

**ECOLOGY OF WHITE-TAILED DEER
IN EASTERN EVERGLADES NATIONAL PARK**

**FINAL REPORT
to the National Park Service**

**J.F. Eisenberg and M.E. Sunkist
Florida Museum of Natural History and
Department of Wildlife and Range Sciences
University of Florida
Gainesville, FL 32611**

**CA-5280-5-8004
Subagreement No. 5, Modification No. 3
Grants 560251912 and 560249712**

**ECOLOGY OF WHITE-TAILED DEER
IN EASTERN EVERGLADES NATIONAL PARK**

**FINAL REPORT
to the National Park Service**

**J.F. Eisenberg and M.E. Sunkist
Florida Museum of Natural History and
Department of Wildlife and Range Sciences
University of Florida
Gainesville, FL 32611**

**CA-5280-5-8004
Subagreement No. 5, Modification No. 3
Grants 560251912 and 560249712**

Acknowledgements

The principle investigators would like to thank the many participants, sponsors, and advocates of this lengthy project, especially the National Park Service and its employees. The National Fish and Wildlife Foundation contributed monetarily as well.

Sonny Bass' cooperation was essential during the final preparation of this report.

The majority of the field work was organized and conducted by Tommy Rae Smith. He deserves credit for continuing aerial locations of deer through many hardships. Cynthia Hunter completed her master's thesis research on the reproduction of the white-tailed deer in ENP and aided greatly in the preparation of the final report. People in Homestead and ENP who were outstandingly helpful were so numerous that we fear we may leave some unmentioned, but we must particularly thank Wyatt Enterprises' pilots, Lynch Inc. pilots, Sue Husari and the Fire Cache, Dr. John Ogden, Frank Draughn, and Dr. W.B. Robertson.

Many thanks are due to the generous GIS computer specialists of the Department of Urban and Regional Planning at UF, especially Dave Lambert, who took the initiative to make room for the 200 Mb of data from the park so that Thia Hunter could sift through it and absorb some of his good teaching.

I. SCOPE AND HISTORY

As increasing attention, funds and research efforts have been applied to the understanding, restoration, and management of the Everglades ecosystem, a proposal was approved to elucidate interactions between deer (*Odocoileus virginianus seminolus*), Florida panthers (*Felis concolor coryi*), and the vegetation, all thought to be unique and essential components (Eisenberg and Sunquist, 1986). The Florida panther, an endangered subspecies, feeds primarily on deer and feral hog (*Sus scrofa*), but the hog has been eliminated from National Park land, thus in Everglades National Park (ENP) deer potentially provide the only large prey available (Maehr et al., 1990; Alvarez, 1993). However, there has been widespread concern that the deer in the Everglades are at insufficient density and of such small body size that they are possibly an inadequate source of sustenance for the panthers (Belden et al., 1988). Information on deer population dynamics was considered essential to management of the panther. The Panther Recovery Plan (USFWS 1987) has been an important ongoing aspect of park research, and this deer study was proposed and approved to provide essential information.

Physiological, behavioral, and reproductive differences between the race *O.v. seminolus* and northern white-tailed deer have long been suspected (Layne, 1988; Richter and Labisky, 1985) but little was known of the ecology of south Florida deer. Only one in-depth study of the natural history of this subspecies had been conducted prior to the present research effort (Loveless, 1959; Loveless and Ligas, 1959) with a later study by Schemnitz (1974).

Deer in ENP are a sedentary (non-migratory) population. No hunting has been allowed anywhere in ENP since its establishment in 1947, but hunting continued uninterrupted in the forest reserves north of the park. Mortality factors acting on deer in ENP were presumed to be panthers, bobcats (*Lynx rufus*), poachers, cars, and natural health factors including possibly nutrition, surface water, disease, and parasites. In this regard we were interested in examining the relative impact of these various mortality factors, the possible differential impacts on different classes of the population, and the implications for management when community interactions were considered. Originally a comparison of hunted and unhunted populations was proposed (Eisenberg and Sunquist, 1986). Richter and Labisky (1985) found a significant difference in deer herd productivity on hunted vs. unhunted sites of similar habitats within Florida. Generally, herd productivity was higher on hunted sites, although densities, pregnancy rates, fetuses/doe, and age-structures varied between sites. Their study provided strong impetus to study and manage the various sub-populations of deer and panthers across Florida on a site-specific basis. This report summarizes a study focused on the unhunted ENP population south and east of Shark River Slough, while a study from 1989

to 1992 directed by R.F. Labisky focused on the hunted Big Cypress National Preserve populations and adjacent deer in ENP north of Shark River Slough.

Deer density in the Everglades appeared lower than elsewhere in Florida or the Piedmont (Harlow and Jones, 1965; Langenau et al., 1984; Newsom, 1984) but the Everglades deer had not been censused thoroughly. A survey-based census of deer and panthers in ENP in 1970 (Schemnitz, 1974) estimated 8 panthers and 1500 deer in the then 5,261 km² ENP, yielding a density of 0.29 deer/km². Densities were even lower in the Water Management Conservation Areas 2 and 3 north of the park at 0.10 deer/km² (Schemnitz, 1974). This difference was possibly due to more intensive hunting and more severe flooding there (Loveless, 1959). The only other authors to survey *O. V. seminolus* (Loveless, 1959; Harlow and Jones, 1965) found the Everglades ecosystem the one least able to support deer in all of non-urban Florida. This was mainly believed to result from the low nutrient availability for deer in the predominantly flooded prairie habitats. Although seasonally flooded bottomland hardwood forests are thought of as the best deer habitat in the southeast Piedmont (Sigler-Eisenberg and Eisenberg, 1985), very little of this habitat exists in the Everglades (Figure 1).

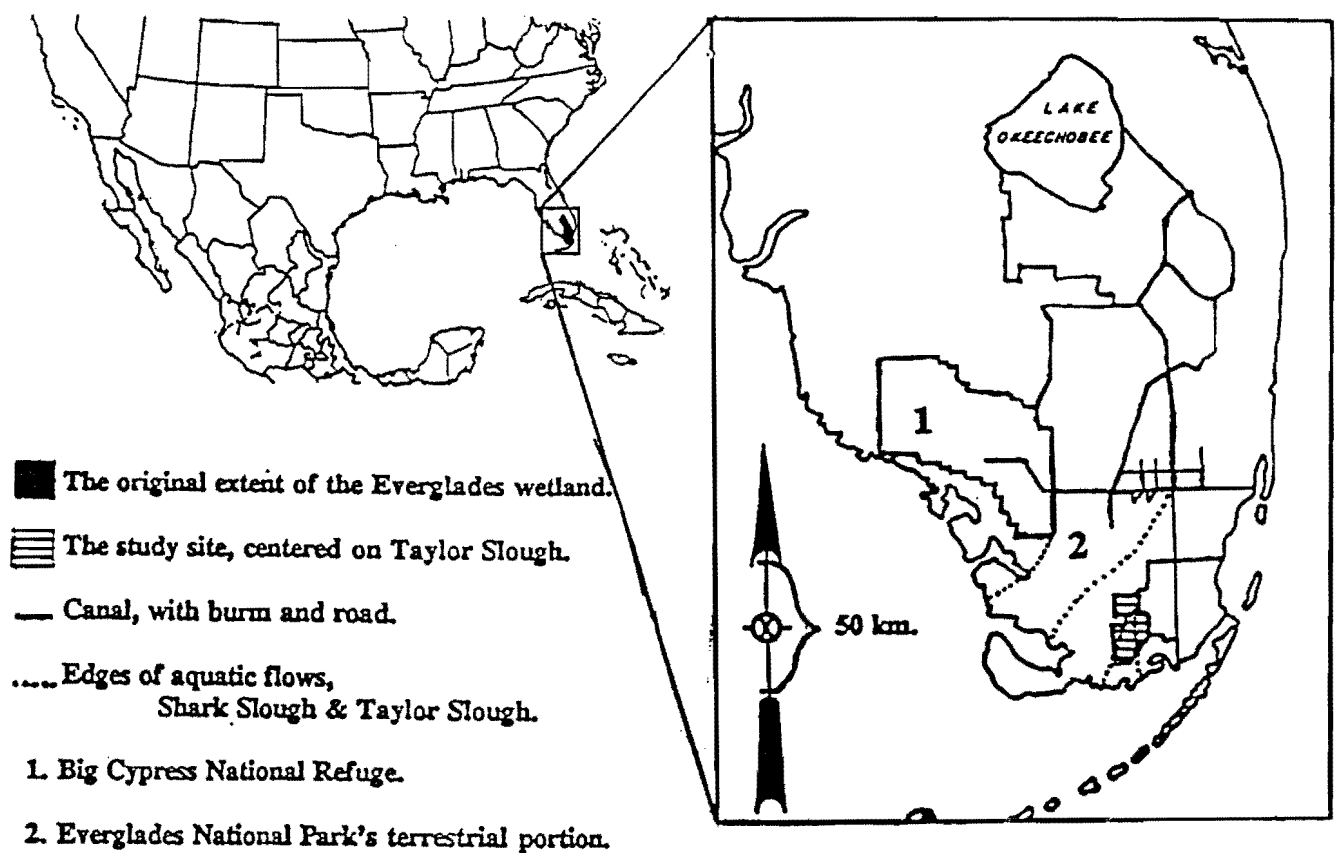


Figure 1. Southern Florida and the now partitioned and partially drained Everglades wetland.

Since the early 1970's the Everglades deer herd has apparently declined and remained at a very low density, relative to historical populations in the Everglades (F. Dayhoff, pers. comm., 1989). The only recorded large-scale die-offs were caused by tick eradication efforts in the 1930's, over-hunting in the conservation areas in the 1960's, and excessive flooding in 1957-8 and in 1982-3. In part the low densities were attributed to a lower fecundity in the deer of the southern flooded region than even in the rest of Florida (Harlow, 1972), despite the state as a whole having deer of lower fecundity than other deer herds north of Florida (Harlow and Jones, 1965). These authors attributed the lower fecundity to possible mineral deficiencies from the food plants growing on infertile soils (Deuver et al., 1986; Kushlan, 1990). This study and the concurrent work on deer in the Big Cypress National Preserve compared densities, reproductive output, predation, and other mortality factors affecting deer in the Everglades.

Study Site

The terrestrial habitats of ENP, covering 5,660 km², are mainly prairies dotted with tree islands of various sorts, and pine flatlands. Sixty-five percent of ENP is classified as tropical savannah (USFWS, 1979), but not much is known regarding changes in this ecosystem's plant or animal components since water control measures were implemented. The entire region can be considered a hyperseasonal savannah (Sarmiento, 1984), controlled by annual flooding that used to coincide with the rainy season of May through October, and now is managed by outputs from canals (Figure 1) in a "rainfall simulation strategy." Although this management scheme has produced wet and dry seasons somewhat similar to the natural system (Walters et al., 1992; ENP unpublished hydrology data), the volume of water has been slowly decreased over the last fifty years, diminishing both high and low extremes of depth that occur seasonally in the park, at the southern end of the wetland (Hunter, 1990, in press).

The Everglades ecosystem is believed to be stable in plant species composition, due to the periodic disturbance of fire and water (Robertson, 1953; Loveless, 1959). The savannah's prairies are of two types. Wet prairies are dominated by one or more of the sedges sawgrass (*Cladium jamaicense*), spikerush (*Eleocharis* sp.), and beakrush (*Rhynchospora* sp.). These prairies are dotted with tree islands or "hammocks" composed of tropical hardwoods, or "domes" of cypress (*Taxodium distichum*). Dry prairies are dominated by the grass called "muhley" (*Muhlenbergia filipes*) and scattered with occasional or clumped hardwoods, especially willow (*Salix caroliniana*), and, where hydroperiod becomes longer, with the herbs common to wet prairies. Parts of dry prairies have no hydroperiod (above ground flooding) at all in some years. Scattered large areas of pinelands

are nearly monotypic (*Pinus elliotii* var. *densa*) forests with thick understories dominated by *Sabal palmetto* (Figure 2).

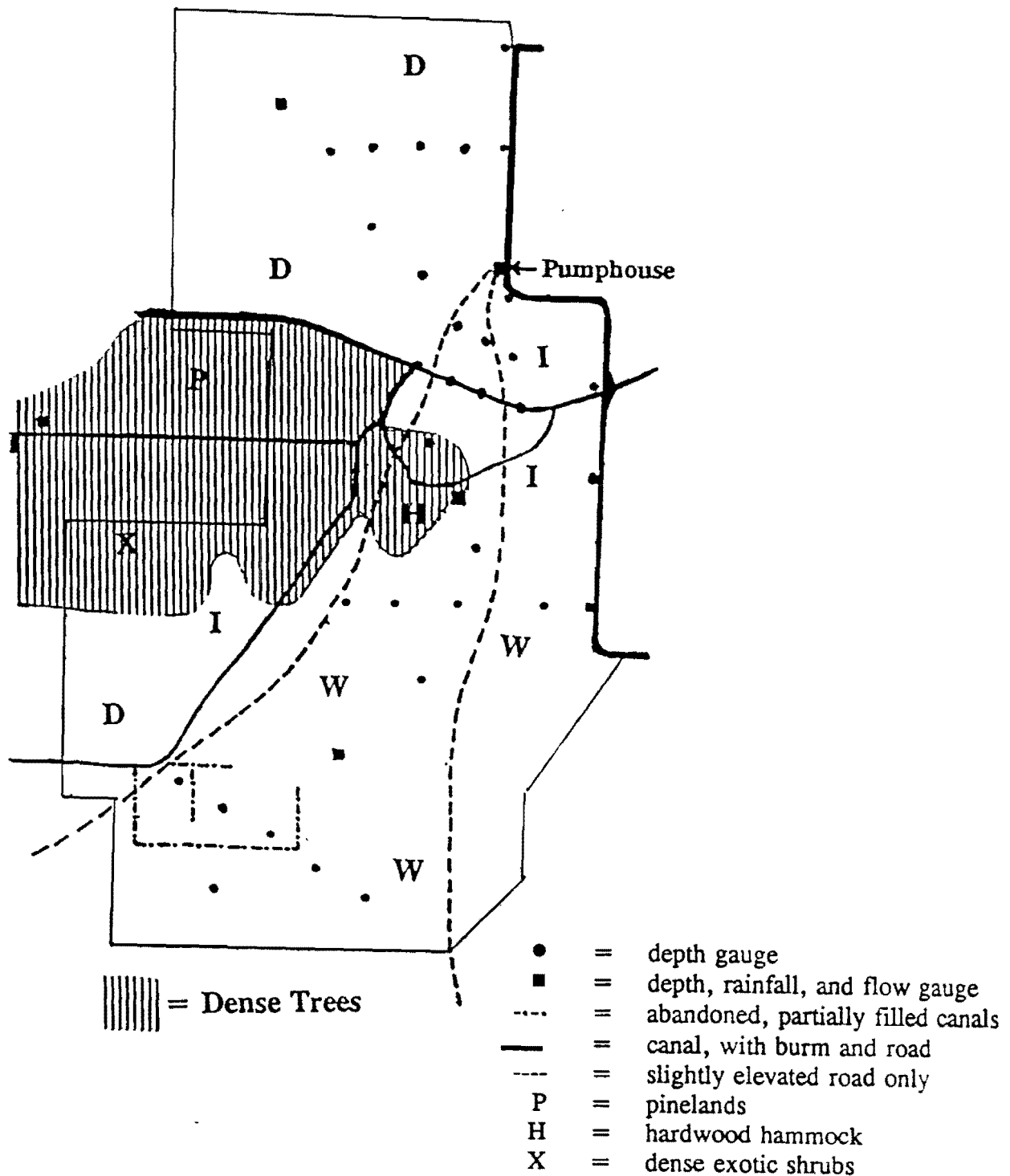


Figure 2. The study site in the Taylor Slough area of Everglades National Park, and the prairies classified as either "wet" (W) or "dry" (D). "Intermediate" (I) prairies were wet in 1988, dry in 1989.

The two areas of the park where water flows almost continuously year-round are called "sloughs," and the study efforts of this report centered around Taylor Slough. This site allowed access to the research facilities and the "hole in the donut." This latter site is a disturbed area now invaded by dense stands of exotic trees such as *Schinus terebinthifolius* and *Melaleuca quinquenervia*. More details of vegetation can be found in Deuver et al. (1986) and Hunter (1990). Ongoing NPS studies of fire management and regeneration, flooding regimes, and flowering phenology were simultaneous with this study and provided useful habitat information in the form of unpublished data from Park Service personnel.

The climate is technically sub-tropical: seasonality is dictated by variation in rainfall, not temperature, although a frost occurs on an average of once every ten years. Rainfall averages 148 cm per year, 81% of which falls during the wet season, usually from late April through October (Schomer and Drew, 1982; Deuver et al., 1986). The intensity [± 34 cm per year], timing, and duration of the wet season are highly variable beginning April, May, or June and extending through August, September, or October. Rainfall often occurs with two noticeable peaks, one in May or June and the second in September (37 years ENP unpublished hydrology data; Schomer and Drew, 1982). The effects of water on deer health and the synchronizing of herd productivity were among the questions of interest addressed in this study. Other objectives, as they changed slightly as fieldwork progressed, are outlined below.

Chronology of Agreements and Objectives for the ENP Deer Project

1. Original Proposal: Eisenberg and Sunquist, 1985 submitted to the National Park Service (NPS).

Objectives: 1) To estimate the demographic characteristics of the deer population at two or three different sites within the Everglades ecosystem, particularly a hunted and an un-hunted site. 2) To determine the physical condition of deer at the different sites. 3) To estimate deer recruitment and mortality at the different sites and, where possible, relate these to predation, hunting, habitat factors, and physical condition of the deer. 4) To determine the seasonal movement patterns of deer at the different sites in relation to habitat types, changing environmental conditions, reproductive condition and, where possible, movement caused by disturbance or predation. 5) To determine forage quality within habitat types at the different sites.

The sites suggested for surveying were: 1) The Hole-in-the-Donut/Taylor Slough area, 2) BCNP's portion of Shark River Slough, 3) Raccoon Point and Bear Island in BCNP. Due

to limited NPS funds, the proposal was changed to begin at only the first site, with follow-up studies at the other sites if more funding became available.

2. Original Cooperative Agreement CA-5280-5-8004 between the NPS and UF: work to be conducted January 1, 1987 through January 1, 1989, with final report due July 1, 1989.

Objectives: 1) To live-capture and mark a sample of approximately 50 deer, stratified by age and sex to represent the natural population. 2) To assess the physical condition of a subsample of approximately 20 deer in cooperation with the Big Cypress Deer condition study (S. Wright, 1987 only). 3) To assess the timing and behavioral characteristics of the breeding season. 4) To assess age-specific mortality factors and rates, natality and recruitment. 5) To elucidate some aspects of habitat use, including dried samples of probable dietary plants identified to species, and possible exclosure experiments.

Fieldwork commenced in January 1987, conducted and administered in the field by Tommy R. Smith. Assistants for various months included José Fragoso, Joseph Dudley, Tadeu Oliveira, and Cynthia Hunter.

3. Modification No. 2 of the Cooperative Agreement, dated September 1986, to be conducted from February 1, 1987 through January 31, 1990.

Objectives: 1) To estimate the demographic characteristics of the population of deer in eastern ENP, including absolute size, density, age structure, and age-specific sex ratios. 2) To estimate recruitment and mortality in the population and relate these to predation, rainfall, habitat utilization, and age and physical condition of deer. 3) To delineate important aspects of the reproductive biology of deer in the study area, including the chronology of breeding and fawning, litter size, and sex ratios at birth. 4) To determine seasonal patterns of movement and activity by deer in relation to habitat types, environmental conditions, and predation.

4. M.Sc. Thesis plan of Cynthia Hunter. Fieldwork to be conducted from January 1988 to August 1989 (late dry to full wet seasons), with thesis to be completed in 1990.

Objectives: 1) To intensively monitor about 10 does each year to determine date and success of fawning. 2) To observe doe/fawn behavior and evaluate habitat use on a micro scale. 3) To record water levels in doe home ranges and correlate any behavioral changes due to water.

5. Modification No. 3 to Subagreement No. 5 of the Cooperative Agreement, dated September 1989, to be conducted from October 1, 1989, but with interim report due January 15, 1989 (unmet obligation at the time), and final report due March 31, 1990. Entitled Dr. John C. Ogden as the service's representative for the agreement. Funding from the National Fish and Wildlife Foundation (Project 89-68) supported this added work.

Objectives: Same as previously with these additions. 1) To evaluate the effects of a large fire (the Ingraham Fire of May 1989) on the deer population, by shifting sampling efforts to the western, burned portion of the study area. 2) To collar a total of 10 adult males, 15 adult females, 10 yearlings, and 10 fawns, about half the sample in the burned half of the study area. 3) To compare deer in burned and unburned home ranges for activity, habitat use, and movements. 4) To establish and refine computer systems and datasets, and begin analyses on, population characteristics and deer habitat use. The final report deadline was extended to December 31, 1990 by letter dated February 12, 1990.

6. Comparable deer project begun in BCNP and extended to the western portion of ENP; January 1989 - 1992. Directed by R.F. Labisky, Department of Wildlife and Range Sciences, University of Florida. Dr. Labisky and students radiocollared and monitored the deer north of Shark River Slough in ENP and the adjacent Big Cypress National Preserve, a hunted population in predominantly wet prairies (separate report series).

7. End of Fieldwork for CA-5280-5-8004. Systematic sampling of deer locations ended in May 1990, but the 42 functional collars were located sporadically until 1992. Data management and analyses commenced.

8. T.R. Smith appointed NPS coordinator [of deer/panther research for southern Florida region]. Appointment April 15, 1991 - April 15, 1993, but terminated in April 1992 when Smith subsequently left for Saudi Arabia in August 1992, with most of the data from this study in his possession and unsummarized. May 1993: the current authors began summarizing what data we could obtain. This report does not preclude further publications planned for peer-reviewed journals.

9. Hurricane Andrew: August 25, 1992. This event may have profoundly affected the deer in the Everglades, but also disrupted communications between Gainesville and ENP for several months.

10. May 1993 the current authors began summarizing what data we could obtain. This report does not preclude further publications planned for peer-reviewed journals.

II. METHODOLOGY

General methods are described below, and more details concerning methods are included in the Results section.

Capture

Initially, dartguns shot from truck, blind, and buildings were used in an attempt to capture deer, but this method proved unsuccessful due to the availability of thick cover for the deer. Box traps were not utilized. After frequent visual sightings of deer in open prairies, the technique of utilizing a shoulder-held gun projecting a net fired from a helicopter was attempted (Barett et al., 1982; Chardonnet and Charity, 1992). A gunner experienced in the use of helicopter net-gun techniques was invited to demonstrate, and 19 deer were caught in 15 hours of flight. This became the chosen technique for capture, and was subsequently used to obtain the sample of deer collared, as represented in Table 3.1. Deer were also recaptured using this technique.

Chase flights by helicopter were limited in duration to a maximum of about ten minutes, varying slightly with environmental temperature. Temperature and chase time were the key factors limiting capture-related mortality, as long chases may result in capture myopathy. No chemical immobilization was necessary: deer were immediately tied, blindfolded, freed from the net, and held on the coolest ground available for an average of 20 minutes while measurements were taken and a radio collar affixed. The pulse and respiration rates of captured deer were monitored while the animal was restrained.

Data collected on each captured animal included: date, time, location, habitat, other animals nearby, total length, tail length, head length, ear length, zygomatic width, neck circumference, height at shoulder, girth, weight, hind foot length, front foot length, toe length, sex, tooth condition, tail fat index, muscle index, pelage condition, ectoparasite index, and samples of blood and vital signs taken. These data were collected by very few personnel, so the subjective assessments were similar for each animal.

Stratification of Sample and Sampling Scheme

After the initial sample of 45 deer was obtained in 1987 by somewhat random searching of open prairies around the HID area, deer could be selected visually and not chased if of an

age or sex that was not needed in the sample. While not completely random nor completely representative of the population, the capture sample represented fairly evenly those deer available in open prairies.

Age was determined by tooth eruption and wear (Severinghaus, 1949), but with no previously collected jaws of known age from the Everglades, accurate aging was only possible after death of many deer: jaws were retained for laboratory analysis. Some deer near the park were shot to obtain samples for assessment of physiological condition. These data are compiled in reports to FGFC (see Forrester, 1992, 1993; McCowan, 1988).

Radio tagged deer were located by telemetry on a rotating diel schedule that allowed one to three locations/animal/week, evenly spaced to cover 24 hours. A subset of the sample was located more intensively for the "fawning ecology study" (Hunter, 1990, and in prep.). That study, conducted from January through July of 1989, included the creation of a digital map of 106 microhabitat types over the Taylor Slough portion of the Park. This map included water-coverage, with the extent of surface water determined by flying systematic transects and noting the sun reflecting from the water and by walking to newly flooded zones and measuring water depths. This information was used for analysis of behavior and habitat use by does during the fawning season (Hunter, 1990).

Telemetry and Mapping of Locations

Collared animals were located by either fixed-wing aircraft or a van. The plane (Cessna 182) had two H-element antennae, one mounted below on each wing strut. Antennae were connected to a receiver through a switch-box which allowed signal reception to be checked on either side of the plane as the pilot was instructed to home in on the deer sought. The van was equipped with an 8-foot telescoping mast supporting two H-element antennae set at the same height but 5 feet apart. This mast could rotate 360° on a marked compass rose, and the two antennae were connected by a null combiner, yielding a silent spot, thus indicating best direction of signal (Cochran, 1980). When fully extended the antenna reached 29 feet above the ground. Signals were clear up to 4 km from the target animals in this flat, open terrain.

Aerial locations were logged to a recognizable hectare square on an orthophoto map of the site by circling over the animal until landmarks were recognized. Hence, this technique could only be used during daylight hours. From dusk through dawn, locations were made from the van by triangulating three fixes on the same animal made within a 30-minute span, or a shorter period if the animal was moving. Approximately 60% of all locations were made by air, 40% by van. All stratified samples by age and sex classes of animals were evenly represented throughout the diel and seasonal cycles. The maps used for the

population study were USGS orthophoto maps on 7.5 minute quad sheets at a scale of 1:24,000, drawn in 1972 from aerial photos. The fawning ecology study (Hunter, 1990, and in press) used a detailed microhabitat map created from 1986 aerial photos and digitized on the Geographical Information System (GIS) to allow more detailed habitat studies. The maps used for analysis of habitat use thus far include Florida Game and Fish's 16-habitat map of Dade County, a 5-habitat broad scale map created by the GIS lab at ENP, and a 176-microhabitat patch map of Taylor Slough.

The program TELEM88 (Coleman and Jones, 1988) was used to delineate minimum convex polygons of deer home range use. These polygons were digitized for some study animals, and overlayed on the various vegetation maps, on which we had already quantified "availability" of various habitats by area. "Use" was then compared to random and to available proportions.

Questions relating to deer habitat use were: What are the major habitats preferred by each age/sex group? Do deer utilize all habitats in proportion to their availability? Do adult females change habitat use at time of fawning or for fawn-rearing? Do deer avoid or respond to rising floodwaters: To what degree do deer and panther home ranges overlap? What effects do fires have on deer, during and in the successional stages following a fire? Do human land use practices affect deer? Can management affect mortality factors of deer?

Other data collected during telemetric locations were activity, habitat, and, if possible, associations with other deer (visual or simultaneous reception). Each radio collar was equipped with an activity switch, which was sensitive to movement of the collar, and activity or inactivity was expressed by different signal pulse rates. Inactivity was triggered by the collar being immobile for 60 seconds, and any motion of the head would switch it back to the "active" phase. Signals were monitored for at least three minutes per fix. If the animal was recorded as inactive for this entire period, it was checked again several hours later. If an inactive signal was obtained two or three times over a 24-hour period, the animal was assumed to be dead or the collar had fallen off, and a walk-in was performed (defined below). All visual locations of deer included a description of behavioral activities and any associations, with great attempts to minimize or prevent disturbance to the animals. For example, although most deer became accustomed to the fixed-wing plane, they would sometimes look up at it, thus triggering an active signal even though there were lying down or resting. If this was seen the animal was recorded as inactive. Most activity readings were obtained before the plane was within a mile of the animal, presumably before it would respond to the presence of the plane.

Walk-ins were the actual locating of an animal by the investigator on foot. As mentioned above, this was routinely done if the animal was believed to be dead, or in some

cases, for visual observation of doe and fawn behavior. Doe and fawn associations were recorded most often from three observation towers placed in the home ranges of does (Hunter, 1990). If a carcass was found, the cause of death was assessed, and if possible, the lower jaw was retrieved for aging. Simultaneously, kills made by collared panthers were examined after the cat left and some jaws of uncollared deer were obtained in this way.

Each radio location (fix) was evaluated for accuracy and only those fixes with ≤ 1 ha error polygons (Heezen and Tester, 1967) were used in the analyses. Radio-collared deer were located biweekly in a stratified pattern of locations spaced through the 24 hours, and evenly distributed over the sex/age categories of the sample. In addition, during the fawning seasons of 1988 and 1989, Ms. Hunter located a subsample of pregnant females an additional 2-3 times per week to obtain an estimate of date of fawning.

Population Censusing

Aerial censuses of the 425 km² study area were flown systematically approximately every other month, and two observers counted all marked and unmarked deer seen along the flight path.

III. RESULTS

Sample Size

Table 3.1 summarizes the captures and recaptures conducted each year. Capture-related mortality was very low. The percent of all deer handled that received injuries or died within three weeks of capture was 6% in 1988, 3% in 1989 and 1990.

Table 3.1. Captures by Netgun of Deer in Eastern ENP.

Year	Captures: Male			Captures: Female			Recaptures: Male			Recaptures: Female			Monitored: Male			Monitored: Female		
	F	J	A	F	J	A	F	J	A	F	J	A	F	J	A	F	J	A
87-89	11	2	13	11	3	24	1	1	4	1	6	3	1	3	8	1	6	16
89-90	7	0	1	2	0	1	1	3	4	1	2	17	4	3	8	4	4	18

F = < 1 yr.; J = 1-2 yrs.; A = 3+ yrs. old.

Sex and Age Structure of Population

As described in Methods, efforts were made to obtain a sample representative of the population as it exists in the prairies of southeastern ENP (Table 3.1). Aging of young deer was usually determined by the tooth eruption schedule of Severinghaus (1949), whose sample was from central Florida. The assumption that eruption would be the same in the Everglades deer was not entirely true. In Severinghaus' study, the permanent third lower premolar was completely erupted by 20 months, while in ENP many yearlings known to be older than this retained the juvenile condition of a deciduous lower premolar. Eruption was not complete in 63% of captured animals 18 to 25 months of age, yet was complete in at least one 24-month old, thus determination of two-year old status was not absolute using this tooth-eruption method. We could not rely on toothwear to accurately age adults; it seems likely that the diet of deer in the Everglades is unique and the wear characteristics for each year are unrecorded. We began a collection of known-age jaws to allow for this comparison in the future. The most precise method of aging dead deer was from cementum annuli counts. Of 64 jaws aged accurately by cementum annuli, the following age groups were obtained. This sample was from collared animals and other carcasses found in the park. The ages identified are included in Table 3.2.

Table 3.2. Age Classes Identified.

Year	0-1 Year	2-4 Years	3-5 Years	5-9 Years	9-14 Years	14+ Years
1987-91	15	23	7	11	7	5

Other estimated ages of live-captured animals indicated a stable age distribution through the period of this study.

While physical size was not used to determine age, it was recorded with an estimate of age and analyzed to assess the hypothesis that Everglades deer are smaller than northern deer. Based on captured animals, fawns weighed from 4 to 25 kg, yearlings from 24 to 34 kg, adult bucks from 38 to 61 kg, and adult does from 26 to 43 kg. Other measurements taken on captured animals are summarized in Table 3.3.

The pregnancy rate was determined by two methods, with slightly different results. By visual examination of females from the air and at capture, no fawns or yearlings appeared pregnant, and only 25% of all yearling females were seen with fawns. However, a physiological examination of does (Forrester 1990, 1992) from a sample collected slightly to

the north of ENP showed that three out of three yearlings were pregnant when killed, and from a sample of does greater than 2 years of age, 50% and 79% of those collected in 1988 and 1989, respectively, were pregnant when killed. This sample provides a minimum estimate of reproduction because some of the does were killed in October, during the rut, negating the possibility of their fertilization just before or after the harvest.

Of all "adult" females collared and monitored in east ENP, the percentage each year observed with a live fawn at any time was 67% in 1987 (but observation not through full fawning season -- 82% pregnancy detected); 86% in 1988 (94% pregnancy detected); 94% in 1989 (87% pregnancy detected); and 91% pregnancy in 1990. None of the harvested females carried twin fetuses, and only one sighting of a doe with twins occurred during the entire study. Hence, twinning in the Everglades appears to be extremely rare, with survival of both young even rarer, thus gross productivity is equal to the pregnancy rate, which we estimate to be about 90% for females ≥ 3 years and about 80% for 2-year-old females.

Table 3.3. Physical Characteristics of Deer Captured in Eastern ENP, 1989.

Sex	Age	N	Weight ¹		Total Length ²		Girth		Hind Foot ³	
			$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
F	≥ 2	23 ⁴	34.9	26-43	159.7	145-171	74.2	64-80	42.7	39-45
M	≥ 2	5	49.3	38-61	174.1	167-181	83.2	75-92	45.4	45-47
F	1	3 ⁵	26.3	26-30	149.3	143-153	67.3	62-71	40.8	41-42
M	1	3	30.8	29-34	155.3	150-161	71.0	67-76	43.3	43.45

¹ kilograms

² total length, cm

³ length, cm

⁴ includes 4 deer collected in health study by Don Forrester

⁵ includes 1 deer collected in health study by Don Forrester

A fat estimate was taken on each animal handled using a scale of 1 (no fat) to 6 (thick fat) by palpating just above the base of the tail. Adult males changed from a pre-rut mean fat index of 5 to a post-rut mean of 2.3. Lactation had a similar effect on females, changing their pre-lactation (late pregnancy) mean of 4 to a post-fawning mean of 1.3. This subjective index is based on a small sample and it has its limitations, but it does indicate a seasonal loss

of condition for both sexes, and a recuperation period sufficient to enter the following breeding season in restored, physical condition.

Estimates of Population Size

Census flights along systematic serpentine transects were flown approximately every other month, with two observers counting marked and unmarked animals visible below and to the sides of the plane. This technique yielded such highly variable results that no reliable density estimate was obtained until the standard deviation of mean estimates shrank to a reasonable level as the number of censuses increased. The mean estimate of density over the 425 km² study area by December 1990 was 0.67 ± 0.24 deer/km². While we cannot completely explain the variation found between surveys, some of it may be due to seasonal movements of males (see reproduction and the overall estimate is comparable to those of previous authors (Loveless, 1959; Schemnitz, 1974).

Table 3.4. Population Characteristics Estimated Each Year in Eastern ENP (see also Table 3.6).

	1987	1988	1989	1990
N	35	35-40	--	--
M-A	x	0.14	--	--
M-J	x	0.60	--	--
M-F	0.67	0.36	--	--
FR	0.78	0.80	0.71	1.0 (burned) 0.90 (unburned)
M:F	3:1	3.4:1	1:2	--
PopEst	x	230	298	--
density	< 1.0/km ²	0.55/km ²	0.67/km ²	0.68/km ²

N = number collared deer monitored for most of that year

M-A = adult mortality recorded among collared animals

M-F = fawn mortality recorded among collared or visually known fawns

M-J = juvenile mortality recorded among collared 1-2 year olds

FR = rate of fawning in does $\geq$ 2 years old and assuming no twinning

M:F = sex ratio of observed adults averaged over year

PopEst = estimate of total number of deer resident in the study area, 425 km²

x = not estimated

Mortality and Predation

1. Assessment of all Mortality Factors

Ectoparasite loads were minor to non-existent on ENP deer. For example, only four of 44 deer captured in 1989 were found with detectable ticks or mites, and these were low loads in September-November. A veterinary survey of a random sample of deer from ENP and Big Cypress (BC) showed the populations to be in good health with low parasite loads (McCowan, 1990; Forrester, 1992). Parasites are not believed to be a significant detriment to deer in the Everglades.

2. Age-Related Mortality

Fawn mortality was significantly higher in wet prairies than in dry prairies ($\text{Chi}^2 < 0.01$) (Hunter, 1990, and in press) and it was greater in male fawns than in females (Smith, 1991). While not all causes of fawn mortality could be determined, the possible differences between the two prairie types are unlikely to derive from different predator pressure. More likely the mortality differences are related to vegetative/phenological differences which influence the health of the lactating dam. There may also be selective behavioral differences in the maternal treatment of male vs. female fawns, if (for example) the female offers more maternal protection to female offspring. The annual mortality rate of yearlings was approximately 28%. For two- to three-year-olds the rate was approximately 16%, and for adults, 4 years old and greater, it was about 22%/year. Rates were not significantly different according to sex or age class except for fawns as noted above.

A Leslie matrix analysis based on the estimated mortality rates indicates that at least 60% survivorship (to adult reproduction) of female fawns is necessary to maintain numbers of females in the population, and hence provide stability. Survivorship of fawns into the "follower stage," at about three months is not uniform by sex or location: fawns of both sexes died during this period in wet prairies (Hunter, 1990, and in press). However, survivorship of female fawns appears sufficient to allow population growth. Observed population growth during the five years of study was lower than the mortality data would predict. There is some (inconclusive) evidence that a skewed sex ratio at birth may exist in the Everglades population, favoring males. In a larger sample of fawns in the Everglades/Big Cypress border region, mortality was similar among sexes. Male fawns had a greater survival rate in only one of three years. Fawn survival rate was higher in BC than in ENP (0.39 vs. 0.10). Deaths were of higher frequency between two and six months of age. Fifty-eight percent of all deaths were from bobcat (*Felis rufus*) predation. Recruitment

ranged from 11 to 26% in BC and 0-13% in ENP (Boulay, 1992). Overall fawn survivorship in that study averaged 24% and loss was attributed mainly to bobcat predation. The situation is not completely comparable to southern ENP, where panther predation exerts a greater impact, but the biology of deer reproduction should be similar.

3. Panther Predation

The following summaries indicate that adult deer are the primary prey of resident panthers in south Florida, especially in ENP where hogs, the other prey capable of sustaining adult panthers (Maehr et al., 1990; Alvarez, 1993), are almost never found. Panther predation may be a significant factor on deer populations where deer are unhunted (Dalrymple and Bass, in prep.; Bass and Smith, in prep.). Where deer are hunted, e.g. BCNP, younger deer are killed more frequently and bobcat predation on fawns seems to be an important population factor (Boulay, 1992; Sargent, 1992). It should be noted that panthers will kill bobcat and where panthers are present, bobcat numbers may be depressed.

Table 3.5. Predation of Deer by Collared Panthers in ENP and Vicinity.

	No. panthers monitored	No. adult study deer killed	No. study fawns killed
1987	6	0	0 incomplete year
1988	7	4	1
1989	7	6	1?
1990	8	9	4

The panther population utilizing ENP remained small throughout the study, but was thought to be at or near carrying capacity for the region (Bass and Smith, in prep.). During the wet season, panthers reduced the area in which they hunted and killed less deer during wet season months of May through September (Dalrymple and Bass, in prep.). Deer comprised 57% of 99 identified kills, and 78% of the biomass killed by panthers in ENP 1987-1990 (Dalrymple and Bass, in prep.). Adult bucks with a mean age of 5.5 years were the dominant age/sex class killed (47% of all deer killed).

4. Conclusions

Although mortality rates varied from year to year, especially among young fawns, the overall rate of recruitment and mortality were consistently low, compared to other deer populations in south Florida. This implies that the population is stable. Perhaps the low density of deer and the low density of panthers reflects limitation by environmental carrying capacity and not by density dependent factors.

Reproduction

Males associated with females from July to October, and with each other in sporadic small groups the rest of the year. Males showed antler velvet from March to mid-June, and shed antlers in December and January. Fawns were dropped from January through early May, with peaks in February and March, the late dry season (Hunter, 1990, and in press).

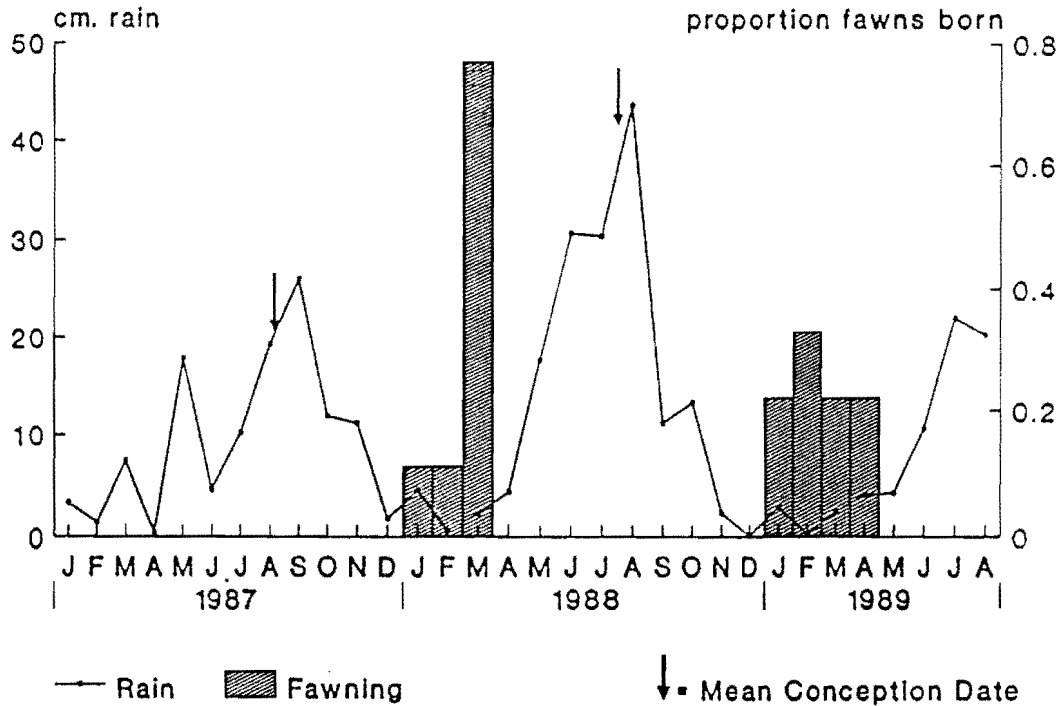
Females seem to associate in permanent matriarchal groups, although two does maintained solitary home ranges throughout the study.

The overall pregnancy rate among females ≥ 2 years old at fawning was 79%. This is a very conservative estimate, as we were unable to verify fawning until the fawn was visible, which precludes any estimates of early neonatal mortality. We can conclude that the female deer in ENP have a high conception rate and sufficient males are available for mating.

Yearling does do not often seem to conceive. This could result from the sedentary, matriarchal social system precluding the youngest females from breeding access to males.

No twinning was observed in the study. Although only six does were killed and examined for fetuses (Forrester, 1992), the careful monitoring of a total of 22 does during the fawning season allows us to conclude that twinning is very rare in the Everglades, or if twinning does occur the mothers are unable to maintain two fawns, and one sibling usually dies soon after birth.

Fawning proved to be synchronized with the late dry season (Figure 3) (Hunter, 1990; Boulay, 1992), and was significantly later in does resident in wet prairies vs. those resident in dry prairies (Hunter, 1990, and in press.) (Figure 4). This was contrary to hypothesized differences in timing, where in wet prairies fawn mortality due to high-water conditions might possibly constrain reproductive success and thereby select for earlier fawning. Instead, although there was significantly more fawn mortality in wet prairies than in dry, fawning must occur later in wet prairies due to nutritional constraints on does (Hunter, 1990, and in press) (see also Figure 5).



wet & dry prairies combined

Figure 3. Fawning seasons in relation to rainfall averaged over the study site, Taylor Slough region of Everglades National Park. Deer conceptions (by backdating from fawning dates) occurred just before the peak of two very different rainy seasons.

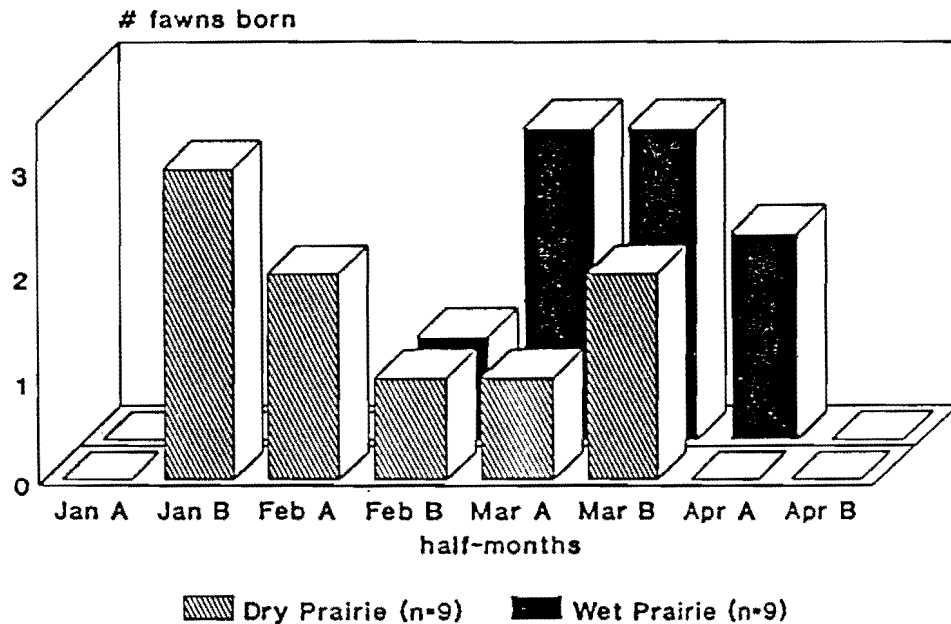


Figure 4. Number of fawns born in the two prairie types, 1988 and 1989, Taylor Slough portion of Everglades National Park. Each block represents fawning events with median date in either the first 15 days of the month (A) or the rest of the month (B). The mean birthdate was significantly different between the two prairie types.

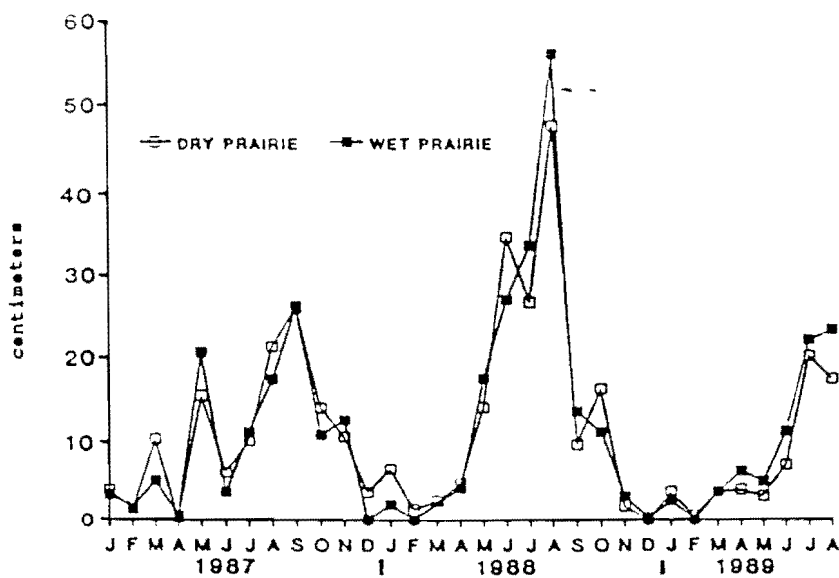


Figure 5. Rainfall on Taylor Slough's dry prairies (station R3110) and wet prairies (station NP67) during this fawning study, Everglades National Park.

Table 3.6. Population Characteristics for White-tailed Deer in Eastern ENP for the Interval January 1987-June 1991 (3 years)*.

	Average or Range Jan '87-June '91
Density (#/km ²)	0.68
Productivity (F/AF)	0.82-0.94
Sex Ratio	
at birth	1:0.7
at 1 year or over	1:2.4
Litter Size (n = 85)	1.0
Age Structure (%)	
0 through 1 year	22
2 through 3 years	33
4 through 5 years	10
>6 years	33
Mortality	
Fawns	0.54
Yearlings	0.24-0.32
Adults (> 2 years)	
Females	0.13
Males	0.19
Recruitment per year (%) (≥ 18 months ≤ 2 years)	1

* Based in part on 35-40 collared deer monitored per year as well as observations of known age deer.

Home Range and Habitat Use

A serious constraint on the analyses of habitat use was the lack of digital data on habitat availability. Although the park has a history of extensive botanical work, and most of the area's floras are quite complete, the quantification of coverage by each community could only be accurately assessed over such a large area with the advent of digital remote sensing data. ENP purchased in 1986 (available in 1987) a complete set of false color-infrared tinted stereoscopic photographs of the entire landholding. An initiation of digitizing and ground-truthing the habitat information from this 1:10,000 scale resource provided the Taylor Slough Microhabitat map (Hunter, 1990). This map was used for a fine-scale (106 microhabitat patch-types, 625 m² cells) analysis of females' behavior during the fawning season. The Florida Game and Freshwater Fish Commission meanwhile created a broad-scale habitat map (16 categories, 1000 m² cells) for the entire state, which was not completely ground-truthed. The inaccuracies were corrected by Hunter, after ground-truthing the previous map. The broad-scale map was used for a study of the annual home ranges of males and females in the core study area, centered around Long Pine Key. Also, some satellite imagery was obtained from the Florida Department of Transportation and classified into six broad landscape types for panther home range analysis (Bass and Smith, in press).

Home-range size estimates for deer were calculated from telemetry locations using the program TELEM88 (Coleman and Jones, 1988), and the core activity area was defined as the 80% isopleth. Home ranges for panthers were estimated from telemetry locations by using the program HOMERANGE (Samuel et al., 1985), the core activity area was defined as the 60% harmonic mean.

Home ranges of adult male deer were larger than those of adult females. Twenty-two overlapping females' home ranges covered 8.15 km², for an average individual area of 37 ha. However, taking overlap into consideration, average core home range area (80% isopleth) for females was 430 ha. Sixteen adult males' home ranges (which barely overlapped) around the LPK area covered 18.05 km², for an average individual area of 1.13 km² (113 ha). Individual core areas for males averaged 12.4 km² (1240 ha). Thus, the density of females was nearly four times higher in these prairies than that of males, and they utilized more of the same habitats and even ranges, than males did. Females showed strong home range fidelity throughout the study, exhibiting a matriarchal hierarchy of social dominance with overlapping home ranges of related females. This pattern was also seen in the Big Cypress deer populations (Zultowsky, 1992). Zultowsky (1992) found female home ranges averaging 5.4 km² in BC and 2.95 km² in ENP. Again water levels did not restrict movement, but home ranges expanded during the dry season. Sargent (1992) found home ranges of males to be 7.0 km² in BC and 2.9 km² in ENP.

Adult bucks utilized dense cover year round much more than adult females did. Collared females were rarely found in the large, dense stands of pinelands, *Schinus*, or hardwoods, while most males' home ranges included these stands. All deer seem to avoid the dense *Schinus* stands present in the "Hole-in-the-Donut," but location as well as capture of deer in any dense tree cover was nearly impossible. Hence, captures emphasized prairie residents, and initial conclusions that deer densities were inversely proportional to distance from LPK or any large tree island (Bass and Smith, in prep.) were compromised. Panthers and adult bucks did utilize the edges of tree islands more than any other habitat (Bass and Smith, in prep.). This "edge effect" probably reflects a stronger need by males for flight cover. Many does were resident year-round in open prairies with little tree cover available. Wet season flooding did not result in any noticeable shifts in home range use of deer (Hunter, 1990, and in press). However, panther home ranges were smaller in the wet season (Dalrymple and Bass, in prep.), and the cats avoided flooded areas, thus the increased fawn mortality in wet prairies during the wet season cannot be explained by panther predation.

The severe drought of 1989 allowed the normal lightning strike induced fires to burn more widely than usual, and about half the study area was burned in the "Ingraham Fire," which was a spectacle second only to the Yellowstone blaze in recent NPS history. But since a policy of controlled and natural burns had been maintained for many years preceding, the fire mainly cleared undergrowth and did not often kill mature trees. The prairie vegetation showed regrowth within a week, while the hardwood hammocks and some pine lands took months to "green up" (ENP Fire Management pers. comm.). Following the fire, deer that were resident in the area did not deviate from normal patterns of home range use. The natural periodic cycles of fire and flood have been (and still are) believed to keep the vegetative communities of the Everglades at equilibrium over time (Robertson, 1953; Wade et al., 1980). The changes that are noted are attributed to human influences on the wetland ecosystem (Walters et al., 1992). In the year following the Ingraham Fire, deer were monitored inside and outside of the burned zone. There was no notable migration of deer into or out of the burned area at any time. Nor was there any notable change in home range use during rising waters when home ranges were 100% inundated (as in the wet year of 1988) (Hunter, 1990). However, historical maximum depths were not reached, so a critical depth where water began to affect deer mobility was not determined. Harlow's (1959) suggestion that 30 cm was the critical depth might be valid, but these depths rarely occur south of the Water Conservation Areas (40 years ENP hydrology data) (Figure 6).

The microhabitat study (Hunter, 1990) analyzed only the fawning females' use of 106 microhabitat patch types: wet and dry prairies, determining their use versus availability. A principle components analysis is underway, indicating so far that shelter elements within the

prairie such as tall grass and willow heads and other shrubbery, are important to does with fawns. Also, the evidence supports the theory of Loveless (1959) and Harlow (1961) that "lilies" (four species of aquatic herbs with flowers) are important to the diets of deer, especially in wet prairies.

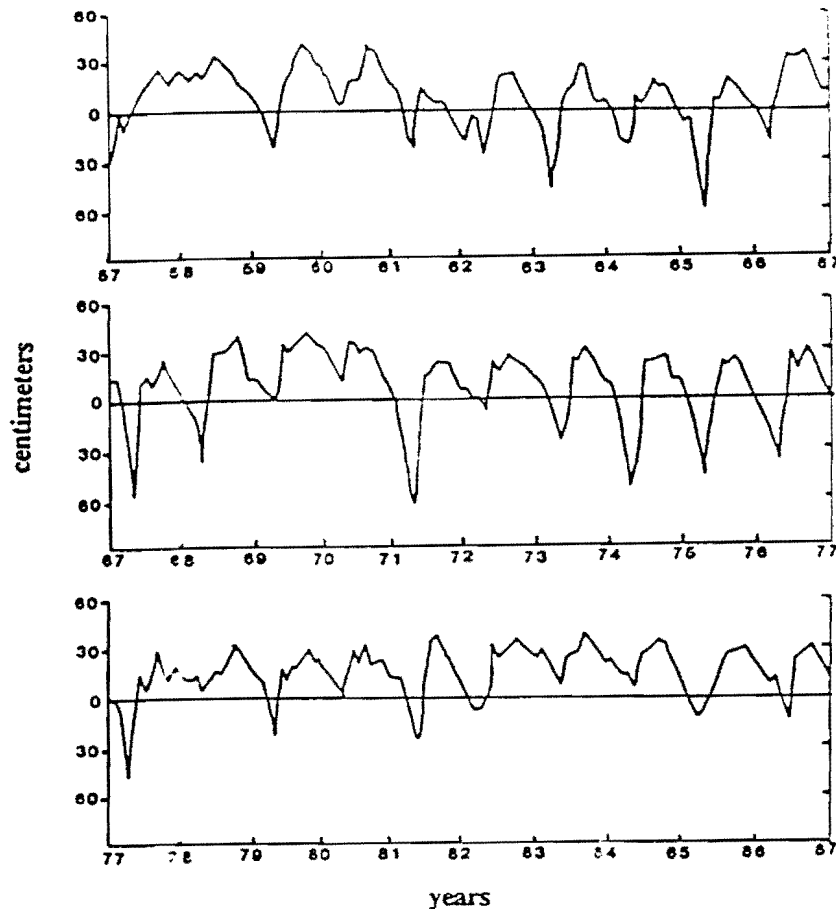


Figure 6. Modelled water table in relation to ground level (horizontal line at 0), from data recorded each year from 1957 through 1987, in typical wet prairie, station P38, Everglades National Park. Year marks are at January.

While investigating the relative rates of success in fawn-rearing in the two types of prairie (wet or dry, defined above, (Hunter, 1990, 1993, in press), it was discovered that does residing year-round in wet prairies had significantly less success raising fawns to the three-month-old follower stage, and that they fawned on average one month later than those does living in the dry prairies. These results suggested a possible nutritional dependency on the part of the mothers during the early wet season, constraining successful lactation to that period when blooming of nutritious flowers occurs.

Miller (1993) contrasted home ranges of males and females with respect to habitat type. In his thesis he distinguished two habitat categories: a) ridges with trees, and b) wet prairies with scattered trees. Both males and females had smaller home ranges on ridges (5.3 km² and 2.5 km²) and larger home ranges if inhabiting prairies (8.2 km² and 6.2 km²). Ridges are characterized by greater cover density and frequency of tree islands in BCNP (Miller, 1993).

IV. DISCUSSION

We found little seasonal variation in density and reproductive output of this relatively K-selected subspecies. Although densities of both deer and panthers are low in eastern ENP compared to ranges farther north, we suspect that they are normal and near carrying capacity. The home ranges and stable, matriarchal social system exhibited by the deer indicate that the Everglades provides a meta-stable environment. Although primary production is low, there is a seasonal peak as the floodwaters arrive, which appears to be the factor influencing the onset of deer reproduction and ultimately the successful rearing of fawns. Hence, reproduction is synchronized, and mortality, although exhibiting seasonal fluxes, probably is important to and perhaps regulating, the juvenile age class number.

Harlow (1961) conducted a thorough analysis of the nutrients available to deer over most of Florida. In the Everglades, he quantified the nutrient content of the 41 food items found in deer rumens, but unfortunately did not assess availability. Although concentrations of minerals and inorganic ions are generally lower in Taylor Slough than in the larger Shark River Slough to the northwest (Schomer and Drew, 1982), they were believed to be sufficient in soil and plant matter such that minerals were not the limiting factor to deer (Harlow, 1961). Instead, the lack of cover and of edible browse were believed to be limiting, at least in the wet prairies (Harlow and Jones, 1965). Camp (1932) reported that cows could not survive in wet prairies of south Florida during flooded months, but their larger body size (and energetic advantage) allows them to obtain a nutritionally better diet than deer can survive on in the same habitat. Comparing deer diets in the Everglades to those in the rest of Florida, Harlow and Jones (1965) claimed the prairies to be the habitat least able to support high densities of deer. The current study showed that deer can and do survive solely in prairie habitats, at low densities and in good health. Densities found in this study were very comparable to those of white-tailed deer in the Venezuelan llanos (Brooks, 1972) (optimum 4/km² = 25 ha/deer) (crude density 2-2.5/km²), a similar habitat, implying this is the carrying capacity of flooded savannahs (Eisenberg, et al., 1979). Authors have

labelled bottomland hardwood forests as the best habitat for deer in southeastern US (Sigler-Eisenberg and Eisenberg, 1985), but the hardwood forests in the Everglades are scattered fragments, utilized for cover and browse, especially by bucks and do not characterize the terrain in terms of dominance. It is possible that the hardwood tree islands are the "best" habitat for deer and are monopolized by the adult males, as has been noted in more crowded deer populations at other locales (LaGory et al., 1991). But it is unlikely that at these low densities, deer of either sex in ENP would be excluded from any habitats by density-dependent factors. Perhaps the more solitary social system of the males promotes utilization of tree cover, while the more grouped females need open habitats to promote cohesion.

The vegetative cover consists of structural characteristics of grasslands as well as interspersions of shrubs and trees, higher interspersions providing better habitat for deer (Moore and Haas, 1973). It seems likely that there is sufficient cover for female deer and fawns in the prairies with minimal tree island stands and that the pre-supposed dependency on tree islands (Loveless, 1959; Miller, 1992) is not necessarily a selective force shaping behavior of Everglades deer.

Flooding did not appear to be a direct mortality factor in the typical Everglades. However, it may be a limiting stress factor in dry prairies, especially to lactating does. This anecdotal evidence supports the theory (McNab, 1963) that animals in xeric regions will have larger home ranges than their conspecifics in mesic regions, which was supported by Rautenstrauch and Krausman (1989) with mule deer (*O. hemionus crooki*). The difference in apparent carrying capacity of prairies in the wet season, and the timing of fawning, is apparently not due directly to the hazards of water, but more to its effects on the vegetation.

Fire management of Everglades habitats did not prove beneficial to deer. Unlike some northern hardwood forests which are maintained and encouraged to regenerate by fire, pine flatwoods with palmetto understories are affected by fire, and open wet prairies need to be burned more often than they are to hold back hardwood encroachment, but this encroachment might be beneficial to the deer. A better land management strategy for the sake of deer and panthers would be to acquire and protect from disturbance land in areas which if disturbed have a potentially high susceptibility to floodwater or saltwater intrusion. The entire Everglades ecosystem is in a state of transition due to pollution, water diversions, urban encroachment, and now Hurricane Andrew. The restoration efforts should utilize the information presented here on the previous stable status of deer and panthers as a minimum baseline. While it is possible the Park can only support 6-8 panthers [the number that has been used since at least the 1960's (Schemnitz, 1974)], it should not be assumed that the ecosystem was supporting its maximum capacity of deer, and there is good evidence that deer might be the factor limiting panthers (Bass and Smith, in prep.)

V. RESULTS PRESENTED, LITERATURE CITED AND INTERIM REPORTS

Appendix I and II list all publications, oral and written, published and unpublished, emanating thus far from the Deer Project. Appendix III lists the literature cited and references. We expect several publications to be accepted in peer-reviewed journals in the next year, and the possibility exists for a book to be published jointly with the Panther Project covering deer-panther interactions.

Appendix I Presentations at Scientific Meetings (Alphabetical)

- Bass, O.L. and T.R. Smith. 1989. Distribution and abundance of Florida panthers and white-tailed deer in eastern E.N.P. *at* Everglades: spatial and temporal patterns as guidelines for ecosystem restoration. Symposium at Key Largo, FL. Proc. eds.: J.C. Ogden and S.M. Davis.
- Hunter, C. 1989. Water and Deer. Poster presented *at* Everglades: spatial and temporal patterns as guidelines for ecosystem restoration. Symposium at Key Largo, Fla., Proc. eds.: J.C. Ogden and S.M. Davis.
- Hunter, C.G. 1993. Radiotracking deer in the Everglades. Invited speaker *at* meeting of Florida Wildlife Care, Inc., Gainesville, Fla.
- Smith, T.R. 1989. Reproductive synchrony and productivity of white-tailed deer in a subtropical wetland. *At* 5th International Theriological Congress, Rome, Italy.
- Smith, T.R. 1990. Recruitment and loss in an un hunted subtropical white-tailed deer population. *At* Biology of Deer: 2nd Annual Symposium. Mississippi State University, Hattiesburg, Miss.
- Smith, T.R. 1992. Predation of white-tailed deer by Florida panthers in the Everglades. *Abstract Only*, American Society of Mammalogists, 72nd Annual Meeting, Salt Lake City, Utah.
- Smith, T.R. and J.F. Eisenberg. 1988. Ecology of white-tailed deer in E.N.P.: preliminary observations in a subtropical wetland. *At* 2nd International Conference on Ungulate Behavior and Management. Texas A&M University, College Station, Texas.

Appendix II

Publications and Unpublished Reports from the E.N.P. Deer Projects*

- Bass, O.R. and T.R. Smith (in prep). 1993. Landscape, white-tailed deer, and the distribution of Florida panthers in the Everglades. Paper presented at: Everglades: spatial and temporal patterns as guidelines for ecosystem restoration. Symposium at Key Largo, Fla., Proc. eds.: J.C. Ogden and S.M. Davis.
- Boulay, M.C. 1992. Mortality and recruitment of white-tailed deer fawns in the wet prairie/tree island habitat of the Everglades. M.Sc. thesis, University of Florida, Gainesville. 77 pp.
- Dalrymple, G.H. and O.L. Bass (in prep). 1993. Food habits of the Florida panther in Everglades National Park, Florida. 35 pp. typescript + figures.
- Eisenberg, J.F. and M.E. Sunkist. 1986. Ecology of the white-tailed deer in Everglades National Park. Proposal to the N.P.S.
- Forrester, D.J. 1990. Studies on the health and diseases of white-tailed deer in Everglades National Park and Big Cypress National Preserve: annual progress report. Coop. Agreement CA-5000-7-8007, Dept. Infectious Diseases, College of Veterinary Medicine, University of Florida, Gainesville. 10 pp + figures.
- Forrester, D.J. 1992. Florida Panthers and Bobcats. Pp. 174-203 in *Parasites and Diseases of Wild Mammals in Florida*. University Presses of Florida, Gainesville. 460 pp.
- Forrester, D.J. 1992. White-tailed Deer. Pp. 275-353 in *Parasites and Diseases of Wild Mammals in Florida*. University Presses of Florida, Gainesville. 460 pp.
- Hunter, C.G. 1990. *Odocoileus virginianus seminolus*: the ecology of fawning in wet and dry prairies. M.S. thesis, University of Florida, Gainesville. 138 pp.
- Hunter, C.G. (in prep). Effects of prairie hydroperiod on timing and success of fawning in Everglades Deer. Resubmitted October 1993.
- Hunter, C.G., R. Lemos de sa, and T. Oliveira. 1989. A GIS analysis of Taylor Slough, Everglades National Park. Unpub. report, Department of Wildlife and Range Sciences, University of Florida, Gainesville.
- Miller, K.E. 1993. Habitat use by white-tailed deer in the Everglades: tree islands in a seasonally flooded landscape. M.Sc. thesis. University of Florida, Gainesville. 105 pp.

- Sargent, R.A., Jr. 1992. Movement ecology of adult male white-tailed deer in hunted and non-hunted populations in the wet prairie of the Everglades. M.Sc. thesis, University of Florida, Gainesville. 66 pp.
- Smith, T.R. 1991. Recruitment and loss in an un hunted subtropical white-tailed deer population. P. 176 *in* The biology of deer. R.D. Brown, ed. Springer-Verlag, New York.
- Smith, T.R. 1991. Effects of hydrology and vegetation on the distribution and abundance of white-tailed deer and Florida panthers in Everglades National Park. Annual Report - FY 1991. South Florida Research Center, unpub. document, Homestead, Florida. 26 pp.
- Smith, T.R., J.F. Eisenberg, and M.E. Sunkist. 1989. Ecology of white-tailed deer in Everglades National Park (CA-5280-5-8004): Progress January 1987-January 1989. Report to Southeast Regional Office of National Park Service, Atlanta.
- Smith, T.R., J.F. Eisenberg, and M.E. Sunkist. 1990. Ecology of the white-tailed deer in Everglades National Park. National Fish and Wildlife Foundation Project No 89-68 Final Report.
- Smith, T.R., J.F. Eisenberg, and M.E. Sunkist. 1990. Ecology of white-tailed deer in Everglades National Park (CA-5280-5-8004): Progress February 1989-January 1990. Report to Southeast Regional Office of National Park Service, Atlanta.
- Zultowsky, J.M. 1992. Behavioral and spatial ecology of female white-tailed deer in the Everglades ecosystem. M.Sc. thesis, University of Florida, Gainesville. 81 pp.

*Includes theses deriving from efforts by R. Labisky and Students as of September, 1993.

Appendix III

Literature Cited and References

- Alvarez, K. 1993. Twilight of the panther. Myakka River Publishing, Sarasota, Fla. 501 pp.
- Barett, M.W., J.W. Nolan, and L.D. Roy. 1982. Evaluation of hand-held net gun to capture large mammals. Wild. Soc. Bull. 10:108-114.
- Bass, O.R., and T.R. Smith (in prep). 1993. Landscape, white-tailed deer, and the distribution of Florida panthers in the Everglades. Paper presented at Everglades: spatial and temporal patterns as guidelines for ecosystem restoration. Symposium at Key Largo, Fla., Proc. eds.: J.C. Ogden and S.M. Davis.
- Belden, R.C., W.B. Frankenberger, and S.T. Schwikert. 1988. Panther habitat use in south Florida. Journal of Wildlife Management, 52(4):660-663.
- Blouch, R.A. 1987. Reproductive seasonality of the white-tailed deer on the Colombian Llanos. Pp. 339-343 in Wemmer, C.M. (ed.), Biology and Management of the Cervidae. Smithsonian Press, Washington, D.C.
- Boulay, M.C. 1992. Mortality and recruitment of white-tailed deer fawns in the wet prairie/tree island habitat of the Everglades. M.Sc. thesis, University of Florida, Gainesville. 77 pp.
- Branan, W.V. and R.L. Marchinton. 1987. Reproductive Ecology of white-tailed and red brocket deer in Suriname. P. 344-351 in Wemmer, C.M. (ed.), Biology and Management of the Cervidae. Smithsonian Press, Washington, D.C.
- Brisbin, I.L. and M.S. Lenarz. 1984. Morphological comparisons of insular and mainland populations of southeastern white-tailed deer. Journal of Mammalogy, 65(1):44-50.
- Brokx, P.A. 1972. A study of the biology of Venezuelan white-tailed deer (*Odocoileus virginianus gymnotis* Wiegmann 1883), with a hypothesis on the origin of South American cervids. Ph.D. dissertation, University of Waterloo.
- Brokx, P.A. 1984. South America. Pp. 525-546 in The white-tailed deer: Ecology and Management, L.K. Halls, (ed.). Stackpole Press, Harrisburg.
- Bunnell, F.L. 1987. Reproductive tactics of Cervidae and their relationships to habitat. Pp. 145-167 In Wemmer, C.M., (ed.). Biology and Management of the Cervidae. Smithsonian Press, Washington, D.C.

- Byers, C.R., R.K. Steinhorst, and P.R. Krausman. 1984. Classification of a technique for analysis of utilization-availability data. *Journal of Wildlife Management* 48:1050-1053.
- Camp, P.D. 1932. A study of range cattle management in Alachua County, Florida. Fla. Agr. Exp. Stn. Bull. 249. 28 pp.
- Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York.
- Chardonnet, P. and S. Charity. 1992. A Marsh Deer (*Blastocerus dichotomus*) capture experiment in Brazil using a net-gun from a helicopter. Pp. 583-588 in "Ongulés/Ungulates 91", Proceedings of the International Symposium, Toulouse, France, September 2-6, 1991, F. Spitz, G. Janeau, G. Gonzalez, and S Aulagnier (eds.). S.F.E.P.M.-I.R.G.M., Paris-Toulouse, France.
- Cochran, W.W. 1980. Wildlife telemetry. Pp. 507-520 in *Wildlife Management Techniques Manual*, 4th ed., S.D. Schemnitz, (ed.). Washington, D.C.: The Wildlife Society.
- Coleman, J.S. and A.B. Jones, III. 1988. User's guide to TELEM88: computer analysis system for radio-telemetry data. Research Series #1, Department of Fisheries and Wildlife, Virginia Polytechnic Institute and State University. Blacksburg. 49 pp.
- Dalrymple, G.H. and O.L. Bass (in prep). 1993. Food habits of the Florida panther in Everglades National Park, Florida. 35 pp. typescript + figures.
- Downing, R.L., B.S. McGinnes, R.L. Petcher, and J.L. Sandt. 1969. Seasonal changes in movements of white-tailed deer. In *Proceedings of a Symposium on White-Tailed Deer in the Southern Forest Habitat*. L.K. Halls, (ed.). U.S. Southern Forest Experiment Station.
- Eisenberg, J.F. and M.E. Sunquist. 1986. Ecology of the white-tailed deer in Everglades National Park. Proposal to the N.P.S.
- Eisenberg, J.F. M.A. O'Connell, and P.V. August. 1979. Density, productivity, and distribution of mammals in two Venezuelan habitats. Pp. 187-210 in *Vertebrate Ecology in the Northern Neotropics*, J.F. Eisenberg (ed.). Smithsonian Institute, Washington, D.C.
- Forrester, D.J. 1990. Studies on the health and diseases of white-tailed deer in Everglades National Park and Big Cypress National Preserve: annual progress report. Coop. Agreement CA-5000-7-8007, Dept. Infectious Diseases, College of Veterinary Medicine, University of Florida, Gainesville. 10 pp + figures.

- Forrester, D.J. 1992. Florida Panthers and Bobcats. Pp. 174-203 *in* Parasites and Diseases of Wild Mammals in Florida. University Presses of Florida, Gainesville. 460 pp.
- Forrester, D.J. 1992. White-tailed Deer. Pp. 275-353 *in* Parasites and Diseases of Wild Mammals in Florida. University Presses of Florida, Gainesville. 460 pp.
- Harlow, R.F. 1959. An evaluation of white-tailed deer habitat in Florida. Technical Bulletin #5. Tallahassee, FL: Florida Game and Fresh Water Fish Commission. 69 pp.
- Harlow, R.F. 1961. Fall and winter foods of Florida white-tailed deer. Quarterly Journal of the Florida Academy of Sciences 24(1):19-38.
- Harlow, R.F. 1972. Reproductive rates in white-tailed deer in Florida. Quarterly Journal of the Florida Academy of Sciences 35(4):165-170.
- Harlow, R.F. and F.K. Jones (eds.). 1965. The white-tailed deer in Florida. Technical Bulletin #9. Tallahassee, FL: Florida Game and Fresh Water Fish Commission. 240 pp.
- Harmoning, A.K. 1976. White-tailed deer dispersion and habitat utilization in central North Dakota. North Dakota Game and Fish Department, P-R W-67-R 13, 14, 15 Phase C Report 199-A.
- Haugen, A.O. and D.W. Speake. 1957. Parturition and early reactions of white-tailed deer fawns. Journal of Mammalogy 38:420-421.
- Heezen, H.R. and J.R. Tester. 1967. Evaluation of radio-tracking by triangulation with special reference to deer movements. J. Wildl. Manage. 31:124-141.
- Heisey, D.M. and T.L. Fuller. 1985. Evaluation of survival and cause specific mortality rates using telemetry data. Journal of Wildlife Management 49:668-674.
- Hirth, D.H. 1977. Social behavior of white-tailed deer in relation to habitat. Wildlife Monograph 53. 55 pp.
- Hirst, S.M. 1975. Ungulate-habitat relationships in a South African woodland/savanna ecosystem. Wildlife Monograph 44. 60 pp.
- Huegel, C.N. 1985. Predator avoidance behaviors that favor fawn survival in white-tailed deer in south-central Iowa. Ph.D. dissertation, Ames IA: Iowa State University. 150 pp.
- Hunter, C.G. 1990. *Odocoileus virginianus seminolus*: the ecology of fawning in wet and dry prairies. M.S. thesis, University of Florida, Gainesville. 138 pp.

- Hunter, C.G. (in prep). 1993. Effects of prairie hydroperiod on timing and success of fawning in Everglades Deer. Manuscript.
- Hunter, C.G., R. Lemos de sa, and T. Oliveira. 1989. A GIS analysis of Taylor Slough, Everglades National Park. Unpub. report, Department of Wildlife and Range Sciences, University of Florida, Gainesville.
- Kushlan, J.A. 1990. Freshwater marshes. Pp. 324-363 *in* Ecosystems of Florida, R.L. Myers and J.J. Ewel (eds.). University of Central Florida Press, Orlando.
- LaGory, K.E., C Bagshaw III, and I. Lehr Brisbin II. 1991. Niche differences between male and female white-tailed deer on Ossabaw Island, Georgia. *Applied Animal Behavior Science* 29:205-214.
- Loveless, C.M. 1959. The Everglades deer herd: life history and management. Florida Game and Freshwater Fish Commission Tech. Bull. #6.
- Loveless, C.M., and F.J. Ligas. 1959. Range conditions, life history and food habits of the Everglades deer herd. *Trans. No. Am. Wildlife Conference* 24:201-214.
- Maehr, D.S., R.C. Belden, E.D. Land, and L. Wilkins. 1990. Food habits of panthers in southwest Florida. *Journal of Wildlife Management* 54:420-423.
- McCowan, J.W. 1988. Big Cypress watershed deer/hog/panther relationships E-1-12 animal performance report. Florida Game and Freshwater Fish Commission, Tallahassee.
- Miller, K.E. 1993. Habitat use by white-tailed deer in the Everglades: tree islands in a seasonally flooded landscape. M.Sc. thesis. University of Florida, Gainesville. 105 pp.
- Moore, K.R. and R.H. Haas. 1973. Remote detection of deer habitat factors. NASA tech report RSC-50. College Stn.: Tex. A&M Univ., Remote Sensing Ctr. 113 pp.
- Newsom, J.D. 1984. The coastal plain. Pp. 367-380 *in* White-tailed deer: Ecology and Management, L.K. Halls (ed.). Stackpole Press, Harrisburg.
- Nue, C.W., C.R. Byers, and J.M. Peek. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 38:541-544.
- Richter, A.R. and R.F. Labisky. 1985. Reproductive dynamics among disjunct white-tailed deer herds in Florida. *Journal of Wildlife Management* 49:964-971.
- Robertson, W.B. 1953. A Survey of the effects of fire in Everglades National Park. National Park Service unpub. report, Homestead. 169 pp.

- Samuel, M.D., D.J. Pierce, E.O. Garton, L.J. Nelson, and K.R. Dixon. 1985. User's manual for program HOMERANGE. Forestry, Wildlife and Range Experiment Station, Technical Reprint #15. University of Idaho, Moscow. 70 pp.
- Sargent, R.A., Jr. 1992. Movement ecology of adult male white-tailed deer in hunted and non-hunted populations in the wet prairie of the Everglades. M.Sc. thesis, University of Florida, Gainesville. 66 pp.
- Schemnitz, S.D. 1974. Populations of bear, panther, alligator and deer in the Florida Everglades. *Florida Scientist* 37(3):157-167.
- Schomer, N.S. and R.D. Drew. 1982. An ecological characterization of the lower Everglades, Florida Bay, and the Florida Keys. U.S. Fish and Wildlife Service, Washington, D.C.: Office of Biol. Serv. FWS/OBS-82/58.1. 246 pp.
- Seber, G.A.F. 1982. The estimation of animal abundance. 2nd Ed. Charles Griffin and Co., London. 654 pp.
- Severinghaus, C.W. 1949. Tooth development and wear as criteria of age in white-tailed deer. *Journal of Wildlife Management* 13:195-216.
- Sigler-Eisenberg, B. and J.F. Eisenberg. 1985. Variation in white-tailed deer populations: a note on the southeast coastal plain. Annual Meeting of the Southeast Archeological Association, Pensacola, Fla.
- Smith, T.R. 1991. Recruitment and loss in an un hunted subtropical white-tailed deer population. P. 176 in *The biology of deer*. R.D. Brown, ed. Springer-Verlag, New York.
- Smith, T.R. 1991. Effects of hydrology and vegetation on the distribution and abundance of white-tailed deer and Florida panthers in Everglades National Park. Annual Report - FY 1991. South Florida Research Center, unpub. document, Homestead, Florida. 26 pp.
- Smith, T.R., J.F. Eisenberg, and M.E. Sunquist. 1989. Ecology of white-tailed deer in Everglades National Park (CA-5280-5-8004): Progress January 1987-January 1989. Report to Southeast Regional Office of National Park Service, Atlanta.
- Smith, T.R., J.F. Eisenberg, and M.E. Sunquist. 1990. Ecology of the white-tailed deer in Everglades National Park. National Fish and Wildlife Foundation Project No 89-68 Final Report.
- Smith, T.R., J.F. Eisenberg, and M.E. Sunquist. 1990. Ecology of white-tailed deer in Everglades National Park (CA-5280-5-8004): Progress February 1989-January 1990. Report to Southeast Regional Office of National Park Service, Atlanta.

- U.S. Fish and Wildlife Service. 1987. Florida panther (*Felis concolor coryi*) recovery plan. Prepared by the Florida Panther Interagency Committee. Atlanta. 75 pp.
- Wade, D., J. Ewel, and R. Hofstetter. 1980. Fire in south Florida ecosystems. U.S. Dept. Agr., Forest Service General Technical Report SE-17.
- Wemmer, C. (ed.). 1987. Biology and Management of the Cervidae. Washington. D.C., Smithsonian Inst. Press.
- Zultowsky, J.M. 1992. Behavioral and spatial ecology of female white-tailed deer in the Everglades ecosystem. M.Sc. thesis, University of Florida, Gainesville. 81 pp.

Appendix IV

ECOLOGY OF WHITE-TAILED DEER
IN EASTERN EVERGLADES NATIONAL PARK
(CA-5280-5-8004)

INTERIM REPORT No. 1
to the National Park Service

Progress: January 1987-January 1989

Tommy R. Smith, Field Coordinator
John F. Eisenberg, Principal Investigator
Melvin E. Sunquist, Co-Principal Investigator

Florida Museum of Natural History
University of Florida
Gainesville, FL 32611

INTRODUCTION

The range of mountain lions (Felis concolor) in North America is strongly tied to the distribution of deer (Dixon 1982). In the western United States (Robinette et al. 1959, Hornocker 1970) and Canada (Spalding and Lesowski 1971), mountain lions prey primarily on mule deer (Odocoileus hemionus). Before they disappeared from eastern North America, mountain lions apparently relied heavily on white-tailed deer (O. virginianus) as a food source (Dixon 1982). White-tailed deer are reported to be important prey of mountain lions in Mexico and Central America (Mendez 1984) and South America (Brooks 1984) as well.

Given this information, it is reasonable to assume that the distribution and abundance of the Florida panther (F. c. coryi) is related to that of white-tailed deer. Indeed, preliminary reconnaissance in south Florida indicates that white-tailed deer are commonly taken by Florida panthers (McBride 1985, Belden and Maehr 1986), but the extent to which populations of the 2 species interact is unknown.

Although Everglades National Park (ENP) and Big Cypress National Preserve (BCNP) provide habitat for most of the present population of Florida panthers, there is much concern over the availability of an adequate prey base in these protected areas and whether active habitat management is necessary, or appropriate, to increase the carrying capacity for deer. Information on density, natality, and mortality of deer populations on these lands is vital for orderly recovery of the Florida panther. Recognizing this, the National Park Service (NPS) has chosen to support population studies of white-tailed deer in conjunction with those of Florida panthers in ENP and BCNP.

In September 1986 the NPS and the Florida Museum of Natural History, University of Florida signed an agreement to cooperatively investigate the population dynamics and habitat utilization of white-tailed deer in the Long Pine Key/Hole-in-the-Donut area (study area) in the eastern portion of ENP. In this report we present a comprehensive summary of activities and findings during the first 2 years of that study; 19 January 1987, when fieldwork began, through January 1989.

OBJECTIVES

The primary objectives of the study are:

- 1) To estimate the demographic characteristics of the population, including absolute size and density, age structure, and age-specific sex ratios.
- 2) To estimate recruitment and mortality in the population and relate these to predation, habitat utilization, and age and physical condition of deer.
- 3) To delineate important aspects of the reproductive biology of deer in the study area, including the chronology of breeding and fawning, litter size, and sex ratio at birth.
- 4) To determine seasonal patterns of movements and activities of deer in relation to habitat types, environmental conditions, and, where possible, to predation.

PRELIMINARY RESULTS

Methodology

In essence, the project began as a pilot study. Attainment of the proposed study objectives hinged on identification of a safe, efficient capture technique that would allow us to obtain a large sample of

radio-tagged deer. In turn, radio-telemetry methods to monitor the movements, activities, and behaviors of radio-tagged deer would have to be adapted to conditions in the study area.

Capture Techniques. Because few signs of deer activity were found in slash pine (Pinus elliotti var. densa) and Brazilian pepper (Schinus terebinthifolius) communities during reconnaissance in January and February 1987, it appeared that the density of deer in the study area was low. Furthermore, there was no activity at 8 bait sites monitored throughout February, and we concluded that conventional box-trap and cannon-net techniques would not be productive. We also obtained a dart rifle during this period and spent several days at White Oak Plantation in north Florida to practice the technique and test drug dosages on semi-wild deer. In March 1987 we began spotlighting along roads in the study area, but after 12 nights, only 1 deer had been captured, and it appeared highly unlikely that a large sample of deer could be obtained with this technique.

We had found during this time, however, that deer were commonly observed from aircraft and could be easily intercepted by helicopter in open prairies surrounding the pine and Schinus forests. Use of the netgun-helicopter technique, which was relatively new but had been successful in open habitats in western United States and Australia, surfaced as a distinct possibility. We solicited the help of an experienced netgunner, Dr. Bart O'Gara, and during a 4-day period in early April 1987, 19 deer were captured. Within 2 months we had acquired a netgun for the project, and since, 61 additional captures have been made (Table 1). Major advantages of the technique include:

- 1) A large number of deer can be captured in a few days at an average cost of approximately \$200-250 per capture, i.e., 0.5 helicopter hours per capture.
- 2) Captures and, hence, composition of the radio-tagged sample can be selected by age, sex, and reproductive condition.
- 3) Deer with problematic or aged radio-collars can be captured at almost any time, and the probability of losing contact with study animals due to failure of radio-transmitters is minimal. This allows extended monitoring of known-age study animals.
- 4) The risk of capture-related injury or mortality is low. Two deer have been killed during capture operations, and 2 others deaths may have been capture-related. This gives a maximum capture mortality rate of 5 percent, which is very low among studies of white-tailed deer. Helicopter chases generally last ≤ 3 minutes and do not appear to cause dangerous physiological stress to deer based on their temperature, heart rate, and respiration. Chemical immobilization is not necessary, and deer are released alert within 30 minutes of capture.

Radio-telemetry Techniques. During the first 3 months of the project, we spent considerable time testing equipment and techniques for obtaining ground-telemetry observations. Although we anticipated doing most of our telemetry from aircraft, our sampling design called for circadian stratification of data on movements, activities, and habitat use, and observations during darkness could only be made from the ground. We placed 'test collars' at various locations in the study area and evaluated the effects of vegetation and antenna placement (i.e., height) on the

Table 1. Captures of white-tailed deer by age-sex class in the Long Pine Key/Hole-in-the-Donut area of Everglades National Park, March 1987-January 1989.

	<u>Adult</u>		<u>Yearling</u>		<u>Fawn</u>		<u>Total</u> ^{1/}
	M	F	M	F	M	F	
Initial captures	13	24	2	3	11	11	64
Recaptures	<u>4</u>	<u>3</u>	<u>1</u>	<u>6</u>	<u>1</u>	<u>1</u>	<u>16</u>
Total	17	27	3	9	12	12	80

^{1/} 1 capture by dart gun; all others by netgun

range and quality of radio-signals received from fixed and mobile ground-to-ground receiving stations. To summarize, we found that:

- 1) Radio signals could be received as far as 12 km from the transmitter, but those received ≥ 6 km away were rarely usable, and to maintain precision, a distance of ≤ 4 km between transmitter and receiver was desirable.
- 2) When either the transmitter or receiver was located in dense cover, e.g., pine or Schinus, signal strength was noticeably reduced, and error in locations was high.
- 3) Elevating receiving antennas to heights of 4-6 km (i.e., atop vehicles and buildings) markedly increased accuracy of locations, and marginally enhanced signal strength.

Lacking elevated structures but having relatively good road access in the study area, we focused on a mobile tracking system. A van was modified to house a 20-ft. telescoping mast that raised a cross boom and dual antennas 12 feet above the roof of the van. A 'null' receiving system was employed and has proven to be exceptionally accurate, giving locations with an average error polygon of about 1 ha. This is the size of cells to which aerial and ground telemetry locations are assigned following the Universal Transmercator (UTM) grid coordinate system.

Sampling Design. At the beginning of the study, when our radio-tagged sample included 15-20 deer, we generally radio-located each animal 3 or 4 times per week (2 or 3 aerial locations and 1 ground location). As the sample increased, the frequency of locations per animal was reduced, but the total number of locations per week was maintained or increased. The ratio of aerial to ground locations in the sample and stratification of

observations over time and by age-sex classes also was maintained. As of 31 January 1989, 7,695 telemetry observations had been made (Table 2). Each observation includes information on range, habitat use, and activity. In addition, aerial observations routinely provide data on social behaviors, fawning, and population structure. Since the initial netgun capture session, the number of deer in the radio-tagged sample has steadily increased toward our goal of 45 (10 adult males, 15 adult females, 10 yearlings, and 10 fawns) (Figure 1). In September 1988, when the sample size reached 42 and included 9 adult males, 17 adult females, 8 yearlings, and 8 fawns, we essentially had attained the number and age-sex composition of radio-tagged deer we had sought. We knew our study objectives were realistic at that point and that the feasibility phase of the project had passed. Given adequate funding and time, we would undoubtedly be able to unravel the story of white-tailed deer in the Everglades, including its relationship with the Florida panther.

Body Size and Growth. Fawns in our study area apparently weigh 2 to 3 kg at birth; 1 fawn estimated to be 7-10 days old weighed 4 kg, and another that was 2-3 weeks old weighed 5 kg. Birth weights of white-tailed deer reportedly range from 1.8 to 3.6 kg (Sauer 1984). Fawns grow rapidly and typically attain weights of 10 kg or more by 2-3 months of age and 20 kg by the end of their first year (Figure 2). The growth rate slows through the second year, and sexual dimorphism becomes distinct (Figure 3). Weights of yearling males in our sample averaged 33 kg compared to 25 kg for yearling females, however, weights of yearlings are related to the time of year (i.e., age in months) when they are captured; generally, at 2 years of age males approach 35 kg and

Table 2. Radio-telemetry observations of white-tailed deer in Everglades National Park, April 1987-January 1989.

Type	Number	Percent
Ground (night)	2262	29%
Aerial (day)	<u>5433</u>	71%
Total	7695	

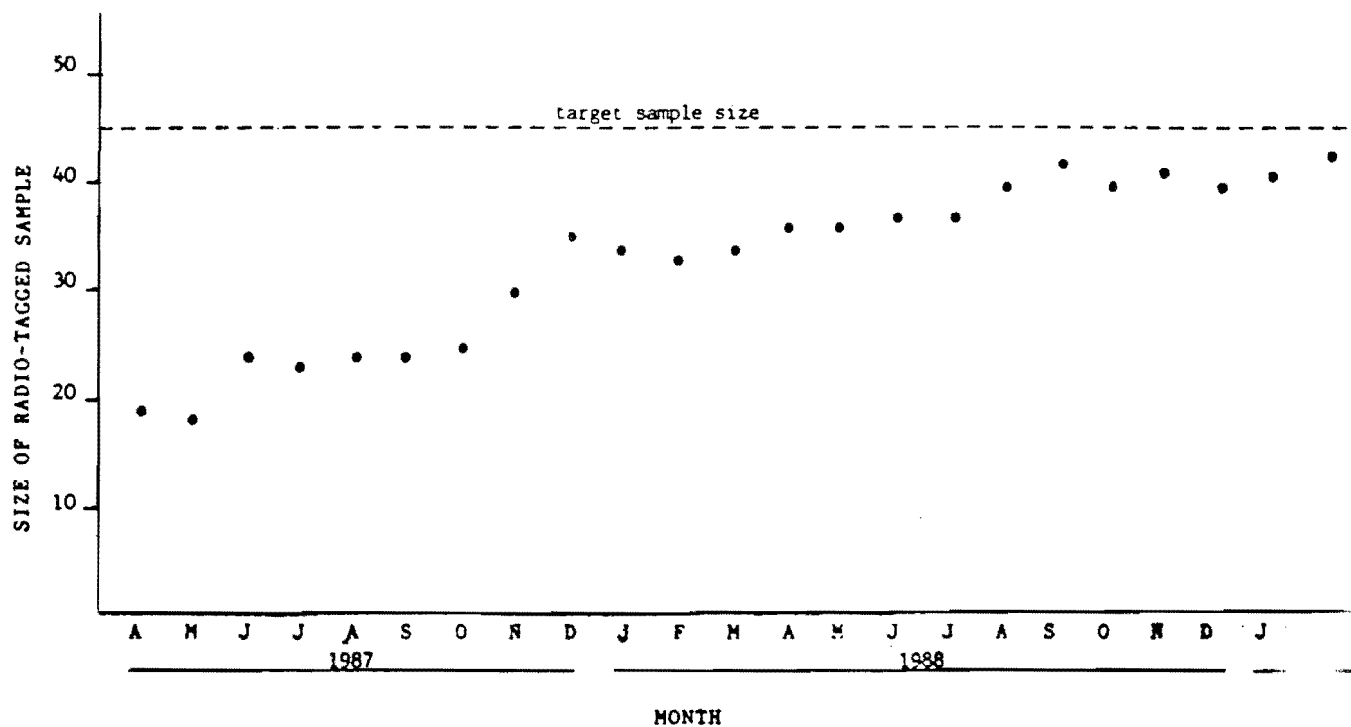


Figure 1. Size of radio-tagged sample of white-tailed deer in Everglades National Park, January 1987 - January 1989.

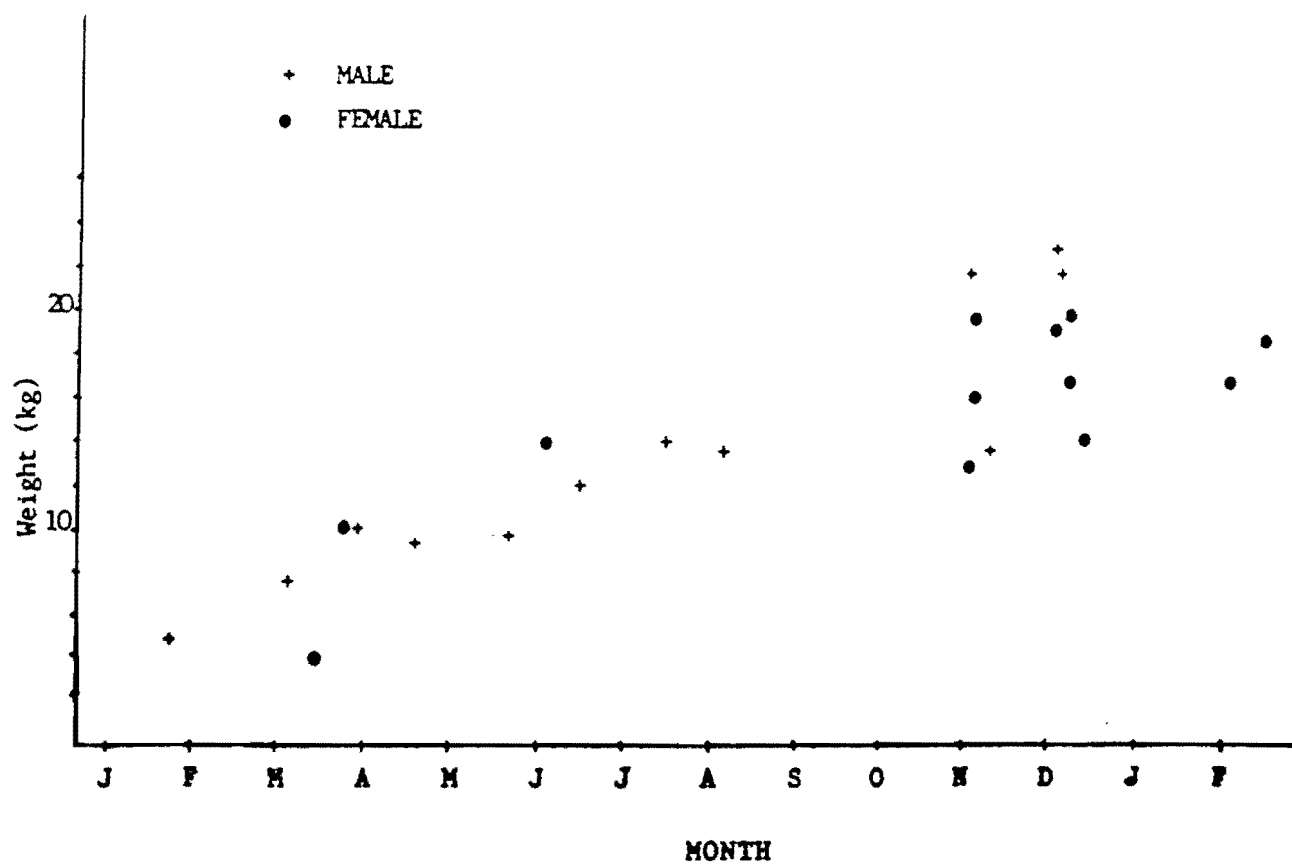


Figure 2. Weights of fawn white-tailed deer by month of capture, Everglades National Park, 1987-1989.

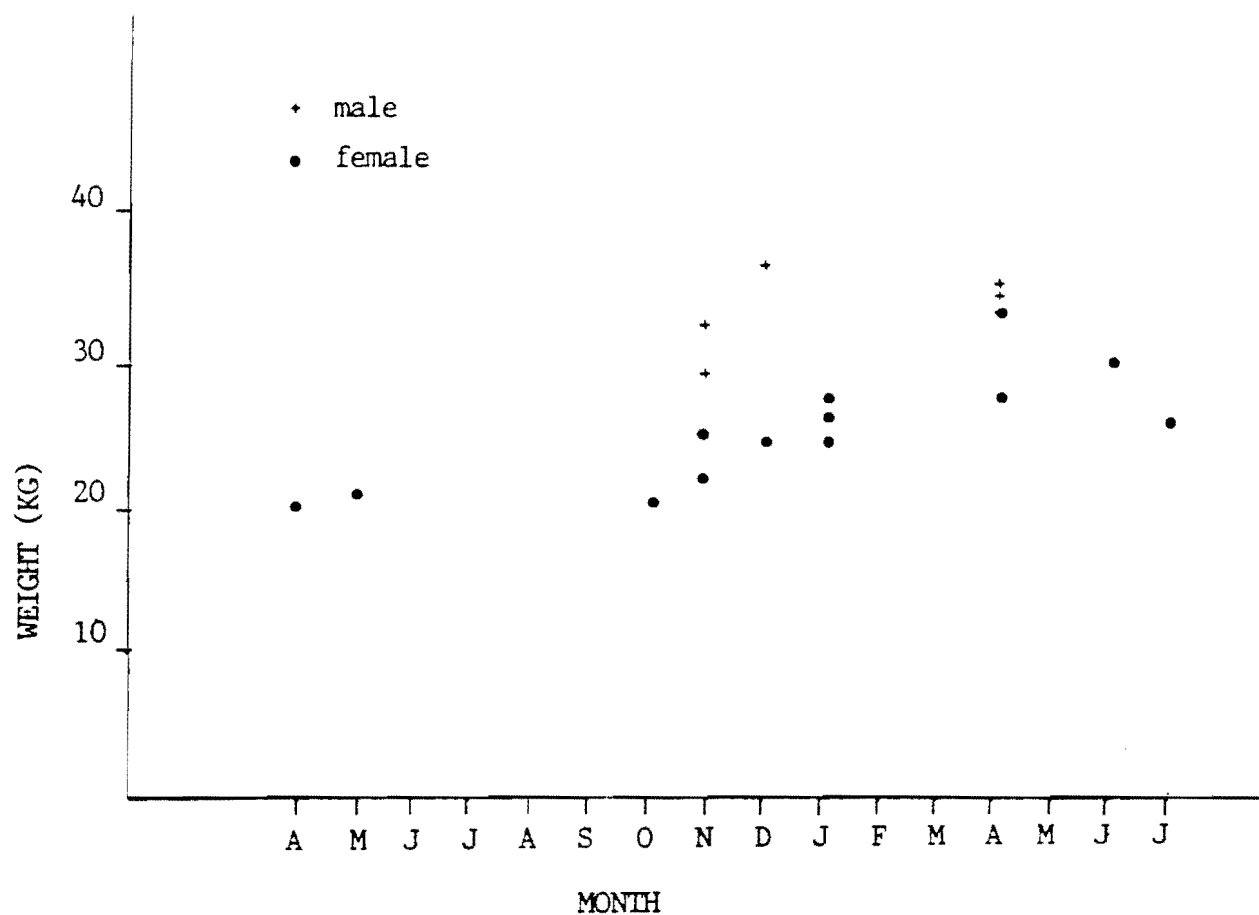


Figure 3. Weights of yearling white-tailed deer by month of capture in Everglades National Park, April 1987-January 1989.

females 30 kg.

Adult (≥ 2 years old) males in the sample average 41 kg and adult females 35 kg (Table 3). Growth apparently continues in both sexes through the third and, possibly, fourth year. White-tailed deer reportedly do not reach full body size until 4 or 5 years of age (Hesselton and Hesselton 1982), and we suspect that age may account for much of the variation in our sample of adult weights. Seasonal nutrition and reproductive condition also may explain much of the variation in weights of adult white-tailed deer (Sauer 1984). As our data base broadens to include larger numbers of observations by age, season, and reproductive condition, we will explore these questions in detail.

Loveless (1959) reported larger weights ($\bar{x} = 52$ kg, range = 42-66 kg) for adult males in the East Everglades north of our study area. Weights of adult females in various parts of BCNP averaged slightly more ($\bar{x} = 38$ kg, range = 31-41 kg) (McCown 1988) than those in our study area, but, unlike our data, were taken at the time when females should have been in their best condition (Sauer 1984)

Health. Physical condition of deer examined in the study area to date ($N = 89$) has been considered good or excellent. No cases of poor, emaciated condition or heavy ectoparasite burdens have been observed. Estimated tail fat of captured deer typically is negligible except for pregnant or heavily lactating females and males in velvet, which often exhibit moderate to heavy deposits of tail fat.

In 1988 our study area was provisionally included as a site in the on-going study of physical condition of deer in ENP and BCNP by the

Table 3. Physical characteristics of white-tailed deer in Everglades National Park, January 1987-January 1989.

Age-sex class	N	<u>Weight</u> (kg)		<u>Total Length</u> (cm)		<u>Girth</u> (cm)	
		Mean	Range	Mean	Range	Mean	Range
adult male	14	41	35-53	165	148-172	79	74-85
adult female	32	35	27-44	155	137-167	74	67-84
yearling male	3	33	30-37	150	144-155	74	71-78
yearling female	10	25	20-35	143	135-154	66	61-70

University of Florida and Florida Game and Freshwater Fish Commission. One yearling and 4 adult females were collected just outside the margin of our study area in late October. Three of the 5, including the yearling, were pregnant and preliminary data indicate that physical condition of deer in the area is generally comparable to that of deer in other areas of south Florida (S. Wright, pers. comm.).

Population Characteristics

Density. In January 1988 we began monthly censuses to gather data for estimating population size and density. Transects are flown at 1 km intervals across the 425 km² study area during early morning or late afternoon for 3 consecutive days (approximately 6 hrs. flight time). When deer are observed, we determine by telemetry if they are marked (i.e., radio-tagged). Petersen estimates are generated for each census based on the proportion of marked deer in the sample.

There is considerable variation among population estimates obtained thus far (Table 4), but much of the variation may be due to sampling error. Population estimates derived from mark-recapture/reobserve data inherently are positively biased, especially when the number of recaptures (or reobservations) is low (Tanner 1978). We have found that 52 percent of the variation in our estimates is explained by the number of reobservations in the sample (Figure 4). Noticeably high estimates are associated with relatively low numbers (e.g., 1-3) of reobservations. At this point, we believe that the estimates obtained when the number of reobservations was > 4 (i.e., approximately 110-160 deer or 0.25 - 0.4 deer per km²) probably are most representative of actual numbers in the population, but much more data are needed to

Table 4. Preliminary estimates of population size and density of white-tailed deer in the Long Pine Key/Hole-in-the-Domut area of eastern Everglades National Park, January 1988-January 1989.

Month	Number Observed	Number Marked <u>1/</u>	Population Estimate	Density Estimate (deer/km ²)
Jan	28	8	113	0.27
Feb	46	10	145	0.34
Mar	13	1	238	0.56
Apr	34	3	315	0.74
May	30	6	159	0.37
Jul	23	4	182	0.43
Oct	34	2	490	1.15
Nov	30	10	121	0.28
Dec	19	2	273	0.64
Jan	32	4	271	0.64

1/ Radio-tagged

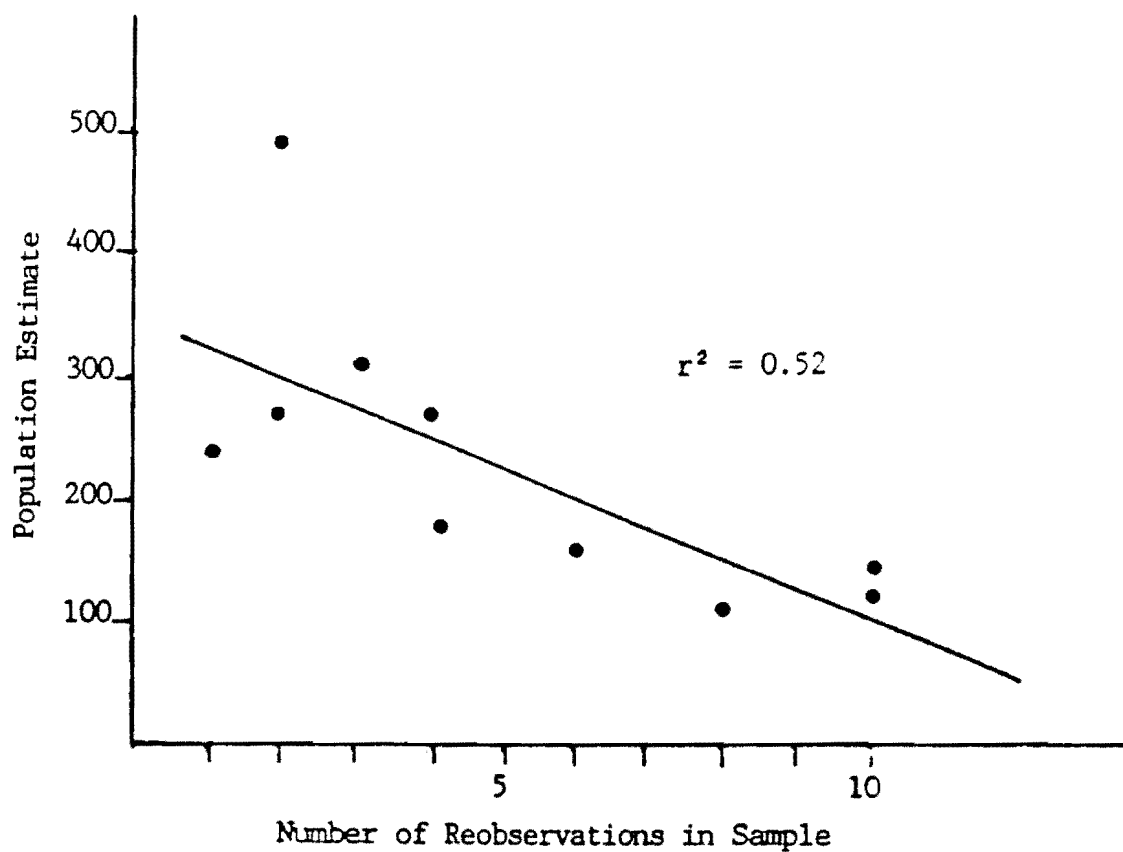


Figure 4. Relationship between population estimates and number of marked deer (reobservations) in census samples, Everglades National Park, January 1988 - January 1989.

determine the degree to which technical, as well as biological biases, e.g., seasonal habitat use and conditions, affect population estimates.

Despite the variation in our estimates, it appears that the density of deer in the study area is markedly low compared to those reported for white-tailed deer elsewhere in its range and relatively low for south Florida. Based on aerial counts, Loveless (1959) estimated a density of 2.2 deer per km² in the eastern portion of the Shark River Slough approximately 50 km north of our study area. Densities of 0.5 deer per km² and 4 deer per km² were derived from track counts in 2 areas of BCNP (McCown 1988). Elsewhere in the species range densities of 3 to 15 deer per km² are common (Teer 1984).

Sex Ratio. Data on sex ratio are obtained from captures, observations during aerial censuses, and fetuses in collected and road-killed deer. Sex ratios of deer ≥ 1 year old in both the random capture sample (when males are not antlered) and aerial observations (when males are antlered) are biased toward females (Table 5). Telemetry data indicate, however, that males typically utilize denser cover than females, especially during the antlerless period, and they may have a low probability of being observed during capture and census operations. In the breeding (antlered) season, males frequently associate with females in open habitats, and the bias from sex-specific habitat use likely is less. Although yearling males with small spiked antlers may occasionally be counted as antlerless (i.e., as female), we believe this bias is negligible and that the sex ratio estimated from census data (1 male:2 females) approximates that of deer ≥ 1 year old in the population.

Table 5. Observed sex ratios of white-tailed deer in Everglades National Park, January 1987 - January 1989.

Age class	Source of data	Sample size	Male:Female ratio
≥ 1 year	capture	22	1:3.4
≥ 1 year	aerial census	77	1:2.1
≤ 1 year	captures and fetuses	29	1:0.9

In contrast, the sex ratio of fawns in our sample approximates unity (Table 5). There is a marked difference, however, between the sex ratios of young and old fawns. Of 14 young (≤ 4 months old) fawns and fetuses handled, 11 were males, whereas among older (≥ 6 months old) fawns in our sample, females predominate 2 to 1, like they do among older deer.

Across the species' range, fawn sex ratios typically are skewed toward males (Verme and Ullrey 1984), and a variety of factors have been shown to affect sex ratios in progeny, including the nutritional state of females at breeding, litter size, and maternal age (Verme 1983), the timing of breeding (Verme and Ozaga 1981), and population density (McCullough 1979). Our sample sizes are too small at this point to draw conclusions regarding sex ratios at conception and sex-specific fawn mortality in the study area. Knowledge of these parameters is vital, however, to developing a model of the population dynamics of deer in ENP. Given the current depth of our radio-tagged sample, we should have adequate data to address these questions by summer 1990.

Age Structure. Deer that we examine are assigned to fawn, yearling, or adult age classes based on patterns of tooth eruption and wear (Severinghaus 1949). Ages of fawns may be further delineated to week or, when older, to month based on eruption patterns. Yearlings and very young 2-year-olds are readily aged based on the condition of their third lower premolar. Often adults are classified as young or old when toothwear is noticeably light or heavy, respectively. Otherwise, we do not believe that adults ≥ 2.5 years old can be reliably assigned to year classes based on toothwear (Gilbert and Stolt 1970), particularly

Table 6. Observed sex ratios of fawn white-tailed deer in Everglades National Park, January 1987 - January 1989.

Age	Source of data	Sample size	Male:Female ratio
<u><</u> 6 months	captures and fetuses	17	1:0.5
<u>></u> 6 months	captures	12	1:2.0

lacking known-age samples from the area.

White-tailed deer may be accurately aged to year classes by the cementum annuli method (Gilbert 1966), but because we do not extract teeth from live-captures, this technique has little immediate application in our study. In the long term, however, it should be useful, especially to age panther kills, and we are extracting teeth from all recovered study animals, road kills, and deer collected in studies of condition. These samples are sent to Matson's Lab in Montana for processing, and to date we have learned that: 1) the first lower premolar appears to provide more accurate and precise estimates of age than incisors, which typically are used, and 2) deer may reach considerable age in ENP; among 13 specimens aged at Matson's, 3 were yearlings, 7 were between 2 and 5 years of age, and 3 were between 9 and 14 years of age. We also have noticed advanced toothwear in several deer in the capture sample. Such representation of older age classes may be indicative of a relatively stable age structure in the Everglades population.

Currently (March 1989) our radio-tagged sample consists of 22 known-age deer, including 2 fawns, 9 yearlings, 6 2-year-olds, 2 3-year-olds, and 3 4-year-olds. If the study continues, many of these animals should be recovered to provide an unprecedented series of known-age specimens for determining the relationships between age, toothwear, and cementum annuli in white-tailed deer in the Everglades. Such information would have lasting value for management and research of both white-tailed deer and Florida panther populations in south Florida.

Reproduction

Chronology of Breeding and Fawning. Antler growth in males, which signals increased testosterone production and preparation for breeding (Verme and Ullrey 1984), apparently begins in March or April in the study area and is complete by early June. All antlered males observed between 14 March and 3 June ($N = 7$) have been in velvet, and all of those observed between 28 June and 16 December ($N = 17$) have had polished antlers. Males apparently lose their antlers in December or January and are antlerless for about 2 months.

Breeding activity may begin as early as June and extend to November, but based on telemetry data, the rut apparently peaks in August, September, and October. Of 22 observations of radio-tagged females accompanied by a radio-tagged male ($N = 11$) or an unmarked antlered male ($N = 11$), 1 occurred in mid-June, 2 in July, 5 in August, 6 in September, 6 in October, and 2 in early November. Crown-rump lengths and weights of 5 fetuses recovered during the study indicate a somewhat earlier peak in breeding; 3 estimated conception dates fell between the last week of July and first week of August, 1 in early September, and 1 in mid-October. Criteria for these estimates were developed from deer north of Florida, however and, because of the substantial geographic variation in body size in white-tailed deer, may not be applicable to our area. If anything, the bias would be toward earlier conception dates due to the relatively small size of deer in south Florida.

The fawning period also may span 4 to 5 months, but most births apparently occur in February, March, and April. In 1987, 12 of 13 (92%) adult females had dropped their fawns by mid-April; the fetus of a

road-killed female was due to be born in early May. More specific information from 1988 indicated that 4 of 11 (36%) females had their fawns in January or February, 4 in March, and 3 in April. One radio-tagged female dropped a fawn during the second week of January this year (1989).

We have found it difficult to determine fawning dates and obtain data on breeding activity, but our preliminary observations clearly indicate that the reproductive cycle of deer in the Everglades is synchronized with seasonal fluctuations in rainfall, i.e., wet and dry seasons. Fawning is restricted to the latter half of the dry season and probably is strongly related to phenological development and the availability of nutritious food. The threats of heavy rainfall and high surface water to fawns also are minimal at that time, but these factors likely play a less important role than nutrition in determining the synchrony of reproduction.

In 1988 we increased the frequency of telemetry observations on adult females in an effort to estimate fawning dates based on movement patterns. This technique appears to be useful, and we are again closely monitoring the movements of adult females during the 1989 fawning season.

Productivity. The estimated overall pregnancy rate among females ≥ 1.5 years old from 1987 to 1989 is 78 percent (Table 7). The rates for 1987 and 1988 were based on examinations of live-captured females and aerial observations of radio-tagged females. Because prenatal mortality in white-tailed deer typically averages about 10 percent (Barron and Harwell 1973, Hesselton and Jackson 1974), these estimates may be low. However, the estimate for 1989, which is lower, was based on the occurrence of fetuses in females recovered in fall 1988. Hence,

Table 7. Pregnancy rates of white-tailed deer in Everglades National Park, 1987-1989.

Year	Sample size	<u>Pregnant or with fawn</u>	
		Number	Percent
1987	18 ^{<u>1/</u>}	14	78%
1988	15 ^{<u>2/</u>}	12	80%
1989	7 ^{<u>3/</u>}	5	71%
	<u>40</u>	<u>31</u>	<u>78%</u>

1/ live-captured, road-killed, and radio-tagged females $\geq$ 2 years old

2/ radio-tagged females $\geq$ 2 years old

3/ females $\geq$ 1.5 years old recovered in Oct-Nov 1988

Table 11. Age-specific rates of mortality among radio-tagged white-tailed deer in eastern Everglades National Park, March 1987-April 1990.

Age	MALE				FEMALE			
	N	# deer years	# deaths	rate	N	# deer years	# deaths	rate
fawn	21	6.9	5	73%	13	4.6	0	0%
yearling	13	7.7	2	26%	14	10.5	4	38%
adult	20	24.8	5	20%	29	53.3	8	15%

white-tailed deer in the Florida keys (Hardin 1974), BCNP (McCown 1988), Rotenberger Wildlife Management Area (Richter and Labisky 1985) and elsewhere in south Florida (Harlow and Jones 1965) commonly produce twins, indicating that habitat quality and/or population turnover (i.e., r-selection) probably are greater in these areas than in the east Everglades.

Mortality

Fawn Mortality. Estimated rates of fawn mortality in 1987 and 1988 are 66% and 36%, respectively (Table 8). This marked difference between years may be partially explained by sampling bias. In 1987 we estimated the number of females that had fawns from observed pregnancy in live-captured individuals as well as from aerial observations of fawns with radio-tagged females. Three of the 12 females that were pregnant when captured that year were not subsequently seen with fawns. In contrast, the estimate for 1988 was based only on aerial observations of fawns with radio-tagged females. We suspect that 2 of 3 females in the 1988 sample actually had fawns but lost them early. If so, and had we handled these females as we did in 1987, the estimate for 1988 would be 46%. Notwithstanding this potential bias, the difference in estimates of fawn mortality in 1987 and 1988 is not especially unusual, because fawn mortality is closely related to maternal nutrition (Ransom 1967, Verme and Ullrey 1984), which may vary considerably between years and by age (Verme and Ullrey 1984) and social rank (Ozaga et al. 1982).

Apparently most deaths among fawns in our study area occur shortly after parturition. Two of 7 (29%) fawns tagged between 17 March and 15 June 1988 died, 1 by predation and 1 apparently of starvation or exposure.

Table 8. Estimated mortality rates of white-tailed deer fawns in
Everglades National Park, 1987 - 1988.

Year	No. females that had fawns	No. Females that lost fawns	Estimated mortality rate
1987	12	8	66%
1988	11	4	36%
Total	23	12	Mean 52%

Conversely, all of 5 fawns tagged between 15 July and 10 November in 1988 and 8 fawns tagged between 3 November and 11 December 1987 survived to yearlings (Table 9). Apparently, two thirds or more of the deaths among fawns may occur within a month or 2 of parturition.

It is likely that rainfall and water levels (ground and surface) are indirectly related to fawn mortality in the study area by the effects of primary productivity and phenological development on maternal nutrition. There have been no severe storms or unusually high water conditions in the area since we began, however, and we cannot speculate on the direct impacts of these conditions on fawn survival.

We also do not have adequate data at this time to determine the effects of maternal age and social structure on fawn survival, because of the lack of known-age deer ≥ 1 year old in our radio-tagged sample. Its complexion has changed however; in 1987 13 females ≥ 3 years old, 3 2-year-olds, and 2 yearlings were tagged; in 1988 the sample included 12 females ≥ 4 years old, 3 3-year-olds, 3 2-year-olds, and 4 yearlings; in 1989, we will be monitoring 12 females ≥ 5 years old, 3 4-year-olds, 3 3-year-olds, 4 2-year-olds, and 4 yearlings. Finally, we are in a position to determine the independent effects of environmental conditions, age (of mothers), and social organization on fawn survival, but data on these individuals must be obtained in 1989 and 1990 to do so. Such information is essential for modeling the dynamics of the Everglades deer population.

Mortality of Yearlings and Adults. The annual mortality rate of radio-tagged deer ≥ 1 year old between April 1987 and January 1989 is 18 percent (Table 10). Mortality rates of adults are based on relatively large sample sizes (i.e, numbers of deer years) and probably are representative

Table 9. Observed mortality rates of radio-tagged white-tailed deer fawns by age in Everglades National Park, 1987 and 1988.

Age	Number radio-tagged	Number of deaths	Mortality rate
$\leq$ 4 months old	7	2 $\frac{1}{1}$	29%
$\geq$ 5 months old	13	0	0%

$\frac{1}{1}$ 1 by a Florida panther

Table 10. Annual mortality rates of radio-collared white-tailed deer by age-sex class in Everglades National Park, April 1987 - January 1989.

Age-sex class	N	No. deer years	No. deaths	Mortality rate
adult male	12	14.5	2	14%
adult female	23	27.9	4	14%
yearling male	3	1.8	1	56%
yearling female	8	6.8	2	29%
all deer $\geq$ 1 year old	46	51.0	9 ^{1/}	18%

^{1/} 6 (67%) of these were killed by radio-tagged Florida panthers

of the population. Those for yearlings, particularly males, are drawn from small sample sizes, however, and are tentative at best. Five male and 4 female fawns radio-tagged in 1988 presently are being monitored, and our sample size (i.e, knowledge) of survival among yearlings will double if monitoring is continued through fiscal 1990.

Other than young (e.g., ≤ 2 months old) fawns, the overall rate of mortality in the Everglades deer population appears to be low. Most of the observed mortality has been from predation; 6 of 9 radio-tagged deer ≥ 1 year old and 1 of 2 fawns were killed by radio-tagged Florida panthers. The cats appear to randomly sample the population; the 6 panther kills include 1 adult male, 3 adult females, 1 yearling male, and 1 yearling female. Four radio-tagged panthers have taken a radio-tagged deer. Additional mortalities include: 1) an adult male that was killed by a hunter on state-owned land adjacent to the eastern border of ENP in late December 1988 - (Although a case could not be made, it is very likely that this deer was killed illegally from a fixed-wing aircraft), 2) an adult female that died of an undetermined but apparently natural cause, 3) a yearling female that starved due to a digestive/dehydration problem that remains unsolved, and 4) a 3-4-month-old fawn that apparently died from starvation or exposure.

Estimates of mortality in un hunted, open white-tailed deer populations are not available for comparison, largely because such populations are rare. Loveless (1959) noted that substantial numbers of Everglades deer died from starvation, malnutrition, or disease during unusually wet years, but otherwise, natural mortality rates appeared to be low.

Movements and Activities

We have not initiated formal analyses of data on movements and activities at this time. Because our objective is to determine the effects of season, environmental conditions, age, sex, reproductive behaviors, and predation on patterns of movement and activity, it would be premature to analyze preliminary data that cannot be adequately partitioned by each of these variables. Furthermore, we lag behind in our data entry chores, largely because of the demands of fieldwork (i.e., data collection). Nonetheless, our experimental design is being closely followed, and we are progressively building a very formidable data set. Approximately 8,000 telemetry observations have been made that include the position (i.e., 1 ha cell), and activity (i.e., active or inactive) of the animal. Great care has been taken to insure that the 160-180 observations made during each 2-week (lunar) sampling period are stratified by age and sex over time (24-hour period).

Home Range. To augment oral presentations as well as this report on progress in the study, we have hand-calculated annual and seasonal home ranges for a few representative deer in our radio-tagged sample (Table 11). These data clearly indicate that: 1) there is much variation in home range size among both adult males and adult females, and 2) adult males utilize distinctly larger ranges than adult females.

Among males, age may partially explain the observed variation; early indication is that younger males utilize smaller areas than older males, but additional data are needed to verify this. Among females, the composition of various habitat (i.e., vegetative) components in the home range and social organization (i.e., hierarchical complexity and

Table 11. Annual home range sizes of adult white-tailed deer in Everglades National Park, April 1987–October 1988.

Sex	N	<u>Annual Home Range (km²) ^{1/}</u>	
		Mean	Range
Male	9	21	9 - 34
Female	6	8	4 - 14

^{1/} calculated by the convex polygon or minimum area method

status) may be 2 important factors related to range size, and we will focus on these parameters in the early stages of our home range analyses.

Home range sizes in the wet and dry seasons appear to be distinctly different among males but not among females (Table 12). Preliminary observations indicate, however, that reproductive behaviors, rather than water levels or food availability, are most directly related to the sizes of seasonal ranges. Increased movements by both adult males and adult females have occurred during the breeding period (June-November), but both sexes remain relatively sedentary between January and April, when males are antlerless or in velvet and females drop fawns. On the average, males utilize 84 percent of their annual ranges during the wet, breeding season compared to 52 percent in the dry, non-breeding season. Females, on the other hand, use their annual ranges with equal intensity in the wet, breeding ($\bar{x} = 75\%$) and the dry, non-breeding ($\bar{x} = 76\%$) seasons.

We have relatively few data on home ranges of yearlings. Females typically travel with their mothers or within their mother's ranges through their second year, and the range sizes of yearling females should closely approximate those of adult females. Between March 1988, when he dispersed from his natal range, and now (January 1989) one yearling male ranged over an area of about 30 km². Another yearling male has utilized a smaller area of 12.5 km² since he dispersed in June 1988. It appears that fawns begin to follow their mothers, at least on a limited basis, at about 2 months of age and are almost always located with their mothers from the time they are 4 months old until the following fawning season.

Although home ranges of white-tailed deer tend to be large in relatively open habitats (Marchinton and Hirth 1984), such as the Everglades,

dispersal behavior by a female (Marchinton and Hirth 1984). If the study is extended and we monitor movements of the 5 male and 4 female fawns presently radio-tagged, we will more than double our information on dispersal.

Habitat Utilization

Similar to the case of movement and activity data, habitat analyses have not been initiated because the data set is not complete yet, and we are behind on data entry. We also face the task of developing and coding a habitat (vegetation) map for the study area from which data for our utilization-availability analysis (Byers et al. 1984) will be extracted. Hopefully, the Geographic Information System (GIS) at ENP will be available soon to relieve us of this chore and provide more accurate and current habitat data for the study area than are presently available. All of our telemetry observations are coded by UTM coordinates which will allow merger of telemetry data files and GIS (habitat) files.

Although we have obtained considerable data on habitat use by adult ($\geq$ 3 year old) males and females, data on yearlings and 2-year-olds are sparse. To reiterate, however, given the current composition of our radio-tagged sample, adequate data for these age classes could be in hand by summer 1990 if the study is extended.

Despite the lack of analytical results, several general patterns of habitat use have been identified during fieldwork that we believe will prove true. These include:

- 1) Males exhibit an affinity to heavy cover; e.g., pinelands, prairies with dense shrub cover, and hardwood hammocks, whereas females tend to occupy more open habitats.

- 2) Deer captured in prairies adjacent to the closed Brazilian pepper forest in the Hole-in-the-Donut seldom use this vegetative community. If they do, it is usually in or at the edge of small openings of natural vegetation within the Schinus.
- 3) During the 2 years of the study, water has not appeared to be a physical barrier to movements by deer, although it undoubtedly affects food availability.
- 4) Males utilize open habitats with greater frequency during the wet season than in the dry season, probably more to gain access to females than to obtain food or water.

Social Organization

Telemetry data and aerial observations indicate that females typically associate in matriarchal groups. The complexity and cohesiveness of these groups vary considerably within the radio-tagged sample and across the study area. At one extreme, we have a group of 8 individuals radio-tagged, including the matriarch, (presumably) her 4-year-old daughter (and her female fawn), her 2-year-old daughter, her yearling daughter, her male fawn, and (presumably) her sister or an older daughter (and her male fawn). All but 2 of these kinships are known, and there are strong theoretical arguments for the presumed relationships based on the levels of association between individuals in the group.

In another case, we have 2 radio-tagged females (a $\geq$ 5-year-old and [presumably] her 3-year-old daughter) that occasionally associate with 3 or 4 other females. We also have a radio-tagged female (with a radio-tagged male fawn) that occasionally associates with 3 or 4 other females. Several other radio-tagged females are members of groups

of 2 or 3 adult females. Conversely, 2 adult females in our sample have never been observed with another female during the 2 years of study, and 3 others rarely associate in groups. Several factors, including habitat quality, density of cover, and predation may be related to the observed variation in hierarchical organization among females, and we will explore these relationships in future analyses.

Outside the rut, males typically associate in bachelor groups of 2 or 3 individuals, but as many as 9 males have been observed together; at this time, they apparently completely dissociate with females. Limited observations indicate that during the rut adult males travel alone.

OUTLOOK FOR THE PROJECT

Two things are apparent from this report: first, the project has been very successful in its first 2 years; considerable data have been obtained on population structure, movements, range, and habitat utilization, and great progress has been made toward satisfying the objectives of the study. Secondly, however, several components of the data set are incomplete. In particular, information on survival, natality, and dispersal among young age classes is sparse.

Throughout the report, we have repeatedly pointed out that, by methodical, patient manipulation, the number of known-age deer in the radio-tagged sample has increased and currently is such that these age-specific data are at hand. In one more year of monitoring, we can double our data on the rates and causes of fawn mortality and the fecundity, mortality, and dispersal of yearlings and 2-year-olds, as well as the productivity and mortality of all deer > 2 years old.

Getting to this point has not happened by accident. Three months into the project, after learning how applicable the netgun capture technique was in the study area, we realized what tremendous potential there was for a comprehensive, in-depth study of the white-tailed deer population in ENP. Accordingly, we restated our objectives to go beyond the original expectations of the study; specifically, we proposed to obtain age-specific data on natality, mortality, movements, and habitat use, focusing on the young age classes in the population. We solicited and were granted support for this transformation by NPS, and Drs. W.B. Robertson and T.R. Smith developed work elements for the project that would extend fieldwork through fiscal 1990 with analysis and write-up in fiscal 1991.

Presently, it appears that these plans may not be realized, and if so, much of the potential productivity of the project will be lost. By investing approximately one-fourth ($\leq$ \$75,000) of the total amount of money already expended (approximately \$300,000), the NPS can double, or better, its return (i.e., the amount of data) from the project. More important than quantity, however, would be the quality (i.e., age-specific nature) of the data which is critical to a thorough understanding of the dynamics of the deer population in ENP.

Successful recovery and management of the endangered Florida panther will largely depend upon knowledge of the existing and potential prey base, particularly populations of white-tailed deer, across its range. We have the opportunity to acquire that knowledge in the east Everglades where perhaps 10-20 percent of the total extant population of Florida

occurs. We encourage the National Park Service to seriously consider our proposal to extend the project and seize that opportunity before it is lost.

LITERATURE CITED

- Barron, J.C., and W.F. Harwell. 1973. Fertilization rates of south Texas deer. *J. Wildl. Manage.* 37(2):179-182.
- Belden, R.C., and D.S. Maehr. 1986. Florida panther food habits. E-1-09 annual performance report. Florida Game and Fresh Water Fish Commission, Tallahassee, FL.
- Brokx, P.A. 1984. South America. Pages 525-546 in J.K. Halls, ed., White-tailed deer, ecology, and management. Stackpole Books, Harrisburg, PA.
- Byers, C.R., R.K. Steinhorst, and P.R. Krausman. 1984. Clasification of a technique for analysis of utilization-availability data. *J. Wildl. Manage.* 48:1050-1053.
- Dixon, K.R. 1982. Mountain Lion. Pages 711-727 in J.A. Chapman and G.A. Feldhamer, eds., Wild mammals of North America. Johns Hopkins Univ. Press, Baltimore, MD.
- Gilbert, F.F. 1966. Aging white-tailed deer by annuli in the cementum of the first incisor. *J. Wildl. Manage.* 30(1):200-202.
- _____, and S.L. Stolt. 1970. Variability in deer age determination. *J. Wildl. Manage.* 34:532-535.
- Halls, L.K. 1978. White-tailed deer. Pages 43-65 in J.L. Schmidt and D.L. Gilbert, eds., Big game of North America. Stackpole Books, Harrisburg, PA.

- Hardin, J.W. 1974. Behavior, socio-biology, and reproductive life history of the Florida Key deer, Odocoileus virginianus clavium. Ph.D. Thesis, Southern Illinois Univ., Carbondale. 243pp.
- Harlow, R.F., and F.K. Jones, Jr. eds. 1965. The white-tailed deer in Florida. Tech. Bull. 9. Tallahassee: Florida Game and Fresh Water Fish Commission. 240pp.
- Hesselton, W.T., and L.W. Jackson. 1974. Reproductive rates of white-tailed deer in New York State. N.Y. Fish and Game J. 21(2): 135-152.
- _____, and R.M. Hesselton. 1982. White-tailed deer. Pages 878-901 in J.A. Chapman and G.A. Feldhamer, eds., Wild mammals of North America. Johns Hopkins Univ. Press, Baltimore, MD.
- Hornocker, M.G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildl. Monogr. 21. 39pp.
- Loveless, C.M. 1959. The Everglades deer herd: life history and management. Tech. Bull. 5. Tallahassee: Florida Game and Fresh Water Fish Commission. 104pp.
- Marchinton, R.L., and D.H. Hirth. 1984. Behavior. Pages 129-168 in L.K. Halls, ed., White-tailed deer, ecology, and management. Stackpole Books, Harrisburg, PA.
- McBride, R.T. 1985. Population status of the Florida panther in Everglades National Park and Big Cypress National Preserve. Contract No. RFP 5280-84-04. USDI National Park Service, Everglades National Park, Homestead, FL. 59pp.
- McCown, J.W. 1988. Annual performance report, Big Cypress deer/panther relationships: deer herd health and reproduction. Study No. E-1-12,

- 7505a, Florida Game and Fresh Water Fish Commission, Tallahassee, FL. 56pp.
- McCullough, D.R. 1979. The George Reserve deer herd: population ecology of a K-selected species. Univ. Michigan Press, Ann Arbor. 271pp.
- Mendez, E. 1984. Mexico and Central America. Pages 513-524 in J.K. Halls, ed., White-tailed deer, ecology, and management. Stackpole Books, Harrisburg, PA.
- Mundinger, J.G. 1981. White-tailed deer reproductive biology in the Swan Valley, Montana. J. Wildl. Manage. 45(1):132-139.
- Ozaga, J.J., L.J. Verme, and C.S. Bienz. 1982. Parturition behavior and territoriality in white-tailed deer: impact on neonatal mortality. J. Wildl. Manage. 46(1):1-11.
- Ransom, A.B. 1967. Reproductive biology of white-tailed deer in Manitoba. J. Wildl. Manage. 31(1):114-123.
- Richter, A.R., and R.F. Labisky. 1985. Reproductive dynamics among disjunct white-tailed deer herds in Florida. J. Wildl. Manage. 49(4):964-971.
- Robinette, W.L., J.S. Gashwiler, and O.W. Morris. 1959. Food habits of the cougar in Utah and Nevada. J. Wildl. Manage. 23:261-273.
- Roseberry, J.L., and W.D. Klimstra. 1970. Productivity of white-tailed deer on Crab Orchard National Wildlife Refuge. J. Wildl. Manage. 34(1):23-28.
- Sauer, P.R. 1984. Physical characteristics. Pages 73-90 in J.K. Halls, ed., White-tailed deer, ecology, and management. Stackpole Books, Harrisburg, PA.

- Severinghaus, C.A. 1949. Tooth development and wear as criteria of age in white-tailed deer. J. Wildl. Manage. 13(2):195-216.
- Spalding, D.J., and J. Lesowski. 1971. Winter food of the cougar in south-central British Columbia. J. Wildl. Manage. 35:378-381.
- Tanner, J.T. 1978. Guide to the study of animal populations. Univ. of Tennessee Press, Knoxville, TN. 186pp.
- Teer, J.G. 1984. Lessons from the Llano Basin, Texas. Pages 261-290 in J.K. Halls, ed., White-tailed deer, ecology, and management. Stackpole Books. Harrisburg, PA.
- Verme, L.J. 1965. Reproductive studies on penned white-tailed deer. J. Wildl. Manage. 29(1):74-79.
- _____. 1983. Sex ratio variation in Odocoileus: a critical review. J. Wildl. Manage. 47(3):573-582.
- _____, and J.J. Ozaga. 1981. Sex ratio of white-tailed deer and the estrous cycle. J. Wildl. Manage. 45(3):710-715.
- _____, and D.E. Ullrey. 1984. Physiology and nutrition. Pages 91-118 in J.K. Halls, ed., White-tailed deer, ecology, and management. Stackpole Books. Harrisburg, PA.

Appendix V

ECOLOGY OF WHITE-TAILED DEER
IN EASTERN EVERGLADES NATIONAL PARK
(CA-5280-5-8004)

INTERIM REPORT No. 2
to the National Park Service

Progress: February 1989-January 1990

Tommy R. Smith, Field Coordinator
John F. Eisenberg, Principal Investigator
Melvin E. Sunkist, Co-Principal Investigator

Florida Museum of Natural History
University of Florida
Gainesville, FL 32611

INTRODUCTION

This report summarizes activities and results of Cooperative Agreement CA-5280-5-8004, Ecology of White-tailed Deer in Everglades National Park, between the United States Department of the Interior, National Park Service (NPS) and the University of Florida for the period 1 February 1989 through 31 January 1990; data from the initial 2 years of study (Smith et al. 1989) are updated throughout. Our investigation is one of several concurrent, NPS-funded research efforts toward recovery of the endangered Florida panther (Felis concolor coryi). It was designed to obtain information on the population ecology of white-tailed deer (Odocoileus virginianus seminolus) in the Long Pine Key/Hole-in-the-Donut area of eastern Everglades National Park (EVER), with particular emphasis on interactions between deer and panther populations. Overall objectives of the study are:

1. To estimate the demographic characteristics of the population, including absolute size and density, age structure, and age-specific sex ratios.
2. To estimate recruitment and mortality in the population and relate these to predation, rainfall, habitat utilization, and age and physical condition of deer.
3. To delineate important aspects of the reproductive biology of deer in the study area, including the chronology of breeding and fawning, litter size, and sex ratio at birth.
4. To determine seasonal patterns of movement and activity by deer in relation to habitat types, environmental conditions, and where possible, to predation.

In June 1989, NPS extended the study into its fourth year (FY90) because: (1) continued monitoring of known-age, radio-tagged deer would considerably increase the return of age-specific data on natality, mortality, and dispersal, which are vital to realistic modeling of the dynamics of the deer population; and (2) following a wildfire that burned about half of the study area in May 1989, a rare opportunity existed to evaluate the effects of fire, a highly touted wildlife management technique that is applicable in national parks, on the population dynamics of deer in the Everglades.

4th year
Still not
thinking
ahead!

RESULTS

Capture Procedure

We have continued to rely exclusively on the netgun-helicopter capture technique. Because deer typically can be captured at will, we are able to control the age and sex structure of the radio-tagged sample and maintain contact with

Table 4. Physical characteristics of white-tailed deer captured in eastern Everglades National Park, 1 February 1989-31 January 1990.

Sex	Age	N	<u>WEIGHT^{1/}</u>		<u>TOTAL LGT.^{2/}</u>		<u>GIRTH</u>		<u>FOOT LGT.^{3/}</u>	
			Mean	Range	Mean	Range	Mean	Range	Mean	Range
M	≥2	5	49	38-61	174	167-181	83	75-92	45	45-47
F	≥2	23 ^{4/}	35	26-43	158	145-171	73	64-80	42	39-45
M	1	3	31	29-34	155	150-161	71	67-76	43	43-45
F	1	3 ^{5/}	27	26-30	147	143-153	66	62-71	41	41-42

1/ kilograms

2/ linear measurements in centimeters

3/ Hind foot length

4/ Includes 4 deer collected in health study.

5/ Includes 1 deer collected in health study.

Table 5. Estimated tail fat of white-tailed deer examined in eastern Everglades National Park between 1 February 1989 and 31 January 1990.

Sex/Reproductive Condition	N	Mean Fat-Index ^{1/}
Adult Male/Pre-Rut	2	5.0
Adult Male/Post-Rut	3	2.3
Adult Female/Early Pregnancy	5	3.0
Adult Female/Late Pregnancy	5	4.0
Adult Female/Lactating ^{2/}	12	1.3

1/ Based on a scale of 0 to 6: 0=none, 2=low, 4=medium, 6=heavy

2/ lactating or recently weaned a fawn

Very light burdens of ticks were observed on 4 (9%) of 44 deer examined in 1989; 3 in September and 1 in November. No captures were made in October, and possibly the prevalence of ticks was highest at that time. However, the lack of fresh lesions or scars from ticks on 12 other deer examined in November, indicated that these ectoparasites were not a threat to the health of deer in our study area during the past year.

For the second consecutive year, eastern EVER was included as a site in a study of health and diseases of white-tailed deer in EVER and BICY by D.J. Forrester, University of Florida. On 21 and 22 November, 6 females (5 adult and 1 yearling) were collected just outside the boundary of our core study area. The results of necropsy and laboratory analyses of that sample should be available by October 1990. Dr. Forrester's work in 1988 indicated that the condition of deer in eastern EVER was a close second to that of deer in the 'Stairsteps' area of EVER and BICY, among 7 sites sampled in south Florida (Forrester and Wright, 1989).

Population Characteristics

Density. Between February 1989 and January 1990, 6 aerial censuses of the study area were flown to generate mark/reobserve data for estimating population density (Table 6). Resulting estimates fall within the range of estimates from the first 2 years of our study. Also like those, they are inversely related ($r=-0.84$) to the number of reobservations (i.e., observations of radio-tagged animals) in individual samples, which lends support to our previous assumption that, typically, density estimates generated from samples when we had few (e.g., ≤ 3) reobservations were positively biased. Regardless of the lack of precision among estimates, it is clear that the density of white-tailed deer in eastern EVER is relatively low. At this time, we believe that a realistic estimate of density for the study area is approximately 0.5 deer/km² (i.e., 1 deer per 2 km² or 1.3 deer/mi²).

Age Structure. Delineation of the relationship between age of deer in the study area and patterns of dental eruption and wear progresses as we obtain specimens from known-age individuals. Patterns of eruption, which were described for white-tailed deer in the northern portion of the species range (Severinghaus 1949) and have become standard aging criteria, appear to be adequate for separating fawns, yearlings, and adults in our study area. An exception, however, is that replacement of the third lower premolar, which reportedly is complete by 20 months of age elsewhere in the species' range, appears to occur relatively late among deer in the Everglades.

Table 6. Density estimates of white-tailed deer (excluding fawns) in the Long Pine Key/Hole-in-the-Donut study area in Eastern Everglades National Park, February 1989-December 1990.

Dates	C ¹	R ²	M ³	N ⁴	Area sampled	D ⁵
26-28 Feb	20	5	41	147	425 km ²	0.35
30-31 Mar	17	1	41	378	425 km ²	0.89
27-28 Apr	17	2	41	252	425 km ²	0.59
8-11 Aug	32	5	35	198	425 km ²	0.47
11-13 Oct	47	3	33	408	525 km ²	0.78
12-14 Dec	31	2	37	405	425 km ²	0.95 ⁶

- 1/ number observed in census (i.e., sample size)
2/ number reobserved (i.e., number of radio-tagged deer in C)
3/ number of marked animals in the population
4/ population estimate for area censused
5/ density estimate - deer/km²
6/ estimate fawns of the 1989 cohort

Among our known-age sample of yearlings and 2-year-olds, replacement of the deciduous third lower premolar was in process in 6 (32%) individuals examined at 17, 19, 20, 22, 27, and 29 months of age; replacement had not begun in 12 (63%) individuals between 18 and 25 months of age and was complete in one 24-month-old. This observation helps clarify early confusion over the ages of a few study animals. For example, 2 females in our initial capture sample, whose third lower premolars were deciduous but whose body lengths and weights approached those of adult females, apparently were 2 years old, rather than yearlings as originally estimated. We also believe that what appeared to be anomalous or broken third lower premolars in a relatively small adult female, actually were erupting permanent teeth of a 2-year-old.

At present, we cannot use toothwear to assign ≥ 2 -year-old deer to year-specific age classes. Although toothwear often indicates if an individual is very young or very old, relationships between toothwear and age in samples available at this time are not consistent, and toothwear aging criteria commonly used across the species range, including south Florida, do not appear to be applicable for deer in the Everglades. Preliminary results of our analyses of cementum annuli in recovered teeth indicate that this technique may be the best available to us for estimating age in adults. We hope to eventually obtain an adequate sample of known-age specimens to describe relationships between toothwear and age in deer of south Florida.

Based on toothwear in deer captured early in the study, it was clear that old (e.g., >5 years old) animals were well-represented in the population. Assuming that sample was unbiased, we suspected that survival rates were high, at least among adult deer, and that the turnover rate in the population was low; both of these factors would lead to a relatively evenly distributed, stable age structure. Data that have since been obtained support our early suspicions. Given data from cementum analyses, age composition in samples of deer ≥ 1 year old that were: 1) collected by our study team (road kills, recovered radio-tagged deer, and deer collected in health studies (N=30), and 2) killed by radio-tagged Florida panthers (N=34) (O.L. Bass, pers. comm.), indicate that a substantial percentage of deer in the population attains an age of 6-10 years, or older (Figure 1); estimated ages of the oldest male and oldest female among these samples were 14 years and 19 years, respectively.

Sex Ratio. Data obtained to date indicate no significant deviation from parity in fetal sex ratio in the population.

Of 8 recovered fetuses that could be sexed, 3 were male and 5 were female (0.6:1 ratio); among 32 fawns randomly live-captured, 19 were male (1.5:1 ratio), giving an overall ratio of 1.2:1 (Table 7). Typically, fawn sex ratios in white-tailed deer are skewed toward males (e.g., Dapson et al. 1979, Dusek et al. 1989), and indeed, if we look only at our sample of live-captured fawns, there is indication that males may predominate early, and that among older fawns, the sex ratio approaches parity. At this time, we have no explanation for the inconsistency between observed sex ratios among fetuses and among live-captured fawns in our study area. Sample sizes are small, however, and hopefully additional data from the 1990 cohort will help clarify the matter.

Among deer ≥ 1 year old, females apparently outnumber males at least 2 to 1 in the eastern Everglades. During aerial censuses between August and December 1989, a male:female ratio of 1:2.2 was observed (Table 8). Data from the first 2 years of the study also indicated that adult females outnumbered adult males by approximately 2 to 1 (Smith et al. 1989).

Reproduction

Chronology. Preliminary data on reproductive synchrony of white-tailed deer in the study area were presented at the 5th International Theriological Congress in Rome, August 1989 (Smith 1989). Those results, as well as data collected since, indicate that reproductive behaviors of deer in the Everglades are synchronized with the annual cycle of rainfall, i.e., wet and dry seasons.

Adult males typically cast their antlers in January and remain antlerless for about 2 months. During the study, no antlered males have been observed between 20 January and 13 March; males that had cast one side of their antlers were observed on 10, 17, and 19 January. Antlerless males (N=13) were observed between 4 January and 14 April (Figure 2). Growth of new antlers commences in March or April, and velvet typically is shed by late May or early June. All males observed between 14 March and 3 June (N=16) have had velveted antlers; no hard antlers have been observed before 19 June. These data, as well as a number of random observations of unmarked males, indicate that the antler cycle may vary by a month or more between individuals or between years.

During the first 2 years of study, the frequency of association between radio-tagged adults and marked or unmarked adults of the opposite sex appeared to be a good indicator of

Table 7. Sex ratios in samples of white-tailed deer fetuses and fawns from eastern Everglades National Park, January 1987-January 1990.

Age	Males	Females	Male:Female Ratio
Fetus	3	5	0.6:1
<2 months	5	2	2.5:1
2-4 months	3	2	1.5:1
≥5 months	<u>11</u>	<u>9</u>	<u>1.2:1</u>
All	22	18	1.2:1

breeding activity; outside of the breeding period, adult males and adult females completely dissociated. This pattern of interaction between sexes was again observed in 1989. Pooling data for the 3 years, it appears that, although a limited amount of association and, possibly, breeding may occur as early as June or as late as November, 90 percent or more of breeding activity occurs between July and October, with a distinct peak in August-September (Figure 3).

Assuming a gestation period of approximately 200 days for white-tailed deer (Hesselton and Hesselton 1982), these data on the timing of breeding coincide with our observations on the fawning season (Figure 4). In 1987, 9 of 13 fawns (69%) in our sample were born by the first week of April, when we began capturing deer; 3 others were born in the second or third week of April, and the estimated birthdate of a roadkilled fetus was 7 May. In 1988 (N=15), and again in 1989 (N=23), the majority of fawns (87% and 93%, respectively) were born between February and April, with births relatively evenly distributed over that 3-month period. Two births occurred in May, 1 in 1988 and 1 in 1989 and 2 in January, 1989. Two females in our 1990 sample (N=20) dropped their fawns in late January.

Productivity. We obtained data on the productivity of 33 females ≥ 1 year old in 1989, including 4 yearlings, 7 2-year-olds, and 22 ≥ 3 -year-olds. The majority of information came from aerial observations; additional data, which were included in our progress report for 1987-1988 (Smith et al. 1989), were obtained from 2 radio-tagged and 5 unmarked females necropsied in October 1988.

Pooling data from aerial observations and necropsies, the estimated overall pregnancy rate among females ≥ 2 years old (age at fawning) in 1989 was 79%, which is comparable to estimates of 78% and 80% for 1987 and 1988, respectively (Smith 1989). We previously proposed that such estimates, derived largely from observations during aerial telemetry, were conservative, and our data from 1989 support that argument. Often, because mothers spend very little time with neonates, we do not sight, i.e., verify, a fawn until 2-3 months after its birth. Estimates of pregnancy rate based on aerial observation may therefore vary in relation to the amount of neonate mortality.

In 1989, we observed fawns with 17 of 18 (94%) ≥ 3 -year-old and 2 of 4 (50%) 2-year-old radio-tagged females during aerial tracking (Table 9), compared to 67% and 86% for ≥ 3 -year-olds in 1987 and 1988, respectively; no fawns were observed with 2-year-olds in either 1987 or 1988. In 1987, we

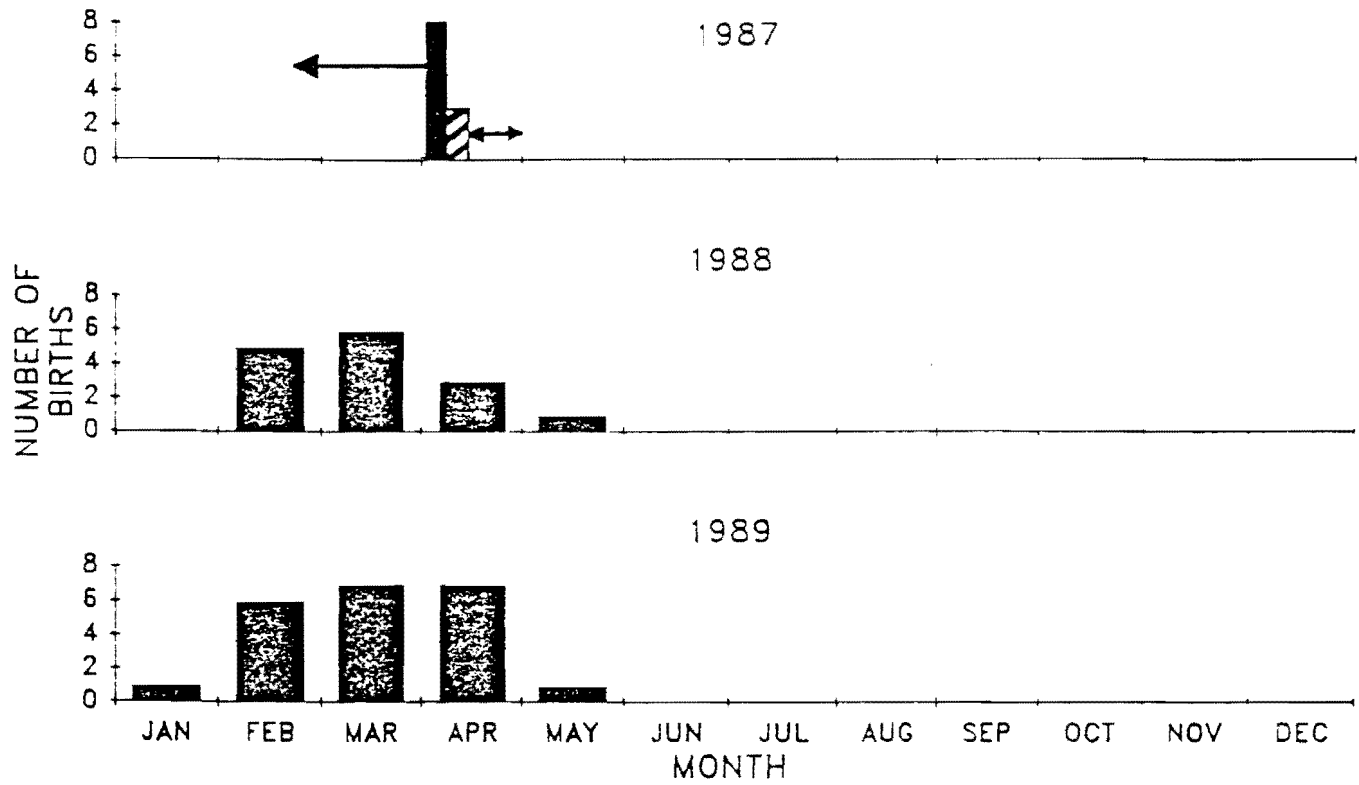


Figure 4. Chronology of fawning among radio-tagged white-tailed deer in eastern Everglades National Park, 1987-1989.

did not begin collecting data until the second half of the fawning season at which time a relatively early wet season had begun; it is quite possible that some females, which were not lactating or pregnant when handled in April, had lost a fawn early in the season and exhibited no external signs of pregnancy. Although flooding was relatively severe and prolonged in 1988, the wet season began late, well past the end of the fawning season. Again in 1989, which was considered a drought year, the wet season probably had little effect on neonatal mortality.

We lack any evidence that demography of the population or environmental conditions may have deterred breeding activities during the course of the study, or that the physical condition of deer influenced rates of conception or resorption. Rather, it appears that the variation in our estimates of pregnancy rate derived from telemetry observations is an artifact of sampling bias associated with annual variation in neonatal mortality, which may depend largely on the timing and severity of wet seasons. Notwithstanding that 3 of 14 (21%) females necropsied between late October and January were barren, we currently believe that the pregnancy rate among ≥ 2 -year-old females (age at breeding) in eastern EVER averages 90% or more. Two of 3 barren females in the necropsy sample were collected in late October 1988, and it is possible that they had yet to breed or had conceived so recently that pregnancy was not detected. Also, given that all of 4 yearling females examined internally have been pregnant, we believe that the rate of pregnancy in this age class is much higher than aerial observations have indicated, probably 80% or greater. Because fawn mortality may be relatively high among young, primiparous mothers (Verme and Ullrey 1984), who often lose their fawns soon after birth (Ozaga et al. 1982), we suspect that the lack of observations of fawns with 2-year-old, radio-tagged females is due to a high rate of neonatal mortality, rather than a low rate of pregnancy, in this age group.

In 1989, only singleton fawns were observed with radio-tagged females (N=19), and each of 5 pregnant females collected in November carried a single fetus. In addition, among 27 random doe/fawn observations during census flights, singleton fawns were observed in 26 (96%) cases. On 14 December we observed an adult female with 2 smaller deer which, after several low passes in the airplane, appeared to be of equal size. If these were twins, and that is inconclusive, they are the only pair sighted during the study. In eastern EVER, there clearly is selection for females that invest in only 1 fawn, and we continue to believe that it is related to low, stable, primary productivity in the system. If litter size is consistently 1, gross productivity of the

Table 10. Mortalities of radio-tagged deer in eastern Everglades National Park, 1 February 1989 - 31 January 1990.

ID No.	Sex	Age	Date	Cause of death
5	M	Adult	5 Dec	panther predation
32	M	Adult	5 May	panther predation
55	M	Adult	1 Oct	panther predation
9	F	Adult	1 Jun	panther predation
43	F	Adult	5 Aug	panther predation
62	F	Yearling	10 Jun	panther predation
58	M	Yearling	25 Aug	unknown natural
67	M	Fawn	11 Oct	unknown natural
68	M	Fawn	2 Sep	unknown natural
39	F	Adult	4 Aug	unknown natural
57	F	Adult	10 Aug	capture-related

21% for adults, and 25% for yearlings, compared to 14%, and 35%, respectively, over the first 2 years of the study. Based on survival among fawns of radio-tagged females, we estimate that the rate of fawn mortality in 1989 was 55%, compared to 67%, and 38%, respectively, for 1987 and 1988.

Mortality rates, and other data on recruitment and loss in the population through April 1990, were recently presented at the 2nd International Symposium on the Biology of Deer (Smith 1990a) (Table 11). Notwithstanding annual variation in age-sex-specific rates of mortality, which will be addressed in the final report, these data indicate that: 1) mortality rates for all age and sex groups in the population, particularly yearling and adult males, are relatively low, leading to the preliminary conclusion that the population is stable in time, and 2) the differential rate of mortality among male and female fawns may be great enough to explain the observed disparity in the adult sex ratio favoring females, even with a fetal sex ratio skewed toward males.

Dispersal

In 1989, 9 radio-tagged yearlings (5 males and 4 females) were monitored. One female was killed by a panther within her natal range in June; the other females have continued to reside in their natal ranges and associate with their mothers and sisters, similar to the behavior of 6 radio-tagged yearling females in 1988.

All yearling males monitored during the study have permanently dissociated from their mothers, but the timing and distance of dispersal from natal ranges have varied. In each case, the yearling male stopped traveling with his mother during the fawning season. One male, who dissociated from his mother in February, immediately dispersed several kilometers outside his natal range. The previous year, his maternal brother exhibited nearly identical behavior. Another male dissociated from his mother in March but since, has remained on the periphery of his natal range and appears never to reassociate with his mother. Each of 3 other males also remained in or adjacent to his natal range following the fawning season but, occasionally, reassociated with his mother until August, when, at approximately 18 months of age, he permanently dispersed several kilometers away. In 1988, an orphaned yearling male who associated with his 2-year-old radio-tagged sister in their natal range, also dispersed in August. Clearly, dispersal behavior is typical among males, however, it is not clear at this time whether such dispersal

constitutes loss from the population. We look forward to forthcoming observations on dispersal behaviors of 5 radio-tagged males from the 1989 cohort.

Recruitment

We consider the age of recruitment to be 1 year. Assuming that litter size is uniformly 1 in our study area, age-specific rate of recruitment represents the percentage of females in a given age class that successfully raises a fawn. In 1989, 8 of 22 (36%) ≥ 2 -year-old radio-tagged females recruited a fawn to the yearling age class; all of these successful mothers were ≥ 3 years old, as were those in 1987 and 1988 when age-specific recruitment rates for females ≥ 3 years old were 26% (N=19) and 53% (N=15), respectively (Table 12).

Using age specific rates of productivity and mortality that we have observed among ≥ 1 -year-old radio-tagged deer during the study, and assuming: 1) a 1:1 sex ratio at birth, 2) 65% annual mortality rate for male fawns and 45% for females, and 3) constant survival rates for adult males and adult females until 15 years and 20 years of age, respectively, life table models were constructed. This preliminary exercise produced estimates of 20-23% for annual recruitment rate and 21-23% for annual mortality rate, indicating stability in the size of the population. Estimates of net recruitment ranged from -12%, to +3%, depending largely upon the recruitment rate of ≥ 3 -year-old females, which produced positive net recruitment when $\geq 45\%$. The per generation rate of increase for females (R_0), also referred to as net reproductive rate or generation ratio, ranged from 0.64 to 1.18; a fawn survival rate of 55% was necessary to produce an R_0 value of ≥ 1.0 , i.e., for females to replace themselves.

Movements, Activities, and Habitat Utilization

Formal analyses of data on movements, activities, and habitat use by radio-tagged deer will not be initiated until field research, i.e., data collection, is terminated later this year. Because of our priority on collecting data that is at hand, and our small staff, we are behind on preliminary analytical chores such as entering telemetry data and digitizing our habitat map. Although we have little to add at this time to information on movement ecology presented in our previous progress report (Smith et al. 1989), a few anecdotal comments are possible.

During the past year, we observed no unusual patterns of movement, activity, or habitat use by study animals, and

after monitoring 12 deer for almost 3 full years and 15 others for 2 years, it appears that the locations and sizes of home ranges of adult deer vary little from year to year. In 1987 and 1988, we found that surface water during the wet season had little effect on movements of study animals; exceptions were 3 young females that temporarily moved outside their ranges in Taylor Slough during the wet season in 1988. Under contrastingly dry conditions in 1989, home ranges likewise appeared to be very stable. Surprisingly, we observed no obvious shifts in home range or habitat use either during or following the Ingraham fire in May 1989, even by animals whose ranges were completely burned (Bass and Smith 1989).

In 1989, several adult males repeated their pattern of annual range use, typically utilizing small, often disjunct ranges with dense cover between January and June, i.e., outside the rut, and then increasing their movements over large areas during the breeding season. In contrast, although their use of vegetative types may vary temporally, females appear to occupy ranges of equal size in the wet (breeding) and dry (fawning) seasons; as we have stated previously, they unquestionably exhibit a greater affinity to open habitats than do males, at all times.

OUTLOOK

We are scheduled to terminate systematic collection of data in June or July 1990, at which time we will have completed 3 full years of field research. Activities will immediately shift to organization and analysis of data, and a final report for the project will be submitted to NPS by 31 December 1990. We have proposed to continue collection of data on a limited schedule as part of a broader effort to coordinate and synthesize research on Florida panthers and white-tailed deer in EVER and BICY (Smith 1990b). The emphasis of such an initiative would be two-fold: 1) to initiate analysis and complete publication of existing data on panther-deer interactions in eastern EVER during FY91, and 2) to establish a framework of technical coordination and interaction among panther and deer studies in EVER and BICY that will lead to a prompt, thorough synthesis of information from the 4 projects once all field research is completed.

Simultaneously, and at a minimal cost, we would continue to gather valuable information on age-specific productivity and mortality of 43 radio-tagged deer currently (June 1990) being monitored in our study area (36 of these transmitters will function at least through January 1991). A large proportion (60%) of this sample is known-age, including 6 fawns, 6 yearlings, 6 2-year-olds, 4 3-year-olds, 2 4-year-

olds, and 2 5-year-olds. We also likely would recover teeth and obtain age estimates for some of 12 adult deer (including 10 females) that have been monitored since 1987, but whose exact ages are not known. Perhaps more importantly, we would avoid the loss of continuous information on predator-prey interactions of Florida panthers and white-tailed deer, which to this point, has come almost exclusively from our study area.

REFERENCES

- Bass, O.L., Jr., and T.R. Smith. 1989. Distribution and abundance of Florida panthers and white-tailed deer in eastern Everglades National Park. in J.C. Ogden and S.M. Davis, eds., Everglades: Spatial and Temporal Patterns as Guidelines for Ecosystem Restoration, A Symposium, Key Largo, FL. (Abstract).
- Dapson, R.W., P.R. Ramsey, M.H. Smith, and D.F. Urbston. 1979. Demographic differences in contiguous populations of white-tailed deer. *J. Wildl. Manage.* 43(4):889-898.
- Dusek, G.L., R.J. Mackie, J.D. Herriges, Jr., and B.B. Compton. 1989. Population ecology of white-tailed deer along the Lower Yellowstone River. *Wildl. Monogr.* 104, 68pp.
- Forrester, D.J., and S.D. Wright. 1989. Studies on the health and diseases of white-tailed deer in Everglades National Park and Big Cypress National Preserve. Annual Prog. Rep., Cooperative Agreement CA-5000-7-8007, Subagreement 6. Southeast Regional Office, National Park Service, Atlanta, GA. 32pp.
- Hesselton, W.T., and R.M. Hesselton. 1982. White-tailed deer. Pages 878-901 in J.A. Chapman and G.A. Feldhamer, eds., *Wild mammals of North America*. Johns Hopkins Univ. Press, Baltimore, MD.
- Ozaga, J.J., L.J. Verme, and C.S. Bienz. 1982. Parturition behavior and territoriality in white-tailed deer: impact on neonatal mortality. *J. Wildl. Manage.* 46(1):1-11.
- Sauer, P.R. 1984. Physical characteristics. Pages 73-90 in J.K. Halls, ed., *White-tailed deer, ecology, and management*. Stackpole Books. Harrisburg, PA.
- Severinghaus, C.A. 1949. Tooth development and wear as criteria of age in white-tailed deer. *J. Wildl. Manage.* 13(2):195-216.

- Smith, T.R. 1989. Reproductive synchrony and productivity of white-tailed deer in a subtropical wetland. Page 836 in Abstracts of Papers and Posters, Vol.II, Fifth International Theriological Congress, Rome, Italy. (Abstract)
- , T.R. 1990a. Recruitment and loss in an unhunted subtropical white-tailed deer population. Page 3 in The Biology of Deer: Program and Abstracts, Second International Symposium on the Biology of Deer, Miss. State, MS. (Abstract)
- , T.R. 1990b. A proposal to coordinate and synthesize research on Florida panthers and white-tailed deer in Everglades National Park and Big Cypress National Preserve. Southeast Regional Office, National Park Service, Atlanta, GA. 4pp.
- , T.R., J.F. Eisenberg, and M.E. Sunkist. 1989. Ecology of white-tailed deer in Everglades National Park (CA-5280-5-8004), Progress: January 1987-January 1989. Southeast Regional Office, National Park Service, Atlanta, GA. 44pp.
- Verme, L.J., and D.E. Ullrey. 1984. Physiology and nutrition. Pages 91-118 in J.K. Halls, ed., White-tailed deer, ecology, and management. Stackpole Books. Harrisburg, PA.

Appendix VI

ECOLOGY OF WHITE-TAILED DEER
IN EASTERN EVERGLADES NATIONAL PARK
(CA-5280-5-8004)

Effects of Hydrology and Vegetation on the Distribution and
Abundance of White-Tailed Deer and Florida Panthers
in Everglades National Park

Annual Report - Fiscal Year 1991
Tommy R. Smith, Field Coordinator

Includes data from CA-5280-5-8004
from February 1990-August 1991

John F. Eisenberg, Principal Investigator
Melvin E. Sunkist, Co-Principal Investigator

Florida Museum of Natural History
University of Florida
Gainesville, FL 32611

TABLE OF CONTENTS

LIST OF TABLES AND FIGURES	ii
EXECUTIVE SUMMARY	iii
INTRODUCTION	i
METHODS	2
RESULTS and DISCUSSION	3
Data Management	3
Population Analysis/Modeling	5
Density	5
Age-structure	5
Sex-ratio	8
Natality	10
Mortality	13
Population dynamics	15
Habitat Analysis	19
Home Range Analysis	20
CONCLUSIONS	21
LITERATURE CITED	24

LIST OF TABLES AND FIGURES

Table 1.	Telemetric observations of white-tailed deer and Florida panthers in Everglades National Park, Dec 1986 - Jun 1991	4
Table 2.	Estimates of population size and density of white-tailed deer ≥ 1 -year-old in the 450 km ² core study area in eastern Everglades National Park, Jan 1988 - Dec 1989	6
Figure 1.	Age composition in 2 samples of white-tailed deer from eastern Everglades National Park, Jan 1987 - Aug 1991	7
Table 3.	Sex ratios of white-tailed deer in eastern Everglades National Park, Jan 1987 - Jan 1991	9
Table 4.	Pregnancy rates of white-tailed deer in Everglades National Park, 1987 - 1990	11
Table 5.	Observed litter sizes of white-tailed deer in Everglades National Park, 1987 - 1991	12
Table 6.	Age-specific mortality among radio-tagged white-tailed deer in Everglades National Park, Mar 1987 - Aug 1991	14
Table 7.	Reproductive recruitment by radio-tagged white-tailed deer in eastern Everglades National Park, 1987 - 1990	17
Table 8.	Interaction of female fawn mortality and sex ratio at birth on per-generation rate of change in female white-tailed deer in eastern Everglades National Park, 1987 - 1990	18
Table 9.	Estimates of composite core activity areas and home ranges Florida panthers radio-tagged in Everglades National Park, 1986 - 1989	22
Table 10.	Estimates of annual home range size of white-tailed deer in Everglades National Park, 1987 - 1991	23

EXECUTIVE SUMMARY

Expanded analysis and synthesis of 4-year data bases on Florida panthers and their primary prey, white-tailed deer, in Everglades National Park was initiated in mid-April 1991 to develop a model of the interaction of hydrology, vegetation, and fire on the dynamics of deer and panther populations. The model ultimately will interface with a broad hydrologic model of the Everglades ecosystem. Objectives during the first half of the 1-year study, initiated 15 April 1991, focus on management and analysis of data on population characteristics, habitat use, and home range.

Presently (August 1991), data bases containing approximately 19,000 telemetry observations of deer and panthers have been edited and updated, and demographic analysis of the deer population is nearly complete. Estimated density of deer in the study area is approximately 1 deer/2-3km², which is very low for the species. Old age classes are well represented among randomly sampled deer, indicative of a stable age structure. Sex ratios among fetuses (N=9) and live-captured fawns (N=52) did not differ significantly from parity, however, the latter sample indicates that sex ratio at birth may be skewed toward males. Pregnancy rate appears to average 90% among $\geq$ 2-year-olds and approximately 80% among yearlings. Litter size is uniformly 1 (N=85). Distinct differential mortality occurred among radio-tagged fawns; 54% in males and 0% in females. This apparently reflects relatively high female survivorship among old fawns, but

it is estimated that neonatal females experience 20-30% mortality. Yearling sex-specific rates of mortality do not differ substantially among older age classes. Life table and Leslie-matrix models have been constructed based on updated estimates of density, age-structure, sex-ratio, productivity, mortality, and recruitment. Pending are 2, more sophisticated computational procedures to 1) generate age- and cause-specific mortality rates with confidence intervals and 2) apply a stochastic simulation model to population data. Data on population structure, productivity, survival, and home range, as well as simple population models uniformly indicate that the density of deer is low and stable in time. Dynamics in the deer population appear to be most influenced by annual variation in fawn mortality.

INTRODUCTION

Dynamics in the Everglades ecosystem are fundamentally related to hydrology (Craighead 1971). Restoration of the system will depend upon an understanding of the direct effects of natural water-delivery and rainfall on the distribution and properties of water in the system and, perhaps more importantly, the more indirect effects of water on the distribution and abundance of plants and animals in the system. Simulation modeling appears to be a feasible tool for developing this understanding, and the National Park Service, in cooperation with other federal and state agencies, is supporting an initiative to refine a hydrologic model for the Everglades ecosystem.

It is important that the hydrologic model includes subroutines for animals at various trophic levels in the system, particularly those secondary and tertiary consumers which draw considerable public and/or legal attention. Paramount among these is the endangered Florida panther (Felis concolor coryi), which rests at the top of the food chain and has become a symbol of the plight of the Everglades.

Companion field studies of panthers and their primary prey, white-tailed deer (Odocoileus virginianus seminolus), were conducted in EVER between 1987 and 1990. Although it was beyond the original scope of work in either project, data bases generated on the 2 species offer the opportunity to delineate, quantify, and model interactions of vegetation, fire, and hydrology on the dynamics of deer and panther populations. Accordingly, a proposal to extend analyses of existing data on deer and panthers was approved for FY91 with the following

objectives:

1. To determine the effects of hydrology, vegetation, and fire on the distribution and abundance of deer and panther populations in EVER, and
2. To assist in the development of a model of these effects that interacts with a broad hydrologic model of the Everglades ecosystem.

METHODS

The details and schedule of procedures to meet objectives of the study were outlined in our original proposal (Smith and Bass 1990). Due to administrative delays, the project was not initiated until 15 April 1991, and the timetable for procedures, listed here as work elements, was revised as follows:

- | | |
|-------------|--|
| Apr-May '91 | - Management of existing data files. |
| Jun | - Analysis of population data and development of simple population models for deer and panthers. |
| Jul-Aug | - Vegetation mapping and utilization-availability analysis of landscapes and vegetative cover by deer and panthers in the core study area. |
| Sep-Oct | - Home range analysis. |
| Nov-Dec | - Analysis of habitat quality (synthesis of results of population, home range, and habitat analyses). |
| Jan | - Multivariate habitat analysis of hydrologic, climatic, and topographic data (if available). |
| Feb-Mar | - Development of deer/panther model. |
| Mar-Apr | - Evaluation of model. |

RESULTS AND DISCUSSION

Due to the delay in startup, we are presently (August) only 3-4 months into the project. Nonetheless, noteworthy progress has been made, as outlined below.

Data Management

Radio-telemetry observations are the foundation of existing data bases on deer and panthers. For panthers, these are exclusively aerial, whereas 21 percent of the telemetry data on deer were collected by ground tracking at night (Table 1). Each telemetry observation includes the location, habitat type, activity (either directly observed or deduced from radio signals), and, frequently, the behavior of the animal at the time. Inclusive, therefore, in these observations is information on reproductive cycles, natality, mortality, habitat preferences, home range, movements, activity rhythms, social interactions, etc., much of which will eventually be incorporated into population, predator-prey, and habitat models for the species.

All aerial telemetry observations made on deer and panthers through June 1991 have been entered in computer data bases and edited for errors using SAS (1988) software for personal computers and LOTUS 1-2-3, respectively. Entry and editing of ground telemetry data on deer is approximately 20 percent complete and progressing. Much of our data management is specific to particular objectives or analyses and is addressed in the appropriate sections.

Population Analysis and Modeling

In order to model the population dynamics of deer in EVER and, subsequently, the interactions of populations of deer and panthers with vegetation and hydrology, accurate estimates of density, age structure, sex ratio, natality, mortality, and recruitment in the deer population must be obtained. We have updated and begun reexamination of our preliminary estimates of these parameters (Smith 1989, 1991, Smith et al. 1989, 1990).

Density. Variance among estimates of population size and density of white-tailed deer in eastern EVER generated from aerial surveys in 1988 and 1989 was very high (Table 2). This apparently was due to positively biased estimates associated with low numbers of reobservations in individual samples, a problem common to population estimates derived from mark/recapture-reobserve data (Tanner 1978). The mean population estimate from samples with ≤ 3 reobservations was 286 (S.D.=87), compared to 145 (S.D.=31) for estimates from samples with ≥ 5 reobservations. Consequently, in our modeling we will use a range of values for density (and carrying capacity) that represents the minimum and maximum values among 95% confidence intervals across estimates derived from samples with ≥ 5 reobservations.

Age Structure. In an earlier report (Smith et al. 1990) we constructed age pyramids of the white-tailed deer population in eastern EVER based on 2 sources of data: miscellaneous recoveries (i.e., roadkills, random live-captures, and deer collected for health studies) and panther kills. These are updated in Figure 1. Both sources of data probably are biased

Table 2. Estimates of population size and density of white-tailed deer $\geq$ 1-year-old in the 450 km² core study area in eastern Everglades National Park, Jan 1988 - Dec 1989.

Date	C ^{1/}	R ^{2/}	M ^{3/}	N ^{4/}	D ^{5/}
Jan'88	28	8	34	113	0.25
Feb	46	10	34	165	0.37
Mar	13	1	32	231	0.51
Apr	28	3	33	247	0.55
May	28	6	33	141	0.31
Jul	17	3	32	149	0.33
Oct	31	2	34	373	0.83
Nov	26	7	32	111	0.25
Dec	16	2	32	187	0.42
Jan'89	32	3	40	338	0.75
Feb	20	5	41	147	0.33
Mar	17	1	41	378	0.84
Apr	17	2	41	252	0.56
Aug	32	5	34	193	0.43
Oct	36	3	31	296	0.66
Dec	26	1	31	405	0.90

1/ number observed in census (i.e., sample size)

2/ number reobserved (i.e., number of radio-tagged deer in C)

3/ number of marked animals in the population

4/ population estimate for area censused

5/ density estimate - deer/km²

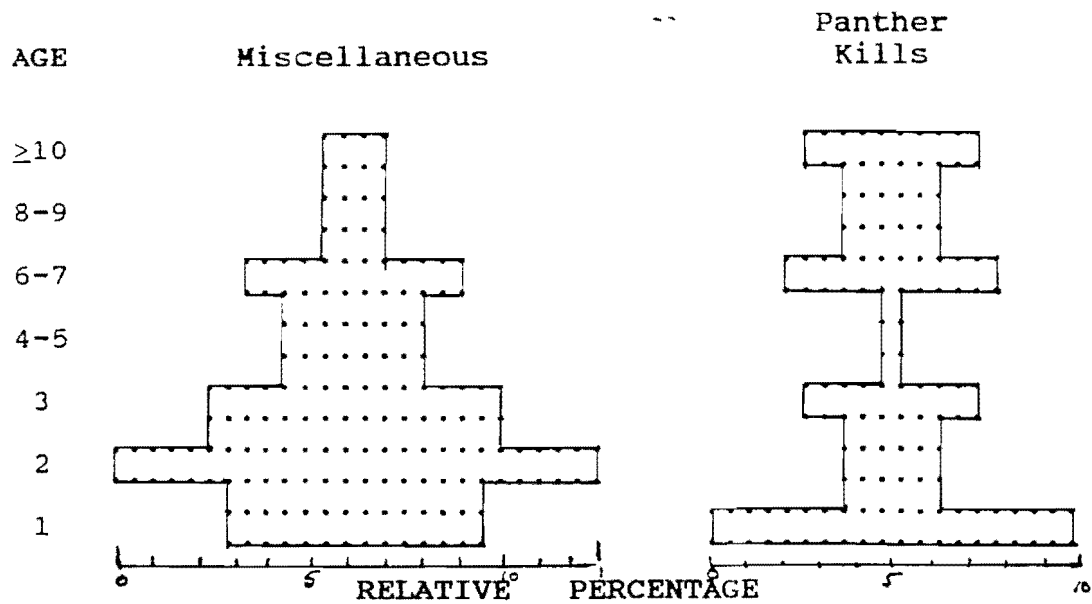


Figure 1. Age composition in 2 samples of white-tailed deer from eastern Everglades National Park, Jan 1987 - Aug 1991. Miscellaneous includes road-kills, random live-captures, and females randomly collected in health studies.

by sampling error, and the degree to which they represent the actual age composition of the population cannot be quantified. However, they are useful to demonstrate that old deer (e.g., ≥ 5 years old) are well represented in the population and, in conjunction with data on age-specific productivity and mortality, support the argument that the age structure of the population is relatively evenly distributed and stable. Although survival rates among fawns and yearlings may vary considerably between years, productivity and survival among older age-sex classes appear to be stable. In simulation models, this will drive the age structure of the population toward stability, regardless of its original composition, therefore the uncertainty over estimates of age composition should have little consequence in the analysis and modeling of the deer population.

Sex Ratio. We have relatively few data on sex ratio at birth, and those in hand are somewhat conflicting. Among 9 fetuses which could be sexed, 3 (33%) were male, whereas 30 (63%) of 43 live-captured fawns were male. Given observed mortality rates of 54% and 0% (pg. 14), respectively, among radio-tagged male and female fawns, we conclude that the skew toward females in our small sample of fetuses is not representative of sex ratio at birth in the population. The cumulative male:female ratio among fawns (1.4:1, Table 3) does not differ significantly from parity ($\chi^2=1.23$, 1 df, $p>0.1$). In modeling we will assume that sex ratio at birth may vary annually from 1:1 to 1.4:1..

We previously argued (Smith et al. 1989) and continue to believe that estimates of sex ratio among deer ≥ 1 year old

Table 3. Sex ratios of white-tailed deer in eastern Everglades National Park, Jan 1987 - Jan 1991.

Age	Males	Females	Male:Female
			Ratio
Fawn ^{a/}	30	22	1:0.7
≥1 yr old ^{b/}	37	88	1:2.4

a/ includes fetuses (N=9) and live-captured fawns

b/ based on aerial censuses during peak of rut (Jul-Oct)

generated from aerial censuses during the rutting period, when association of males and females is greatest (Smith 1989), are relatively unbiased. In modeling we will use the 1:2.4 ratio of males to females which was observed among yearling and older deer on censuses during the peak of rut (Jul-Oct) (Table 3). In addition to the argument based on behavioral observations, it is clear that the observed differential mortality among radio-tagged male and female fawns could produce a 1:2 sex ratio among yearlings. Further, given the relatively small variation in mortality rates between sexes and within age-classes among radio-tagged deer ≥ 1 year old (pg. 14), a 1:2 sex ratio should remain relatively stable throughout adult age classes.

Natality. Reproductive parameters of particular relevance to modeling the deer population are age-specific pregnancy rates and litter sizes. Estimated pregnancy rates for 1990, based on observations of 21 radio-tagged females and in utero examination of 6 females collected in health studies, were similar to those observed in the 3 previous years of study (Table 4). Hence, we maintain our earlier conclusions that: 1) estimates of pregnancy rate in 1987 were biased low due to the type and timing of sampling, 2) pregnancy rates average approximately 90 percent for ≥ 2 -year-olds and 80 percent for yearlings and are relatively stable from year to year, and 3) female fawns are not reproductively active (Smith et al. 1990).

Observations on litter size in 1990 and 1991 also were consistent with those in previous years (Table 5). Only singleton fawns were observed among 6 litters in utero and 23

Table 4. Pregnancy rates of white-tailed deer in Everglades National Park, 1987-1990.

age-class ^{a/}	1987		1988		1989		1990	
	N	%	N	%	N	%	N	%
fawn	3	0%	6	0%	4	0%	2	0%
yearling	4	0%	2	50%	8	75%	4	75%
≥ 2-yr-old	17	82%	16	94%	23	87%	23	91%

^{a/} age at breeding

Table 5. Observed litter sizes of White-tailed deer in
Everglades National Park, 1987-1991.

Period	Type of Observation			
	in utero		telemetry	
	N	Mean size	N	Mean size
1987-1989	6	1.0	50	1.0
1990-1991	6	1.0	23	1.0

litters of radio-tagged females, bringing our totals for each source of data to 12 and 73, respectively, since 1987 without an observation of twinning. In addition, we have yet to observe twins in over 100 incidental observations of family units during telemetry and census operations. Clearly there is selection for a litter size of 1 in the population, and we will use this in our modeling.

Mortality. Data from 1990 and 1991 increased our previous sample of mortality among radio-tagged deer by approximately 20 percent. Much of the increase was in samples for fawns and yearlings, which substantially strengthens our estimates of mortality in these age classes. This was particularly useful to clarify differential mortality between male (54%) and female (0%) fawns (Table 6), which, as mentioned earlier, appears to explain the preponderance of females among yearling and older deer. Our data indicate that mortality rates may be somewhat lower for males than females among yearlings and young adults, but in older deer, survivorship appears to be higher for females than males.

We are comfortable that these estimates approximate overall age-specific rates of mortality in the population. However, the small size of annual samples for yearling and young adult age-classes limits the usefulness (i.e., defendability in modeling) of observed year-to-year variation in mortality for these groups. This may be overcome by generating unbiased estimates of mortality, around which confidence intervals can be constructed (Heisey and Fuller 1985). These intervals will be used as estimates of variance in mortality rates for our modeling.

Table 6. Age-specific mortality among radio-tagged white-tailed deer in Everglades National Park, Mar 1987-Aug 1991.

Age	Sex	<u>Sample size</u>		Annual mortality rate
		N	# deer years	
fawn	male	26	11.1	54%
	female	17	7.5	0%
yearling	male	19	12.7	24%
	female	17	12.4	32%
2-3 yrs	male	23	14.1	14%
	female	22	17.0	18%
≥4 yrs	male	9	11.4	26%
	female	22	33.1	18%
all ≥2 yrs	male	21	32.0	19%
	female	30	60.0	13%

This approach will further allow statistical comparison of age- and cause-specific rates of mortality. Microcomputer program MICROMORT, which calculates unbiased estimates of cause-specific mortality rates, has been obtained and is presently being studied for application to our telemetry data on deer and panthers.

Population Dynamics. A life table analysis of preliminary data indicated that, given observed stability in pregnancy rates and mortality among deer ≥ 2 years old, fawn survival, hence, reproductive recruitment, appears to drive the dynamics of the white-tailed deer population in eastern EVER (Smith 1991). Assuming a 1:1 sex ratio at birth, pregnancy (birthing) rates of 80% and 94%, respectively, and mortality rates of 38% and 15%, respectively, for yearling and ≥ 2 -year-old females, and a uniform litter size of 1, the life table model indicated that a survival rate of $\geq 55\%$ among female fawns was necessary to maintain the female segment of the population, i.e., a per-generation increase of ≥ 1.0 . Recent incorporation of updated estimates of age-specific mortality only slightly changed the life table model, which now indicates that 60 percent survival among female fawns is critical. A 'Leslie matrix' (Leslie 1948), based on the assumptions of the life table model, also projects that a survival rate of 55-60 percent among female fawns will maintain female numbers and, hence, population stability.

Based on the life table model, if mortality among female fawns were negligible, as we observed in the radio-tagged sample, the deer population would have increased substantially between 1987 and 1991. However, reproductive recruitment by radio-tagged females during that period indicates otherwise. Based on age-

specific recruitment rates, i.e., the proportion of females that raised a fawn to 1 year of age, among radio-tagged females, net recruitment to the population over the 4-year period was 1%, ranging from a 6% loss in 1987 to a 9% gain in 1990 (Table 7). Dispersal of young males from the core study area, where the density of deer may be higher than elsewhere in the eastern Everglades (Smith and Bass, in press), may account for an additional annual loss as great as 7% (Smith 1991), however, it does not explain the discrepancy in population projections between the model based on observed mortality among radio-tagged fawns (increase) and the model based on observed recruitment among radio-tagged adult females (stable).

To explore this question we turned to the parameter for which there was least resolution, i.e., sex ratio at birth. Indeed, we found that if the fawn sex ratio is skewed toward males, as in our capture sample, a survival rate of approximately 75%, rather than 60%, among female fawns is necessary to maintain stability in the female segment of the population (Table 8). Presently, it appears infeasible to assume that mortality among female fawns approaches zero. Rather, considering recruitment rates among radio-tagged females, we hypothesize that annual mortality of female fawns averages 20-30% and occurs primarily at the neonatal stage, when sex differences in survival typically are least among ungulates (Clutton-Brock 1991).

Our life table analysis has provided simple, deterministic models of the structure and dynamics of the EVER deer population,

Table 7. Reproductive recruitment^a by radio-tagged white-tailed deer in eastern Everglades National Park, 1987-1990.

Year	<u>age-specific recruitment</u>				<u>net recruitment rate</u>	
	<u>2-year-olds</u>		<u>>3-year-olds</u>		<u>observed</u>	
	N	%	N	%	observed	estimated ^{b/}
1987	3	0%	16	38%	- 0.06	- 0.05
1988	2	50%	14	64%	+ 0.08	+ 0.05
1989	4	0%	17	47%	- 0.03	- 0.01
1990	3	33%	14	71%	+ 0.09	+ 0.08
1987-90	12	17%	61	54%	+ 0.01	+ 0.01

a/ recruitment of offspring to yearling age class

b/ assumes a recruitment rate of 17% for 2-year-old females, i.e., the observed mean for this age-class for 1987-1990.

Table 8. Interaction of female fawn mortality and sex ratio at birth on per-generation rate of change in female white-tailed deer in eastern Everglades National Park, 1987-1990. (Assuming 80% and 90% pregnancy rates and 32% and 18% mortality rates, respectively, for yearlings and $\geq$ 2-year-olds).

fawn mortality rate	Per-Generation Rate of Increase ^{a/}	
	sex ratio at birth	
	1:1	1.4:1
5 %	1.49	1.25
10 %	1.44	1.22
20 %	1.26	1.07
30 %	1.08	0.91
40 %	0.97	0.82

a/ # gains/# losses

and delineated parameters to which models of the population may be particularly sensitive. Our objective, however, is to apply stochastic population and systems models to the data that predict responses of the deer population to fire, hydrology, vegetation, and predation. To this end, we have obtained 2 simulation models from experts in the field: Bob Lacey, Brookfield Zoo, Chicago and Reg Barrett, Univ. California, Berkeley. Application of our data to these models will begin soon.

Habitat Analysis

Our recent analysis of interactions between landscape, deer, and panthers (Smith and Bass, in press) was an important, initial step toward delineating relationships between vegetation (i.e., habitat) and the distribution and abundance of deer and panthers. Digital data on plant communities generated from satellite imagery were obtained from the Florida Department of Transportation and reclassified into 6 landscape categories based on vegetational structure, hydrology and land-use. Using the Geographic Information System at EVER, these data were coupled with telemetry observations to quantify the availability of landscapes and their usage by individual panthers. Then, using utilization-availability analysis (Byers et al. 1984) we tested the hypothesis that the distribution of panthers across landscapes in and adjacent to EVER was random.

Findings of that analysis relevant to vegetation were:

1. Panthers utilized forested landscape, either as continuous pinelands or hammocks in open prairies, more than expected.
2. Relatively mesic landscapes, i.e., sloughs and mangrove forest, were avoided by panthers.

3. Breeding female panthers utilized insular ranges centered around forested Long Pine Key, whereas young, non-breeding panthers explored disturbed, open landscape outside the park.
4. The affinity of breeding female panthers to Long Pine Key apparently is due to relatively high availability of prey (deer) and hunting cover at the forest-prairie edge.
5. It appears, therefore, that acquisition of large prey (deer) limits the breeding density of panthers in EVER and determines its carrying capacity for panthers, estimated at 6-9.

We will follow similar procedures in a more detailed analysis of habitat relationships once an accurate, small-scaled vegetation map of the area is obtained. We had hoped that a truthed vegetation map based on satellite imagery would be available within the timeframe of our project, but that appears unlikely and that the formidable task of vegetation mapping will fall on our shoulders. Therefore, with the assistance of Juliane Struve, an intern from Germany, we have begun this effort. Based on observations during telemetry flights, vegetation in approximately 15,000 1-ha cells is being classified into one of 25-30 habitat types and coded, with accompanying UTM coordinates, into a SAS database. From this, we will generate a skeletal habitat map with GIS and then fill-in gaps using aerial photographs of the area.

HOME RANGE ANALYSIS

Estimates of the size and vegetative composition of home ranges of deer and panthers are fundamental to our analyses of habitat use and population dynamics. Much of the necessary preliminary work in refining a home range analysis was

accomplished in our study of the effects of landscape and white-tailed deer on the distribution of panthers in EVER (Smith and Bass, in press). For that analysis, we reformatted and applied telemetry data to 2 home range programs, TELEM88 (Coleman and Jones 1988) and HOMERANGE (Samuel et al. 1985), to generate estimates of core activity areas and home ranges of individual panthers and deer (Tables 9 and 10). This output was easily reformatted and coupled with landscape data using GRASS on the GIS.

Once a vegetation map of the study area is complete, we will return to the home range analysis for estimates of seasonal and annual ranges of deer and panthers. Again using the GIS, vegetative composition (including fire history) and hydrologic conditions in individual ranges will be quantified, providing the necessary data for analysis of associations between habitat quality and the dynamics (i.e., productivity and mortality) of deer and panther populations.

CONCLUSIONS

We are firmly on schedule in the project and pleased with the progress and quality of work to date. Most of the basic population analyses have been completed, and we are ready to apply the results to a stochastic simulation model. We also have made considerable progress in home range and habitat analyses. Computer software for both procedures is on-line and has been preliminarily applied to telemetry data.

These are major steps toward our final objective of developing a subroutine that simulates responses of deer and panther populations to vegetation, fire, and hydrology.

Development of an accurate, fine-scaled vegetation map of the study area will be a major hurdle in the overall project, but we are confident that this will be complete within 2-3 months and cause no delay in our scheduled completion of the project.

Table 9. Estimates of composite core activity areas and home ranges of Florida panthers radio-tagged Everglades National Park, 1986-1989.

id	sex	age	number of locations	estimate size	
				core activity area ^{a/}	home range ^{b/}
14	F	adult	976	108	350
15	F	adult	505	150	430
16	M	subadult	904	515	1,917
21	F	subadult	469	112	342
22	F	subadult	434	129	514
27	F	adult	451	352	747

a/ area within the 60% activity area isopleth generated by the harmonic mean estimator (Dixon and Chapman 1980), in km^2

b/ modified minimum area estimator (Harvey and Barbour 1965), in km^2

Table 10. Estimates of annual home-range size of white-tailed deer in Everglades National Park, 1987-1991.

sex	age-class	N	mean	s.d. ^{a/}	range
male	adult	24	12.4 km ²	6.0	3-29 km ²
	subadult	7	10.5 km ²	8.7	5-26 km ²
female	adult	53	4.3 km ²	2.3	1-12 km ²
	subadult	11	4.2 km ²	3.2	1-13 km ²

a/ standard deviation