DISTRIBUTION, ABUNDANCE, AND DEMOGRAPHY OF WHITE-TAILED DEER IN THE EVERGLADES

MARTY FLEMING - ***National Park Service, Everglades National Park, 40001 SR 9336, Homestead, FL 33030.***

NOTE: The author chose to use the following report for these proceedings.

Distribution and Abundance of White-Tailed Deer in the Florida Everglades

By: D. Martin Fleming[1], James Schortemeyer[2], and John Ault[3]

[1] National Biological Service, Everglades National Park Field Station, Homestead FL.
[2] Florida Game and Fresh Water Fish Commission, Naples, FL.
[3] Florida Game and Fresh Water Fish Commission, Lake City, FL.

ABSTRACT

The large size of white-tailed deer, their role as a major herbivore in the Everglades, as well as significant and well publicized die-offs related to high water conditions, and their importance as a key prey base for the endangered Florida panther, have focused attention on the Everglades deer herd. However, no data are available on the relative distribution and abundance of deer in the Everglades in relation to systemwide landscape patterns and temporal characteristics. Objectives of this study, therefore, were to (l) document seasonal and annual changes in their relative distribution and abundance systemwide, (2) identify environmental correlates influencing the distribution and abundance patterns observed, with particular reference to hydrologic parameters, and (3) assess changes in deer distribution and abundance in response to intensive, regional water management regulation initiated in the early 1960s.

Systematic aerial surveys were conducted over the freshwater, interior wetlands of the system during the wet (August/September) and late dry season (May/June) months from 1985 -1989 to document deer distribution and abundance. Annual productivity estimates (number of fetuses per adult doe) from harvested does in the northern Everglades and annual recruitment indices (number of 3+ month old fawns in population) for the entire study area were also obtained during this study period.

Highest average densities of deer observed occurred in wetlands characterized by seasonal water level fluctuation and intermediate hydroperiods. Estimated average breeding date occurred on 30 July, and ranged from 26 July to 1 August. Estimated breeding dates of individual deer (n=69) ranged from 13 May to 10 September. Annual average productivity over the study period was 1.18 (n=69) and ranged from 1.0-1.33. Annual productivity was related to average marsh water depths during the gestation period (September-January). Peak fawning was well synchronized with seasonal changes in the hydrologic regime and occurred during the middle of the dry season (February/March), at a time when numerous dry sites are normally available for fawning. Fawn survivorship was inversely related to average marsh water depths during the fawning season (January-May) of each study year in drainage basins with pronounced seasonal water level fluctuations. In such drainage basins, total numbers of deer fluctuated in relation to seasonal and annual changes in marsh water depths.

Comparison of deer herd population estimates from this study with those of previous studies conducted in the 1950s suggest that a major reduction in deer numbers within the northern Everglades has occurred. Environmental factors believed related to this decline, including wetland drainage and impoundment associated with intensive, regional water management practices initiated in the 1960s, are discussed along with critical hydrologic restoration elements.

INTRODUCTION

The Everglades has long been recognized

for its diversity of flora and fauna. Generally, the terrestrial component of the Everglades faunal community has received considerably less attention than aquatic or semi-aquatic components. White-tailed deer, the only large herbivore of the Everglades, constitute the best known terrestrial species. Their large size and role as a major herbivore in the system, as well as significant and well publicized die-offs related to high water conditions, have focused attention on the Everglades deer herd.

More recently, considerable attention has been focused on white-tailed deer as a prey base for the Florida panther. Maehr et al (1990) documented that deer constitute a minimum of 40 - 50 percent of the panther's diet. While wild hogs, another large mammal, are abundant and important as a panther prey item elsewhere in Florida, observations during this study indicate that they are absent or rare throughout much of the Everglades.

In the Everglades region, deer inhabit a variety of landscape types, including the pinelands and high ridges that extend into the wetlands from upland landscapes, adjacent peripheral wetlands, the mosaic of sawgrass and wet prairie savannahs and sloughs that comprise the interior, freshwater wetlands, as well as the coastal mangrove forests. The highest relative density of deer, however, occurs in the tree island prairies of the interior wetlands that provide feeding areas, escape cover, and reproductive habitat for a variety of native animals (Gunderson and Loftus, 1993). The terrestrial component of these tree island prairies has always constituted an integral feature of the Everglades landscape.

Unfortunately, human-induced perturbations within the Everglades have generally resulted in adverse long-term impacts on flora and fauna, including terrestrial species. Thus, as wetlands were either drained for development, or impounded for water supply and/or flood control purposes, the Everglades deer herd declined. As a result of this habitat loss and degradation, deer are rare or absent on that half of the Everglades landscape which has been either urbanized or agriculturalized or within deep water impoundments.

Past studies of the Everglades deer herd have been conducted within the upper reaches of the Everglades catchment area only (Loveless, 1959; Loveless and Ligas, 1959). No data are available on the relative distribution and abundance of deer in the Everglades in relation to systemwide landscape patterns and temporal characteristics.

The objectives of this study, therefore, were to: (1) document seasonal changes in the relative distribution and abundance of the Everglades deer herd systemwide, (2) identify the environmental correlates influencing changes in the distribution and abundance patterns observed, with particular reference to changes in surface water conditions, and (3) assess changes in deer distribution and abundance in response to intensive, regional water management regulation initiated in the early 1960s.

ECOLOGICAL FACTORS AFFECTING DEER POPULATIONS

White-tailed deer are highly adaptive, occurring over a wide range of climatic and habitat conditions, and capable of reproduction at an early age, with local populations comprised of several overlapping generations (Baker, 1984). Population size is maintained through individual longevity, low reproduction countered by great parental care, complex social behavior which permits gregariousness, and capabilities of exploiting patches of habitat in space and time (Wilson, 1975; Geist, 1980). Fundamental environmental characteristics that affect their population dynamics and abundance in the Everglades include thermal, hydrologic, salinity, and fire regimes, as well as the topographic and landscape features of the system. These fundamental characteristics directly influence deer and their habitat.

The Everglades is located at the convergence of the Gulf of Mexico and South Atlantic coastal plains. This region is characterized by a mild climate (mean annual temperature from 10-20 C), a high precipitation rate (from 40-160 cm per year), and a long growing season (from 185-300 days) (Short, 1986). Forage quality and availability, as compared to deer requirements for cover or water, are believed to be major limiting factors to deer range carrying capacity in Florida. Deer are ruminants, with small stomach capacities, and are selective for high quality forage to meet their nutritional needs (Short, 1986). The abundance of quality forage, therefore, often determines deer herd size and rates of increase. In the Everglades, even with a long growing season, relatively infertile soils limit the production of quality forage (Harlow and Jones, 1965).

Food plants of deer can be classified into three principal types: (1) soft and hard mast, (2) cool (or dry season) grasses or forbs, and (3) leafy browse. In the Everglades landscape, the availability of mast appears to be restricted. In overdrained peripheral or dry prairie habitats, the availability of quality dry season forbs may also limit deer carrying capacity. In deep water portions of impounded marsh areas, browse availability is also reduced. Major foods in the Everglades include forbs such as Nymphaea odoratra, Crinum americanum, and Hymenocallis tridentata and leafy browse (Salix amphibia and Sambucus simpsonii) (Loveless, 1959).

Deer nutritional requirements vary by season of the year in relation to an individual's age and reproductive status, and the weather (Short, 1986). Cycles of change in deer body weights and food consumption rates over an annual period are related to these seasonal nutritional requirements. Deer dietary requirements for phosphorus and nitrogen in forage also vary seasonally and influence habitat suitability (Harlow and Jones, 1965; Harlow, 1972; Short, 1986).

In the coastal plain, the nutritional value of forbs and broadleaved browse plants decline rapidly after the late spring/early summer. Other food items then become important during the remainder of the year. In forest habitats, hard and soft mast, and the evergreen leaves of woody browse plants, provide highly palatable and digestible foodstuffs for the remainder of the year. In coastal herbaceous wetlands such as the Everglades, where mast availability is limited, forbs and evergreen browse remain important throughout the year, but their nutritional value diminishes (Short, 1986).

Climatic stress on deer can occur when air temperatures average 27 C (80.6 F) and relative humidity averages 75% (Short et al, 1969). In the subtropical latitudes of the Everglades, average monthly temperatures and relative humidity at or above these ranges occur from June through September, with temperatures of 32 C or above (> 90 F) occurring on one half to two thirds of the days during these months (National Oceanic and Atmospheric Administration, 1985).

The hot, humid summer/wet seasons typical of this climate can influence deer food consumption rates, the reproductive physiology of does, and the growth rate and survival of fawns (Short et al, 1969), as well as water consumption requirements for deer of all age classes (Marchinton and Hirth, 1984). Heat-related stress to deer during such climatic conditions that cause diminished food consumption rates may also affect the nutritional status and health of adults and young (Short et al, 1969). This period of climatic stress also coincides with a rapid decline in the nutritional value of fast growing vegetation and can create nutritional deficiencies that may weaken individuals and increase their susceptibility to accident, predation, and/or disease (Short et al., 1969).

Other factors such as intra- or interspecific competition may limit deer numbers. The restricted distribution of feral hogs in the Everglades limits potential competition with deer. However, competition among deer for food and space can be significant. Such intra-specific competition is often related to the sex and age classes of individuals comprising a deer herd in relation to population density, habitat conditions, and/or weather. Deer populations can increase temporarily above the sustaining level of their food supplies (Watt, 1968).

When intra-specific competition is significant, deer survival, growth, and reproductive success decline. Fawn mortality may increase dramatically, and older deer may suffer from malnutrition, resulting in poor physical condition, increased susceptibility to disease, predation and/or accidental death. A general decrease in productivity (40 - 50 %) and/or growth with decreased nutritional plane have also been reported, including reduced fawn pregnancies, ovulations per doe, fawns per doe and body size (Morton and Cheatum, 1946; Cheatum and Severinghaus, 1950; Taber, 1956; Taber and Dasmann, 1957; Julander et al., 1961; Klein, 1964; Severinghaus and Tanck, 1964; Mautz, 1978). In addition, an increasing proportion of male fawns at birth may result with decreasing nutritional plane (Verme 1965, 1969).

Under prolonged severe climatic conditions, competition among deer for food can result in high mortality, particularly of young and old deer, as stored fat reserves and food availability decline (Severinghaus, 1972; Mautz, 1978; Halls, 1978). In the impounded marshes of the northern Everglades, periodic "die-offs" of deer have occurred as a result of malnutrition and/or starvation. Such occurrences are a result of periodic high water levels, forcing deer onto tree islands over extended periods until all available food plants have been consumed. Browse lines occur during these periods, with high resulting mortality of deer, particularly fawns (Loveless,1959; Harlow and Jones, 1965). Publicity of such die-offs has necessitated a management/harvest strategy that now maintains the deer herd in these impounded marsh areas to post-flooding population levels (FGC, 1983).

Deer habitat quality has also been affected by changes in the system's hydrologic regime. Changes in overland flow volumes, and the timing and distribution of these flows during the recent past period of water management, by either overdrainage or the construction of impoundments, have altered the hydroperiods and stage durations of formerly occupied prairie habitats by deer throughout the Everglades (NPS, 1990). Overdrainage of both peripheral, marl prairie or interior wet prairie habitats within the upstream portions of impounded marsh areas has resulted in increased oxidation rates of mucks and frequency of deep muck fires. These events have resulted in the loss of tree island communities important to deer as a source of both browse and cover in these open grassland habitats (Schortemeyer, 1980). The excessive water depths and stage durations that characterize downstream surface water pools that form in these impounded marsh areas, have also reduced the areal extent and suitability of tree island prairies formerly occupied by deer throughout the northern Everglades (Dineen, 1974).

Such alterations in the natural hydrologic regime also affect the variety and seasonal sequence of plant foods available to deer. The natural adaptation of native vegetation to soil-water-climatic conditions or regimes that affect plant succession have been altered in areas of drainage or impoundment (Davis, 1943). Deer metabolic requirements for maintenance, growth, and reproduction change seasonally. As the digestibility and nutrient composition of forages also change seasonally, deer must feed on a greater variety of food plants to meet their energy needs (Short, 1986). Low deer abundance in marsh areas characterized by hydroperiod extremes may also reflect this reduction in the variety or interspersion of plant species in overdrained or impounded Everglades wetlands.

Deer population dynamics and abundance can also be affected by predators. Ungulate-predator relationships, or the role of predation as a limiting factor of ungulate populations, however, have been extensively debated in the scientific literature and reviewed by Connolly (1980). In modern times, the reduction or elimination of most large predators in ungulate ranges has often relegated predators to a secondary role in influencing or limiting ungulate numbers (Robinette, 1956; Huffaker, 1970; Connolly, 1980). The influence these predators have on regulating ungulate populations appears to increase with the relative numbers or ratio of predators to prey (Mech, 1970). Such predator-prey ratios are dynamic, changing over time (Keith, 1983). The age, sex, and/or physical condition of individuals killed by predators is related to a wide array of factors. These may include environmental factors, prey densities, prey conditions, predator density, and food availability.

In the Everglades, two predator species, panther and bobcat, both exist and prey upon white-tailed deer (Smith and Bass, 1991; Labisky et al., 1991). Panther are now rare, with only approximately 30 - 50 documented individuals occurring in adjacent habitats and the Everglades (Maehr, 1990). Recently, Labisky et al. (1991) have suggested that bobcat predation may be impacting deer recruitment in a ridge complex along the southwestern edge of the Everglades. " High bobcat density, low alternative prey availability, nutritional stress on deer, and coincident parturition cycles for both predator and prey," are proposed as factors contributing to the high level of bobcat predation documented. Alligators may also prey upon white-tailed deer in the Everglades. However, such predation is infrequent, with other prey items constituting most of alligator diets (Fleming, 1993).

Predation, as a limiting factor on localized populations of deer in the Everglades, may occur in particular activity ranges of individual panthers and/or in high elevation landscapes occupied by other terrestrial predators, such as bobcat (Labisky et al., 1991). However, environmental factors that affect the availability of high quality forage appear to be the determinate variables influencing deer carrying capacity and population dynamics throughout most of the Everglades deer herd range.

In general, Everglades deer herd contingent characteristics portray a population with a relative low abundance, low productivity, and smaller body size than that documented for other populations in the more northern portion of the species range (Newsom, 1984). Deer in southern Florida also occur in lower densities (Schemnitz, 1974) and have a lower fecundity (Harlow, 1972) than in other areas of the state.

Fundamental environmental characteristics of the Everglades that may contribute to these relative differences include: (1) the comparatively low fertility of the dominant soils, (2) resultant low nutrient availability in forage plants, (3) climatic stress, related to high summer temperatures and humidity and a rapid decline in the nutritional value of fast growing forage, all of which occur during critical periods of adult deer reproductive cycles (peak ovulation in does and spermatogenesis in bucks), and during a period of rapid growth in young deer, when food intake and nutritional requirements are highest, and (4) the periodic restriction of deer movements to high ground during periods of prolonged high marsh water depths, that can affect a deer's nutritional status and physical condition, and subsequent survival, growth, and reproductive performance.

STUDY AREA

The study area included most of the freshwater interior grasslands of the Everglades, encompassing approximately 506,818 hectares (1,251,800 acres) (Figure 1). Mixed agricultural and urban development border the study area to the north and east, fresh to slightly brackish mangrove estuaries to the south, and cypress swamp to the west.

Elevation ranges from 6 m. msl (19.7 ft.) in the northern reaches to 0.3 m msl (1.2 ft.) in the southernmost reaches of the study area. Elevational gradients are slight and, except for several local topographic features (predominately ridges), decline on average approximately 3 cm per km from upper to lower reaches of the study area.

Limestone bedrock in the interior marshes of the study area is overlain with deep muck deposits in the northern reaches, gradating to shallow deposits and exposed, eroded limestone bedrock in the southern reaches. High elevation marshes bordering the study area to the east are overlain by organic and inorganic marls and, to the west, by sandy marls. Mixed, unclassified tidal marls and mucks underlie the coastal estuaries to the southeast, south, and southwest of the study area. Depressions or solution holes in the underlying bedrock also create open water ponds or "alligator holes" that occur throughout the freshwater wetlands.

Prominent vegetational patterns of the study area include extensive dense sawgrass prairies, interspersed with tree island and wet prairies in the northern reaches and a mosaic of sawgrass, tree island prairies, wet prairies, and sloughs in the southern portions, bordered by extensive marl prairies to the east and west, and mangroves to the south.

Rainfall is seasonal, with eighty percent occurring between May and October, followed by pronounced fluctuations in marsh water depths (MacVicar, 1981). However, impoundment of overland flows in the northern reaches of the study area into water conservation areas (WCAs) has resulted in the formation of semi-permanent to permanent, deep, surface water pools in the downstream portions of each WCA. In the downstream areas of each impoundment, tree island and wet prairies have been replaced by slough/aquatic plant communities. During peak rainfall periods, water depths within these WCAs frequently exceed regulatory limits, necessitating releases through water control structures to downstream reaches of the Everglades (NPS, 1990).

Normal discharges from these impounded marshes, downstream through Shark River Slough (the historical central flowway of the southern Everglades) are currently based on a rainfall - delivery formula. Considerable variation in seasonal and annual flows through the slough have characterized recent water deliveries. These deliveries have resulted in increasingly frequent drydowns of extended duration and magnitude in the slough during the dry season months, and high seasonal flows during the wet season months, compared to documented and estimated natural flows before intensive regional water management regulation was initiated in the 1960s (Craighead, 1968: Perkins and MacVicar, 1991; Johnson and VonHatten, 1991).

The marl prairies bordering the eastern edge of Shark River Slough in the southern Everglades have also been impacted by recent water management practices. Overdrainage to benefit agricultural activities on adjacent lands has resulted in a major reduction in the depth and duration of seasonal inundation (Johnson and Fennema, 1989) and the subsequent invasion of exotic trees and shrubs throughout these peripheral wetlands (Hofstetter, 1988).

METHODS

Data collection

White-tailed deer relative distribution and abundance were documented using systematic aerial transect counting techniques (Norton-Griffiths, 1978). East-west oriented transects across the predominant, topographic gradients of the study area, and spaced at 2 km. intervals from north to south, were flown in June (low water) and in August/September (high water), 1985-1989. Navigation of transects was conducted by reference to a Loran C navigational aide. Survey height (61.5 m agl), strip width (100 m), and ground speed (80 knots) were standardized for all surveys to minimize and hold constant visibility bias.

A left and right observer counted all deer seen within 100 m strip widths (a 10 percent systematic sample of the study area). Surveys were flown from one half hour after sunrise to mid-morning, to avoid later daylight hours when deer were inactive.

Surface water conditions were qualitatively described by empirical observations during each survey flight. Surface water conditions and hydropattern maps were developed based on the dominant water condition in each cell as described in Fleming, 1993. Marsh water depths and stage duration curves at hydrologic index stations in each of the drainage basins comprising the study area were also used to document and describe water conditions.

Breeding and parturition dates in the central Everglades were determined by examination of harvested deer during November/December, 1981-1985. Ages of embryos from harvested pregnant does were estimated by measurements of crown-rump lengths (Harlow and Jones, 1965). Breeding/conception dates were estimated by backdating from the collection date. Parturition dates were estimated by assuming a 200 day gestation period (Hesselton and Hesselton, 1982).

Annual productivity and recruitment have been measured in the northern Everglades for 8 years (1981-1988) prior to and during the study period. No productivity estimates were obtained in the southern Everglades as part of this study. However, indices of annual recruitment were obtained for the southern Everglades during the study period (1985-1989).

Productivity was defined as the number of fetuses per adult doe. Productivity estimates for deer in the northern Everglades were obtained from examination of hunter-killed does.

Annual recruitment was indexed as the number of fawns reaching 3+ months of age divided by the estimate of the total population, including fawns. Annual recruitment indices were obtained by aerial survey flights along established survey lines during late May or early June of each year. The number and location of all adult and large spotted fawns were recorded to obtain fawn/adult ratios, as an index of annual recruitment for geographical subareas of the study area.

Data analyses

Deer count data and coordinates of these observations were processed as described in Fleming (this volume) and the distribution and abundance of deer mapped on a 2 x 2 km cellular grid developed for aerial surveys in the study area. Descriptive statistics for several distribution and abundance parameters were also calculated as described in Fleming (1993).

To describe seasonal changes in deer distribution and abundance in relation to landscape patterns within the study area, a hierarchial, landscape classification analysis was conducted of the study area, following the methodology as described in Astel et al. (1969) and Fleming et al. (1993).

Descriptive statistics, mean deer densities +/- one standard error, and occupancy (percent of total numbers) by landscape categories within the study area were then calculated for each wet and dry season survey flight to describe and compare deer use of these landscape categories in response to variation in hydroperiod.

The relationship of annual productivity and recruitment to average marsh water depths at hydrologic index stations in subareas or drainage basins of the study was examined through the use of simple univariate regression analysis.

RESULTS

Everglades deer herd relative distribution and abundance

Deer were not distributed evenly over the study area (Tables 2 - 4). During most surveys conducted when marsh water depths were high (exceeding 50 cm), highest deer densities occurred in moderately dry landscapes. High occupancy areas during these months were normally restricted to higher elevations, including rock outcrop/ridges, adjacent peripheral wetlands, the edges of central sloughs, and tree islands within slough habitats. During surveys conducted when water levels are typically low (< 20 cm. marsh water depth), deer were more evenly distributed.

Deer distributions were generally related to surface water conditions, regardless of the season. Greatest concentrations of deer were observed in high elevation marsh sites during periods of increased overland flows that normally occurred during the August/September surveys. However, deer were also observed concentrated in these same areas whenever unseasonably, high water levels occurred during the June surveys (Table 5).

Geographical subareas that were consistently occupied by disjunct, local concentrations of deer throughout the study period included: (1) peripheral or marl prairies to the east and southeast of Shark Slough within the southern Everglades; (2) a prominent outcrop/ridge forming a divide between the Big Cypress Swamp and interior wetlands of the Everglades, including adjacent marl and tree island prairies bordering and to the northwest, west, and southwest of Shark Slough; (3) tree island/wet prairies in south-central Everglades mainland (WCA3B); (4) within the sawgrass prairies of the northern reaches of the Everglades catchment basin included within the study area (upstream portions of WCA2A, WCA3A North, and WCA3A South) (Figures 2, 3).

Deer numbers in tree island/wet prairie habitats in the central flowway of the southern Everglades were highest during the June surveys in years with pronounced, dry season water level declines. Concurrent, slight increases in deer numbers occurred in the headwater regions of adjacent mangrove estuaries as the interiors wetlands dried and water levels also declined in the estuaries. However, numbers of deer observed in the estuary headwaters during all surveys were consistently low. Numbers observed in this region declined during the wet season months, as water levels increased. Deer densities in the deep water, downstream portions of the water conservation area impoundments of the northern, and overdrained peripheral wetlands of the southern Everglades, were also consistently low (Table 3).

The relative abundance or average densities of deer were consistently lower in marsh areas characterized by either (1) artificially extended hydroperiods and high stage durations resulting from impoundment, or (2) by severely reduced hydroperiods and low stage durations as a result of overdrainage. Marsh areas with approximate annual hydroperiods greater than nine months and characterized by high marsh water depths of prolonged duration, as well as marsh areas with annual hydroperiods of less than 2-3 months that dried down severely every year, supported low average densities (Table 3, Figure 4) and relative occupancy rates (Table 4).

Everglades deer herd breeding and parturition dates

Estimated annual breeding and parturition dates of individual deer in the northern Everglades were also variable. The estimated average breeding date from 1981-1985 occurred on 30 July, and ranged from 26 July to 1 August over the 5 year period (Table 6). Estimated breeding dates of individual deer during this period ranged from 13 May to 10 September. The estimated average parturition date occurred on 15 February, and ranged from 12 February to 17 February during the 5 year period. Estimated parturition dates for individual deer ranged from 29 November to 29 March. This fawning season is well synchronized with seasonal changes in the hydrologic regime and occurs during the mid-dry season months, at a time of rapid drying of the marsh floor when numerous dry sites are available for fawning. Fawns born during this period are approximately 3+ months old when marsh water depths begin rising again with the return of spring rains.

Everglades deer herd annual productivity in relation to environmental factors

Annual average productivity estimates for deer in the northern Everglades varied from year to year in relation to annual changes in average marsh water depths during the late wet/early dry season months (September - January) (Figure 5). The mean number of fetuses per doe over the study period was 1.18 (n=69) and ranged from 1.0-1.33 (Table 7). The occurrence of two fetuses per doe was observed in approximately 25% (17) of the does examined, and ranged from a low of 12% to a high of 40%.

Everglades deer herd annual recruitment in relation to environmental factors

Annual recruitment also varied from year to year and by drainage basin. Although annual recruitment over the entire study area was relatively constant, recruitment varied greatly among years in different drainage basins (Table 8). Recruitment was inversely related to average dry season marsh water depths during the fawning season of each study year (January-May) in drainage basins with pronounced seasonal water level fluctuations (Figure 6). Annual recruitment declined sharply in such basins when average water depth exceeded 45 cm (1.5 feet). Annual recruitment was less variable in relation to annual changes in marsh water depths in the higher elevation drainage basins of the northern Everglades which have a more pronounced topographic gradient. Recruitment in areas with a relatively steep topographic gradient was not as strongly correlated with water depth as in areas with a more gradual gradient.

Everglades deer herd population dynamics in relation to environmental factors

Total numbers of deer in geographical subareas of the study area fluctuated in relation to seasonal and annual changes in marsh water depths. These fluctuations were caused by changes in productivity and recruitment to breeding age classes of the Everglades deer herd (Figure 7). During wetter years with above normal marsh water depths throughout the dry season months, deer were restricted to higher elevation sites in geographical areas or basins with normally pronounced fluctuations in seasonal water levels. Deer productivity and fawn survivorship in such areas during these years decreased, as well as subsequent estimates of total deer numbers in each of these geographical subareas. During lower rainfall years and dry season marsh water depths, deer productivity and fawn survivorship increased in these areas, as well as the subsequent total number of deer.

DISCUSSION

Geographical subareas of the Everglades landscape that supported the highest average densities of deer were characterized by seasonal fluctuations in water levels and intermediate hydroperiods. Overdrained or impounded prairie habitats with reduced seasonal and annual variability in water levels, and either short or long hydroperiods, supported consistently low deer densities. Habitat suitability appears correlated to the seasonal fluctuation in marsh water depths in an area in relation to drainage characteristics of the local topography, associated soil type and development, and the resultant interspersion of vegetational associations and related seasonal availability of quality food plants.

The reduced deer abundance in deep water, impounded marsh may be attributed to more restricted movements of deer in such areas, affecting their ability to obtain a sufficient year round diet. The lower relative numbers of deer observed in overdrained marshes, compared to higher observed densities of deer in wetland areas with more normal ranges of seasonal water level fluctuation, may reflect less desirable range characteristics. Such characteristics may be the result of a reduction in forage quality, related to the rapid drying and decreased palatability of vegetation in these areas during the dry season months. Deer distribution and abundance appears to be adversely affected by extremes in hydroperiod conditions.

White-tailed deer abundance in the headwater region of coastal mangrove forests was also low, compared to deer occurrence in upstream, freshwater wetlands. High ground in these coastal mangrove forests is primarily restricted to coastal beach and dune ridges, the elevated banks of tidal rivers, and to local topographic features in the headwaters of the upper estuaries.

The availability of free standing sources of potable drinking water to deer, as well as the availability of dry/firm ground, vary with the wet to dry season rise and fall in mean sea level (Marmer, 1954), and with increased local rainfall and sheet flow into the estuaries from upstream, freshwater marshes during the wet season months. The salinity regimes that characterize these coastal estuaries also vary both spatially and temporally, from freshwater surface lenses that result from local rainfall during the wet season months (Mozatti, 1983), to brackish and hypersaline conditions (>40 ppt) that characterize much of the area during the late dry season (Odum et al., 1982; NPS, unpub. data). Although Klimstra et al (1974) have determined that mangrove spp. may be an important deer food, the limited availability of high/firm ground during the wet season months, and the limited availability of free standing sources of potable drinking water during most dry season months, apparently restrict deer utilization of these coastal landscapes.

Annual average productivity estimates of does in the freshwater wetlands of the northern Everglades were low compared to those reported for deer occurring on more fertile soils throughout the species geographical range (Verme, 1967), but were similar to those reported for deer herds elsewhere in Florida (Harlow and Jones, 1965). The correlation of annual average productivity to annual average late wet/early dry season (September - January) water depths indicates that peak productivity occurs at intermediate marsh water depths. High water restricts movement and thus availability of quality forage for pregnant does, while low water conditions may adversely impact the production of quality forage. Deer productivity would be expected to be more constant in marsh areas with only minor seasonal fluctuations in water depths.

Water level fluctuations during the latter dry season months also influenced fawn survival. Rapidly declining marsh water levels during the middle of the dry season (peak fawning period) allow fawns the necessary time to reach sufficient size and mobility before water levels begin to rise in the early wet season. Fawn mortality factors appeared to be correlated to high marsh water depths of extended duration during this fawning period. Such high water depths restricted deer distribution and may have affected doe and/or fawn nutrition, susceptibility to disease, and/or death from predation or accidents. Causal mechanisms may include: (1) restricted movements and insufficient and/or increased competition between fawns and older deer for food, (2) an increased incidence of disease or parasites resulting from malnutrition and/or the overcrowding of deer on restricted high ground/escape refuges, (3) an increased vulnerability of fawns to predation, resulting from restricted movements of both fawns and potential predators to high ground, and/or (4) accidental deaths of fawns related to the rough texture or characteristics of high terrain, e.g. rock outcroppings/eroded bedrock/solution holes. Topographic relief, where present, may therefore ameliorate fawn mortality associated with high water conditions.

The drainage patterns formed by the underlying topographic contours in the Everglades directly affect deer distribution. Deep water and extended inundation of the central sloughs limit most deer occupancy in these areas to tree island habitats during wet periods. Tree islands in the wet prairies of the interior Everglades, as well as ridges bordering the central sloughs of the southern Everglades, provide the only available high ground for escape habitat during seasonal or periodic high water conditions or events. Deer occupancy is less variable and deer distribution more uniform in the shallow, seasonally-inundated, peripheral wetlands or marl prairies to the east and west of these interior central sloughs.

Important environmental characteristics that limit the carrying capacity, or size and rates of increase in the Everglades deer herd, include: (1) the relatively infertile and shallow soils that limit the availability of high quality forage, (2) the relatively flat gradient or slope of the terrain, with limited topographic relief to provide escape habitat during high water or flood conditions, and (3) the extensive open grassland savannas, or reduced variety of forage plants, that characterize much of the Everglades landscape.

Landscape features that provide habitat heterogeneity associated with increased deer abundance include: (1) aberrations in the local topography that provide high ground and support scattered hammocks or tree islands, (2) the grainess (micro-heterogeneity) or presence of solution or pot holes in high elevation peripheral wetlands or rocklands and associated hammocks or stands of tropical trees, (3) the seasonal inundation characteristics of wet prairie and slough habitats, (4) the spatial and temporal characteristics of related fire regimes that maintain the interspersion of native plant communities, as well as (5) the seasonal sequence or phenology of plant growth and successional patterns.

Water management practices that have reduced this habitat heterogeneity appear to have affected deer abundance, particularly in the impounded marsh areas of the northern Everglades. The relative abundance of deer documented during this study in the northern Everglades represents a significant decrease in numbers since the mid-late 1950s, a time period coinciding with the development of the WCAs. Loveless (1959) estimated the deer population of the Everglades Wildlife Management Area (EWMA) during this period at 7,000 or one deer per 40 ha. The EWMA corresponds to the northern portion of the current study area and includes Water Conservation Areas 2 and 3. Our estimates for these areas varied from 1650 in 1985 to 860 in 1988. The high estimate represents a 76 percent decrease of the 1959 population estimate. However, survey methods were not directly comparable. Although Loveless conducted systematic aerial surveys using approximately the same height, strip width, and ground speed as our surveys, he also varied survey height to better count deer encountered in groups and when flying over more woody terrain. Such practices would be expected to reduce visibility bias relative to the constant height flown during our surveys. His survey also included correction factors for visibility bias which accounted for 20-30 percent of the estimated 1959 deer population. This same estimate is reduced to approximately 5000 animals, if uncorrected for visibility bias. Our high estimate (1,650) still represents a large decrease (67%) in the deer herd size. We conclude that a major reduction in the deer herd size has occurred in the northern Everglades as a result of habitat degradation from impoundment and associated water management.

The increased water depths in these impounded marshes, as well as the continuing human settlement of peripheral wetlands along the eastern edge of the Everglades, have also reduced the availability of adjacent high ground as escape habitat for deer during periods of high water. The response of the deer herd to the loss of wet prairie-tree island and peripheral wetland habitat is best demonstrated by the variability in annual fawn survival rates during extended high water periods and related adult mortality. The biotic instability of the deer herd to such high water events is further intensified in the reduced spatial extent of the post-drainage Everglades landscape. A greater proportion of the remaining natural wetland area is subjected to extended periods of deep water during such events, restricting the movements of deer within a limited area of high ground, relative to the pre-drainage landscape. The extensive tree island-wet prairie and peripheral wetlands of the historical landscape, and attenuated seasonal fluctuations in regional water levels, contrast sharply with the pronounced, seasonal, water level fluctuations and remnant tree island and peripheral wetlands that characterize post-drainage conditions. An increased instability and reduction in the size of the Everglades deer herd may be expected in relation to these changes.

Environmental conditions of the historical or pre-drainage landscape that would have contributed to the stability of the Everglades deer herd included: (1) lower seasonal variability in water level fluctuations, and (2) a reduced magnitude and frequency of flood and drought events, as well as (3) a greater spatial extent and diversity of suitable habitat types. Pre-drainage conditions also provided moderate water depths suitable for deer over a greater portion of the area throughout most of a year (NPS, 1990).

The extent that such changes in pre-drainage conditions affect the Everglades deer herd stability, or to what extent interactions among deer (biotic feedbacks) are destabilizing, depend to a great degree on these fundamental environmental characteristics. In the post-drainage Everglades landscape, biotic instabilities in the deer herd that result from high water events are more likely to develop into severe oscillations or population reductions, as such high water events are more likely to impact the entire area for prolonged periods. The human settlement of adjacent upland habitats, the limited dispersal tendency of deer, and their low fecundity reduce the herd's resilience or ability to recover from such environmentally-induced instabilities. Increased competition among deer for food in high water conditions that impact a greater proportion of the post-drainage landscape, may also result in increased malnutrition and vulnerability to disease, accidental deaths, predation, or starvation. Such biotic feedback would further intensify deer herd instability, relative to pre-drainage conditions.

Changes in the system's hydrologic regime are not the only long-term changes that may adversely affect the persistence of the Everglades deer herd. The continuing rapid rate of sea level rise (Hoffman et al, 1983) may also result in further reductions of suitable deer habitat by decreasing freshwater plant communities that are of high food value. Other adverse changes in habitat characteristics include the invasion of exotics into overdrained marshes, and the establishment of monotypic stands of unpalatable plant species as a result of nutrient enrichment related to agricultural runoff. The replacement of native plant community mosaics by such monotypic stands further reduces important habitat heterogeneity and the ability of deer to meet their critical dietary needs.

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