequent years necessitated long-distance movements.

Restricted movements by the sheep also may have reduced energy expenditures and decreased their vulnerability to predation in an unfamiliar area.

Predation also may have provoked shifts in distribution. In one instance, the herd moved to a new area after being chased by a coyote (*Canis latrans*). On another occasion, a nursery band moved 2 km after a mountain lion took a lamb. J. Wehausen (University of California, White Mountain Research Station, personal communication) observed the Mount Baxter herd abandon a wintering area in response to increased mountain lion predation.

The failure of rams and ewes to segregate during the first year may have been due to disorientation in their new location. The absence of a strict social hierarchy typically found in established herds (Goldsmith 1988) also may have curtailed sexual segregation. Finally, Geist (1971) observed that rams in British Columbia remained with natal bands until they were 2 or 3 years old. Thus, the rams may have failed to disperse because they were less than 2 years old when reintroduced in 1986.

Although a combination of factors is likely to have been involved, the most significant influences on the Lee Vining Canyon herd's pattern of home range establishment during the first year were the absence of traditional movement patterns and disorientation in a new location. Increased knowledge of their new surroundings fostered range expansion in the second year. Establishment of summer ranges in areas visited previously provides the strongest support for this interpretation. The rapidity with which members of the 1988 supplement adopted the movement and distribution patterns of their predecessors also strengthens this idea. The presence of continuous habitat and accompanying absence of visual obstructions may have promoted further range expansion (Geist 1971).

The development of stable migration patterns after only 2 years suggests traditions can arise rapidly. Further evidence is provided by increased sexual segregation, which may indicate that the Lee Vining Canyon herd began functioning more like an established mountain sheep population.

Population Dynamics

The Lee Vining Canyon herd grew slowly during the first 3 years of the study. Annual growth rates during this period were well below those reported by previous studies of reintroduced mountain sheep (Woodgerd 1964; Hansen 1984) and contrasted sharply with annual growth rates recorded later in the study. The low rate of growth is attributed to heavy predation on a small population. The problems of small population size were further exacerbated by unexpectedly high postrelease mortality and the emigration of three ewes and two lambs to Bloody Canyon.

From 1989 to 1991, annual growth rates rose dramatically (Fig. 7), nearly attaining the theoretical maximum (Buechner 1960; Woodgerd 1964; Streeter 1970). The sudden rise in growth rates seemed to result from increased lamb production while the number of deaths remained relatively constant.

Two events contributed to the increase in lamb production. The most significant was the 1988 supplement, which increased the number of reproductive

aged ewes in the Lee Vining Canyon herd from 5 to 12. Although the natality rate in 1987 was high, only five lambs were born. Recruitment the next year barely offset deaths (Fig. 7). Despite a lower natality rate and a higher number of deaths in 1988, the addition of seven adult ewes boosted total lamb production so that the absolute number of recruits was greater.

Lamb production rose again in 1989 when ewes born at Lee Vining Canyon first entered the breeding population. The loss of both female lambs to post-release deaths in 1986 precluded recruitment of any females into the 3-year-old age class until 1989. Sierra Nevada mountain sheep ewes typically have their first lamb at 3 years (Wehausen 1980). Thus, adult females lost to emigration and death between 1986 and 1988 were not replaced. Steady erosion of the herd's reproductive potential during those years was finally arrested when ewes born at Lee Vining Canyon began lambing in 1989.

The number of deaths in the Lee Vining Canyon herd remained relatively constant after the second year (Fig. 7). This was due, in part, to the reduced probability of detecting deaths as the proportion of radio-collared sheep in the herd declined. It may also have been a consequence of territorial behavior among mountain lions (Hornocker 1970), resulting in a constant density of lions in Lee Vining Canyon. Because each mountain lion could only take a certain number of sheep, the number of lion kills would remain relatively constant.

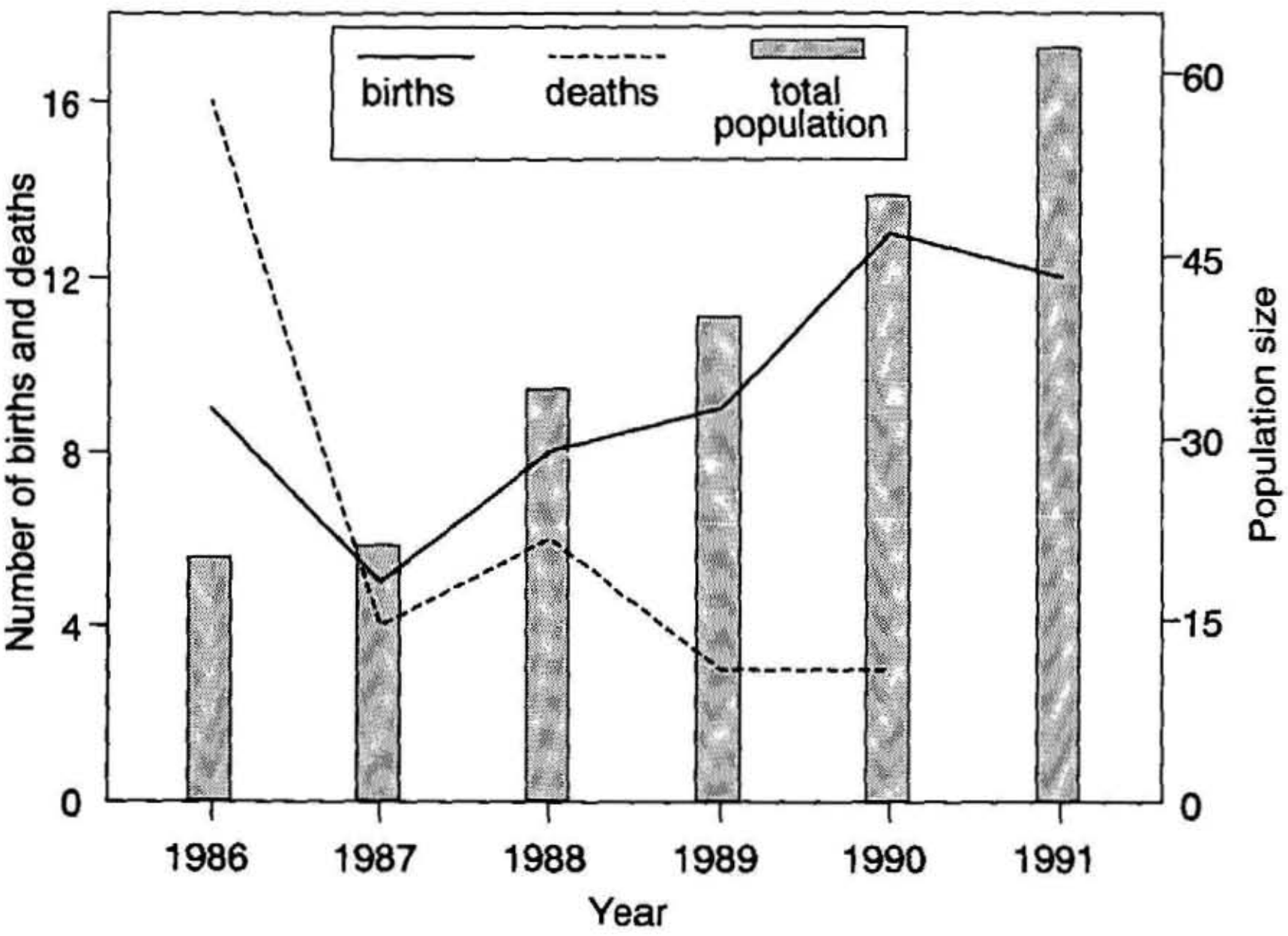


Fig. 7. Population dynamics of 27 bighorn sheep reintroduced to Lee Vining Canyon, Mono County, California, in March 1986. Population sizes represent end-of-year totals. Total population size shown for 1988 includes 11 additional sheep added in March 1988.

The adult sex ratio of 68 rams per 100 ewes was within the range seen in established mountain sheep herds (Streeter 1970; Geist 1971) and was virtually identical to the 67.7:100 observed by Wehausen (1980) at Mount Baxter. The adult sex ratio, however, was largely the product of random selection during the two reintroductions and, thus, is not particularly meaningful.

The mean ratio of yearlings to ewes of 47:100 was 1.5 times greater than the figure McQuivey (1978) deemed necessary for maintaining a stable mountain sheep population in Nevada and exceeded the ratio of 40:100 that Wehausen (1980) felt was indicative of population increase in the Mount Baxter herd. However, age ratios are difficult to interpret or may be misleading (Murphy and Whitten 1976; Caughley 1977) if changes in ratio result from increased adult mortality. Because adult mortality remained relatively constant, we interpreted the shift towards younger age classes in 1990 and 1991 as an increasing trend.

Habitat Suitability

Results of vegetation classification are consistent with previous work on alpine vegetation in the Sierra Nevada. Taylor (1984) described communities corresponding to the *Podistera–Phlox*, *Ribes*, *Artemisia–Monardella*, *Carex–Juncus*, *Trisetum–Trifolium*, and *Deschampsia–Carex* communities found on summer range. He reported the *Podistera–Phlox* community from stable, metamorphic substrates where snow cover was sparse in winter and moisture availability was low during the growing season. Pemble (1970) described a similar association but did not find it limited to metamorphic substrates. He regarded it as the most common association in the Sierra alpine (Pemble 1970:135). This association seemed to be the most common vegetation type within home ranges of ewe–juvenile groups and was used for resting and traveling as well as foraging.

Mesic sites on the Lee Vining Canyon herd summer range varied in species composition and cover. Some mesic sites were misclassified by TWINSPAN as members of the *Podistera–Phlox* community because of the presence of *Festuca ovina*, *Sitanion hystrix*, or *Ribes cereum*, indicator species for xeric communities. Additional sampling, stratified to focus on mesic sites, might provide a more detailed and useful classification of these complex communities. Alternatively, these sites may represent small, poorly developed examples of communities that thrive under more benign conditions and may have been sampled at the extreme of their environmental tolerance. Better developed examples of these communities as described by Pemble (1970) and Taylor (1984) were not observed and may not occur in the study area.

Fifteen of 51 forage sites were misclassified by the linear discriminant function. The forage sites most strongly identified as random sites had sparse vegetative cover, no surface water, and were located far from escape terrain or had low visibility. All forage sites misclassified because of sparse cover, however, contained important forage species.

The *Salix–Carex* and *Deschampsia–Carex* communities were the easiest forage sites to predict (100% correctly classified) because they offered moist

conditions, abundant herbaceous cover, and were often near cliffs. Forage sites in the *Ribes* type were correctly classified nearly as often (89% of the time), and forage sites in the *Podistera–Phlox* community were correctly identified 68% of the time. Sites in the *Podistera–Phlox* community probably represent opportunistic foraging strongly influenced by the abundance of that community.

Ewe groups repeatedly visited snowmelt-fed or spring-fed sites. These sites offered the highest vegetative cover and species diversity per unit area. Although these areas were limited in size (typically 10–15 m diameter) and number, repeated use highlights their importance. Higher cover and protracted phenological development at these sites are likely to increase the overall amount of green forage and prolong its availability. Forage moisture content as well as plant nutrient status may be most important during late summer and early fall months when sources of moisture become scarce elsewhere.

Annual patterns of forage quality paralleled those of other California mountain sheep herds (Hebert 1973; Wehausen 1980). The decline in fecal crude protein levels from a high in early summer to lower levels during winter reflects patterns of plant phenology. Pattern alone, however, is insufficient to make conclusions about absolute forage quality. Other considerations necessitate treating apparent fecal protein levels with caution.

Fecal nitrogen concentrations may be elevated when the diet includes a large proportion of species containing phenolic compounds (Mould and Robbins 1981). These species include shrubs and some herbs (Nagy et al. 1964; Swain 1979). These compounds may reduce protein digestibility by complexing with dietary and microbial proteins in the rumen (McLeod 1974). The result is an increased level of fecal protein without a corresponding rise in diet quality. This effect seems to be mitigated when these species contribute less than a third of the diet (Leslie and Starkey 1985). The winter diet of the Lee Vining Canyon herd included up to 60% shrub species. Thus, fecal protein levels during this period may be unreliable and should be interpreted with caution.

Reproductive success is related to body condition in ungulates (Thomas 1982; Saether and Haagenrud 1983). High ratios of lambs to ewes in the herd from 1986 to 1989 indicate forage quality is probably comparable to that available to other rapidly growing populations (Chow 1991). Because of the problems associated with fecal protein as an indirect measure of forage quality, reproduction rate is a more reliable index of overall habitat quality.

Management Implications

Current population size and a steadily increasing growth rate allow the Lee Vining Canyon reintroduction to be labeled a qualified success. However, an analysis of population statistics from 121 herds of mountain sheep showed that those having fewer than 50 animals were extirpated within 50 years (Berger 1990). A similar fate could befall the Lee Vining Canyon herd without some management intervention.

Goodman (1987) modeled the demography of small populations and concluded that long-term persistence required reducing population fluctuations

resulting from environmental variables. Effects of environmental variables can be ameliorated by either manipulating habitat or reducing mortality (Goodman 1987).

At present, habitat analysis and the high rate of lamb production suggest forage resources in Lee Vining Canyon are sufficient for reproduction and survival. Thus, habitat manipulation to increase forage productivity seems unnecessary. Removing shrubs and trees on the winter range, however, would increase visibility and facilitate predator detection by the mountain sheep.

Because forage resources seem adequate, ensuring persistence of the Lee Vining Canyon herd requires lowering mortality to increase its growth rate. A higher growth rate would shorten the herd's period of vulnerability to extirpation from disease, predation, and inbreeding. A larger population would increase the probability of herd survival in the event of a major disease epizootic (Foreyt and Jessup 1982; Foreyt 1989). Greater numbers would also dilute the effects of predation, reduce the potential for inbreeding depression (Skiba and Schmidt 1982; Ralls et al. 1986; Schwartz et al. 1986; Berger 1990), and provide a buffer against extinction from stochastic events.

Predation was the major source of known deaths. Data from the first 3 years of the study indicate that predation can significantly influence the growth rate of a small population. If the goal is to maintain a maximum rate of increase, managers need to consider continuing mountain lion removal from Lee Vining Canyon for several more years. The removal of mountain lions would require monitoring to document its efficacy. Those making the decision must weigh the costs and effectiveness of short-term predator control against the long-term objectives of Sierra Nevada mountain sheep management.

In July 1988, a domestic sheep strayed onto the winter range of the Lee Vining Canyon herd. Luckily, the ewes inhabiting that area had departed 3 weeks earlier. However, the incident underscores the continued concern over catastrophic loss because of disease. The propensity for adult rams to wander long distances (Geist 1971; Wehausen 1980) and presence of grazing allotments within 5 km of Lee Vining Canyon maintain the potential for disease transmission from domestic stock. Disease remains the greatest threat to the long-term survival of the Lee Vining Canyon herd (Foreyt and Jessup 1982; Foreyt 1989), and consideration should be given to reduce or eliminate the threat.

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