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ECOLOGY OF WHITE-TAILED DEER IN EASTERN EVERGLADES NATIONAL PARK--AN OVERVIEW

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ABSTRACT

A population of white-tailed deer (*Odocoileus virginianus seminolus*) was studied in the eastern Everglades National Park from 1987 to 1992. The data for the interval January 1987 to June 1991 are summarized in this publication. During this interval, from 35 to 40 deer were monitored annually. Deer were captured utilizing a shoulder-held gun projecting a net, and fired from a helicopter. Captured deer were fitted with a radio collar and, thereafter, located by telemetry from both the ground and a fixed wing aircraft. Aerial locations were logged to a recognizable hectare square. Minimum convex polygons of deer home range use then were determined. Individual females occupied ranges of approximately 37 ha and males 113 ha, but seasonal differences in range use indicated that some males may have an annual range exceeding 12 km^2. There was considerable overlap of home ranges, especially among individual females and their presumptive offspring. The population density was estimated to be 0.68 deer/km^2. Adult females produce a single young; twinning was not recorded. During the course of this study, recruitment into the population was low. Mortality rates varied from year to year, especially for young fawns. The population appeared to be stable. During the course of the study, the panther (*Puma concolor*) was present. Deer comprised 57 percent of 99 identified panther kills in the eastern Everglades National Park and adjacent areas. Adult

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bucks with a mean age of 5.5 years were the dominant age/sex class killed (47% of all deer). We conclude that, although densities of both deer and panthers are low in the eastern Everglades National Park, they were normal and near carrying capacity or stable.

RESUMEN

Se estudió una población de ciervos de cola blanca (*Odocoileus virginianus seminolus*) entre 1987 y 1992 en la parte oriental del Parque Nacional Everglades. Esta publicación sumariza la información obtenida entre enero de 1987 y junio de 1991. Durante este periodo se monitorearon 35 a 40 ciervos al año. Los ciervos fueron capturados usando una red projectada por un rifle desde un helicóptero. A cada ciervo capturado se le colocó un radio collar gracias al cual los animales pudieron ser localizados usando telemetría desde tierra o desde una avioneta. Las localizaciones obtenidas desde la avioneta fueron registradas en cuadriculados de una hectárea. Los ámbitos de hogar de los ciervos fueron entonces determinados usando polígonos convexos mínimos. Hembras y machos ocuparon ámbitos de hogar de 37 y 113 Ha, respectivamente. Variaciones estacionales indicaron que algunos machos habrían tenido ámbitos mayores que 12 km^2. Los ámbitos de hogar se sobreimpusieron considerablemente. Las hembras y sus presuntos descendientes ocuparon rangos de hogar sobrepuestos en gran medida. La densidad poblacional fue estimada en 0.68 ciervos/km^2. Las hembras adultas parieron una sola cría no registrándose mellizos. El reclutamiento de la población fue bajo durante este estudio. La tasa de mortalidad varió de año a año especialmente en los cervatillos jóvenes. La población apareció estable. Pumas (*Puma concolor*) estuvieron presentes durante el curso de este estudio. Un 57% de las 99 presas capturadas por puma e identificadas en la parte oriental del Parque Nacional Everglades fueron ciervos. Ciervos adultos macho de 5.5 años en promedio fueron la clase de edad y sexo dominante (47% de todos los ciervos). Nosotros concluimos que aunque la densidad de ciervos y pumas en la parte oriental del Parque Nacional Everglades es baja, ambas poblaciones son normales y se encuentran cerca de su capacidad de carga.

ACKNOWLEDGEMENTS

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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 the Everglades National Park (ENP) and aided greatly in the preparation of the final report. José Fragoso and Tadeu Oliviera served as part-time field assistants. 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 Incorporated pilots, Sue Husari and the Fire Cache, John Ogden, Frank Draughn, and W. B. Robertson.

Many thanks are due to the generous Geographical Information System (GIS) computer specialists of the Department of Urban and Regional Planning at the University of Florida, especially David Lambert, who took the initiative to make room for the 200 MB of data from the park so that Cynthia Hunter could sift through it and absorb some of his good teaching.

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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 (*Puma 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 (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, contaminated 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 age 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. A parallel study from 1989 to 1992 directed by R. F. Labisky focused on the hunted populations in Big Cypress National Preserve 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; 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 5261 km^2 ENP, yielding a density of 0.29 deer/km^2. Densities were even lower in the Water Management Conservation Areas 2 and 3 north of the park at 0.10 deer/km^2 (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* and as part of a state survey (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 (Sigler-Eisenberg and Eisenberg 1985), very little of this habitat exists in the Everglades (Fig. 1).

Since the early 1970s 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

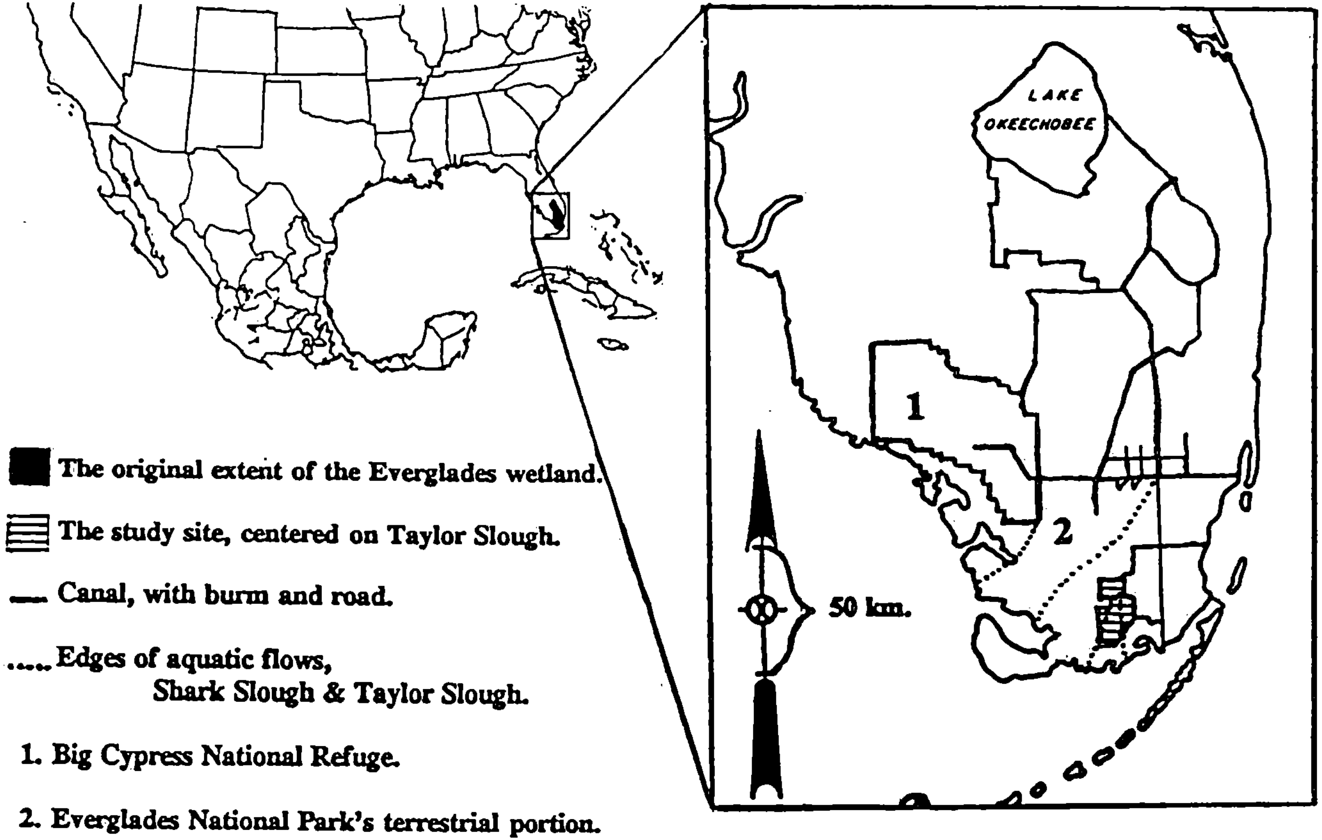


Figure 1. Southern Florida and the now partitioned and partially drained Everglades National Park wetland.

die-offs were caused by tick eradication efforts in the 1930s, overhunting in the conservation areas in the 1960s, and excessive flooding in 1957-1958 and in 1982-1983. 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 5660 km^2, are mainly prairies dotted with tree islands of various sizes and pine flatlands. The Everglades is classified as 65% 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 (Fig. 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 unpubl. hydrology data), the volume of water has been slowly decreased over the last 50 years, diminishing both high and low extremes of depth that occur seasonally in the park at the southern end of the wetland (Hunter 1990).

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 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* (Fig. 2).

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 terrebinthifolius* 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.

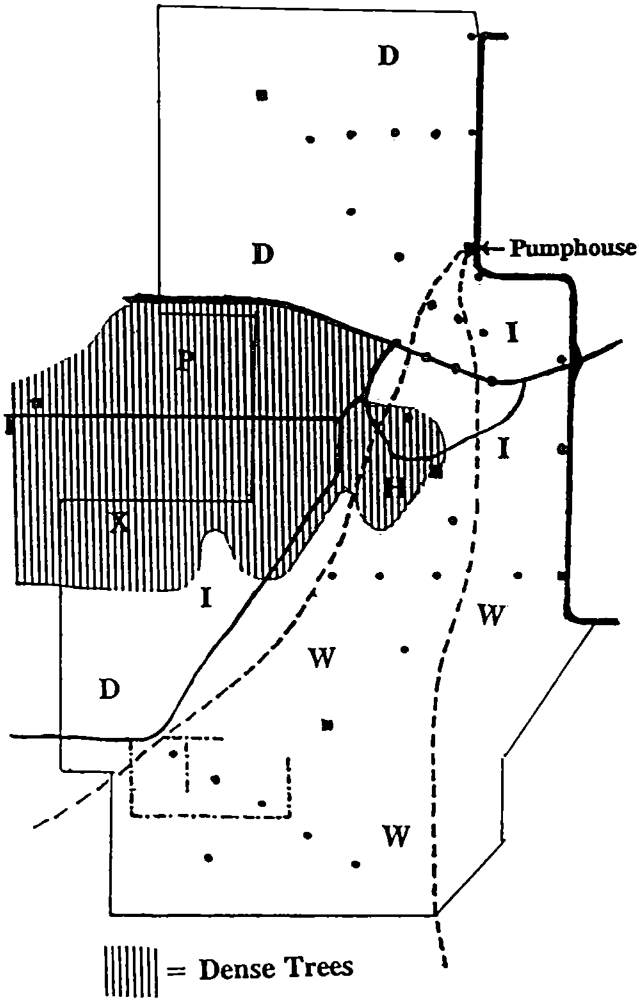
The climate is technically sub-tropical: Seasonality is dictated by variation in rainfall, not temperature, although a frost occurs on an average of once every ten years. Rainfall averages 148 cm per year, 81 percent of which falls during the wet season, usually from late April through October (Schomer 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 unpubl. 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.

METHODOLOGY

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

Capture

Initially, dartguns shot from blinds, buildings, and a truck 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



● = depth gauge
■ = depth, rainfall, and flow gauge
-..-. = abandoned, partially filled canals
—— = canal, with burm and road
---- = slightly elevated road only
P = pinelands
H = hardwood hammock
X = dense exotic shrubs

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 and dry in 1989.

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 1. Deer were also recaptured using this technique.

Chase flights by helicopoter were limited in duration to a maximum of about 10 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 the 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 1990, 1993b; 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). 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. Antenna 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 2.4-m telescoping mast supporting two H-element antennae set at the same height but 1.5 m 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 ft above the ground. Signals were clear up to 4 km from the target animals in this flat, open terrain.

Aerial locations were logged on an orthophoto map of the site to a recognizable hectare square 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 triangulation using two 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 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) 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 overlaid 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 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 they 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.

Population Censusing

Walk-ins were 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, one of us (Hunter) located a subsample of pregnant females an additional 2-3 times per week to obtain an estimate of the fawning date.

Aerial censuses of the 425 km^2 study area were flown systematically approximately every other month, and two observers counted all marked and unmarked deer seen along the flight path.

RESULTS AND COMPARISONS

Sample Size

Table 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 percent in 1988 and 3 percent in 1989 and 1990.

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 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 capture

Table 1. Captures by netgun of deer in eastern Everglades National Park.

	Captures		Recaptures		Monitored	
	M	FM	M	FM	M	FM
1987-1989						
F	11	11	1	1	1	1
J	2	3	1	6	3	6
A	13	24	4	3	8	16
1989-1990						
F	7	2	1	1	4	4
J	0	0	3	2	3	4
A	1	1	4	17	8	18

M = male; FM = female; F = < 1 yr; J = 1-2 yrs; A = 3+yrs.

animals 18-25 months of age, yet was complete in at least one 24-month old, thus determination of 2-year-old status was not absolute using this tooth-eruption method. We could not rely on tooth wear 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 in the park. The ages identified are included in Table 2.

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 percent of all yearling females were seen with fawns. However, a physiological examination of does (Forrester 1990, 1992b) from a sample collected slightly to the north of ENP showed that 3 out of 3 yearlings were pregnant

Table 2. Age classes identified.

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

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.

Other estimated ages of live-captured animals indicated a stable age distribution throughout 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.

In the eastern ENP, for each year the percentages of collared and monitored "adult" females observed with a live fawn were: 1987, 67% (but observation not through full fawning season--82% pregnancy detected); 1988, 86% (94% pregnancy detected); 1989, 94% (87% pregnancy detected); and 1990 (91% pregnancy detected). 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 ENP 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.

A fat estimate was taken on each animal handled using a scale of 1 (no fat) to 6 (thick fat) by palpitating just above the base of the tail. Adult

Table 3. Physical characteristics of deer captured in eastern Everglades National Park during 1989.

Sex	Age	N	Weight[1] X	Weight[1] Range	Total length[2] X	Total length[2] Range	Girth X	Girth Range	Hind foot[3] X	Hind foot[3] 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	25-30	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 included 1 deer collected in health study by Don Forrester

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 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 km^2 study area by December 1990 was 0.67 ± 0.24 deer/km^2 (Table 4). While we cannot completely explain the

Table 4. Population characteristics estimated each year in eastern Everglades National Park (also see Table 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) 0.9 (unburned)
M:F	3:1	3.4:1	1:1	–
PopEst	x	230	298	–
Density/km²	<1.0	0.55	0.67	0.68

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 ≥ 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 km^2
x = not estimated

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).

Mortality and Predation

Assessment of All Mortality Factors

Ectoparasite loads were minor to non-existent on ENP deer. For example, only 4 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 National Park (BCNP) showed the populations to be in good health with low parasite loads (McCowan 1990; Forrester 1992b). Parasites are not believed to be a significant detriment to deer in ENP.

Age-related Mortality

Fawn mortality was significantly higher in wet prairies than in dry prairies ($Chi^2 < 0.01$) (Hunter 1990); and it was greater in male fawns than in females (Smith 1991b). 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 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 2- to 3-year olds the rate was approximately 16%, and for adults, 4-years old and greater, it was about 22% per 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 percent 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). 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.

Panther Predation and Comments on the Bobcat

The summaries in Table 5 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 hunted (Dalrymple and Bass in press; Smith and Bass 1994). 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 bobcats, and where panthers are present, bobcat numbers may be depressed.

Table 5. Predation of deer by collared panthers in Everglades National Park and vicinity.

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

* incomplete year

The panther population utilizing ENP remained small throughout the study, but was thought to be at or near carrying capacity for the region (Smith and Bass 1994). During the wet season, panthers reduced the area in which they hunted and killed less deer from May through September (Dalrymple and Bass in press). Deer comprised 57 percent of 99 identified kills and 78 percent of the biomass killed by panthers in ENP 1987-1990 (Dalrymple and Bass in press). Adult bucks with a mean age of 5.5 years were the dominant age/sex class killed (47% of all deer killed).

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 densities of deer and panthers reflects limitation by environmental carrying capacity and by density dependent factors.

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 BCNP than in ENP (0.39 vs 0.10). Deaths were of higher frequency between two and six months of age. Bobcat (*Lynx rufus*) predation accounted for 58 percent of all deaths. Recruitment ranged from 11% to 26% in BCNP 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 the southeastern ENP, where panther predation exerts a greater impact, but the biology of deer reproduction should be similar.

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). 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 percent. 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 females 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 1992b), the careful monitoring of a total of 22 does during the fawning season allows us to conclude that twinning is very rare in the ENP, 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 (Fig. 3) (Hunter 1990; Boulay 1992) and was significantly later in does resident in wet prairies vs those resident in dry prairies (Hunter 1990) (Fig. 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 than in dry prairies, fawning must occur later in wet prairies due to nutritional constraints on does (Hunter 1990) (see also Fig. 5).

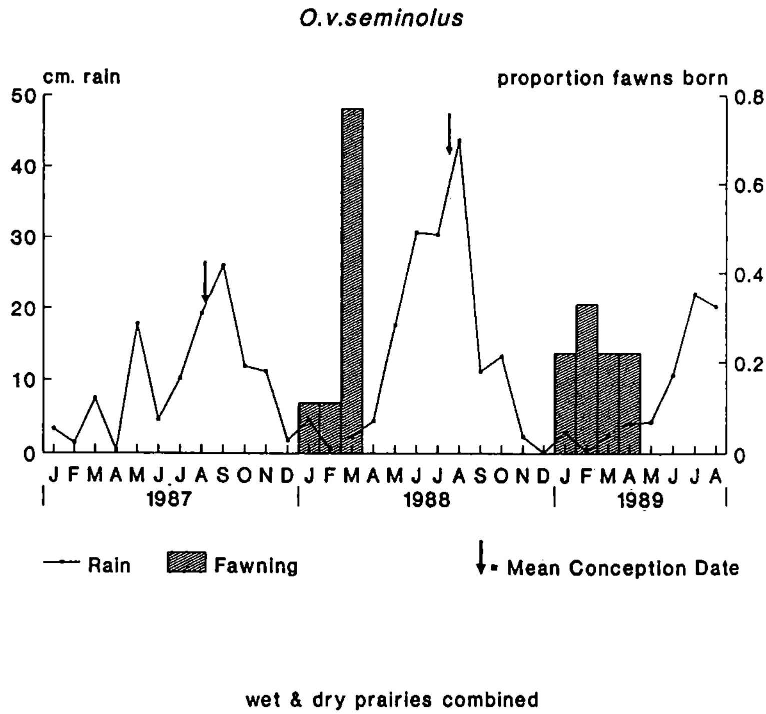


Figure 3. Fawning seasons in relation to rainfall averaged over the study site, Taylor Slough region of Everglades National Park. Deer conceptions (by backdating from fawning dates) occurred just before the peak of two very different rainy seasons (Hunter 1990).

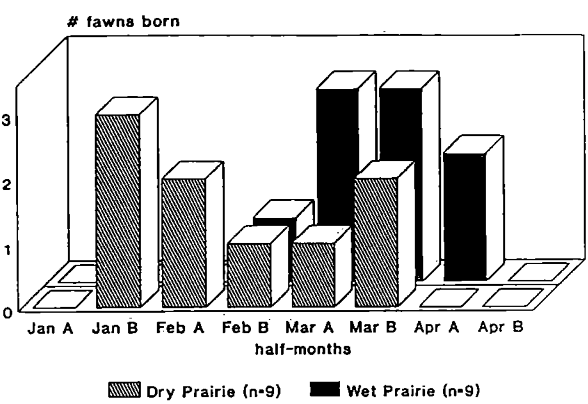


Figure 4. Number of fawns born in the two prairies types, 1988-1989, Taylor Slough portion of Everglades National Park. Each block represents fawning events with median date in either the first 15 days of the month (A) or the rest of the month (B). The mean birthdate was significantly different between the two prairies types (Hunter 1990).

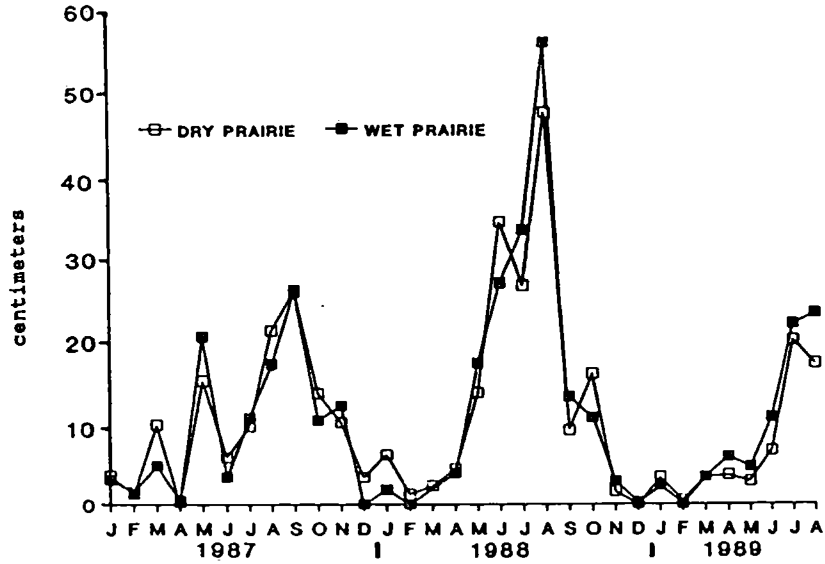


Figure 5. Rainfall on Taylor Slough's dry prairies (station R3110) and wet prairies (station NP67) during this fawning study, Everglades National Park (Hunter 1990).

Home Range and Habitat Use--Results and Discussion

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 flora are quite complete, the quantification of coverage by each community could be assessed accurately over such a large area only 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 a 10,000-scale resource provided the Taylor Slough Microhabitat map (Hunter 1990). This map was used for a find-scale (106 microhabitat patch-types, 625 m^2 cells) analysis of females' behavior during the fawning season. The Florida Game and Fresh Water Fish Commission meanwhile created a broad-scale habitat map (16 categories,

Table 6. Population characteristics for white-tailed deer in eastern Everglades National Park for the interval January 1987-June 1991 (3 years).*

	Average or RangeJan 87-Jun 91
Density (#/km^2)	0.68
Productivity (F/AF)	0.82-0.94
Sex ratio	
at birth	1:0.7
at 1 yr or over	1:2.4
Litter size (n = 85)	1.0
Age structure (%)	
0-1 yr	22
2-3 yrs	33
4-5 yrs	10
< 6 yrs	33
Mortality	
Fawns	0.54
Yearlings	0.24-0.32
Adults (>2 yrs)	
Females	0.13
Males	0.19
Recruitment per year (%)	
(≥18 mon ≤3 yrs)	1

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

1000 m^2 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 (LPK). Also, some satellite imagery was obtained from the Florida Department of Transportation and classified into six broad landscape types for panther home-range analysis (Smith and Bass 1994).

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 percent isopleth. Panthers home ranges for were estimated from telemetry locations by using the program HOMERANGE (Samuel et al. 1985); the core activity area was defined as the 60 percent harmonic mean.

Home ranges of adult male deer were larger than those of adult females. Overlapping home ranges for 22 females covered 8.15 km^2, 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. Home ranges (which barely overlapped) around the LPK area for 16 adult males covered 18.05 km^2, for an average individual area of 1.13 km^2 (113 ha). Individual core areas for males averaged 12.4 km^2 (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 also was seen in the BCNP deer populations (Zultowsky 1992). Zultowsky (1992) found female home ranges averaging 5.4 km^2 in BCNP and 2.95 km^2 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 km^2 in BCNP and 2.9 km^2 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 the 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 (Smith and Bass 1994) were compromised. Panthers and adult bucks did utilize the edges of tree islands more than any other habitat (Smith and Bass 1994). 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). However, panther home ranges were smaller in the wet season (Dalrymple and Bass in press), 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, it mainly cleared undergrowth and did not often kill mature trees. The prairie vegetation showed regrowth with in 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 noted changes 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 or when home ranges were 100 percent inundated (as in the wet year of 1988) (Hunter 1990). However, historical maximum depths were not reached, so a critical depth where water begins 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) (Fig. 6).

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

While investigating the relative rates of success in fawn-rearing in the two types of prairie (wet or dry, defined above) (Hunter 1990; 1994), it was discovered that does residing year-round in wet prairies had significantly less success raising fawns to the 3-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:

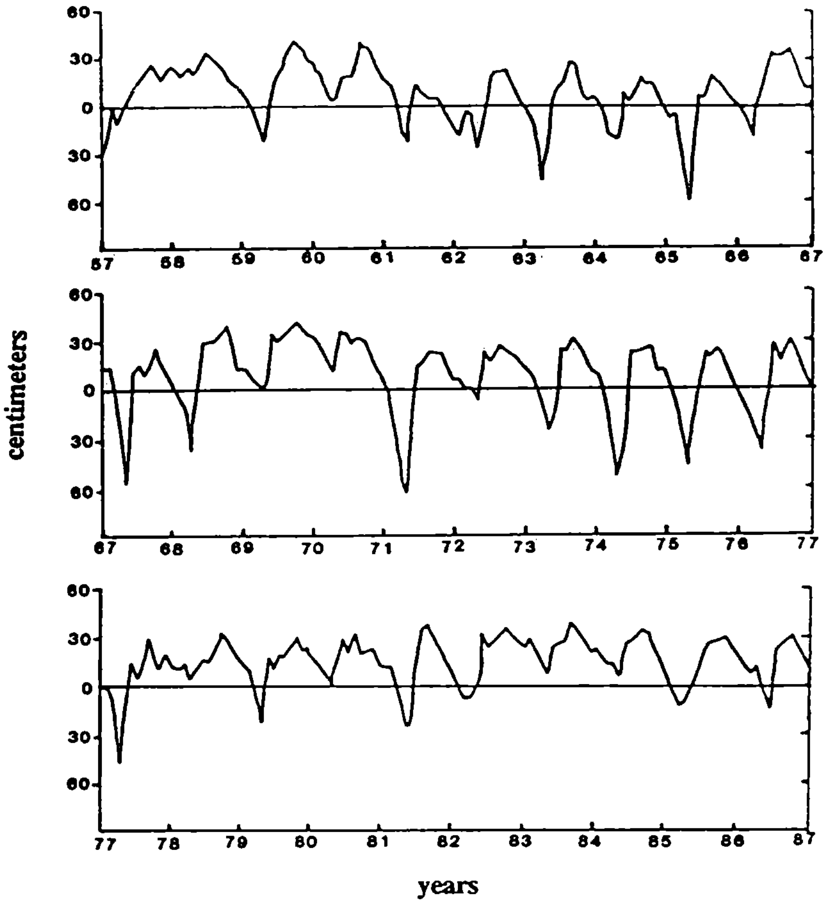


Figure 6. Modelled water table in relation to ground level (horizontal line at 0), from data recorded each year from 1957 through 1987, in typical wet prairie (station P38), Everglades National Park. Year marks are at January (Hunter 1990).

(1) ridges with trees, and (2) wet prairies with scattered trees. Both males and females had smaller home ranges on ridges (5.3 km^2 and 2.5 km^2) and larger home ranges if inhabiting prairies (8.2 and 6.2). The ridges are characterized by greater cover density and frequency of tree islands in BCNP (Miller 1993).

GENERAL 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, 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 that on which deer can survive 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 (Brokx 1972) (optimum 4/ km^2 = 25 ha/deer; crude density 2.0-2.5/km^2), a similar habitat, implying this is the carrying capacity of flooded savannahs (Eisenberg et al. 1979; Stuwe 1985). Authors have labelled bottomland hardwood forests as the best habitat for deer in the southeastern United States (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 interspersion of shrubs and trees, higher interspersion 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 presupposed 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 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 1960s [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 have been the factor limiting panthers (Smith and Bass 1994).

NOTE: This publication is an abbreviated version of the project final report submitted to the U.S.N.P. by J.F.E. and M.E.S. The priority of authorship reflects the actual field efforts and data analyses. The total data set for E.N.P., developed by T.R. Smith, will be analyzed and submitted for separate publications by Smith and associates.

J.F.E.

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