FOODS OF WHITE-TAILED DEER IN THE FLORIDA EVERGLADES: THE SIGNIFICANCE OF *CRINUM*

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ABSTRACT - The year-round food habits of white-tailed deer (*Odocoileus virginianus seminolus* Rafinesque) were studied in the wet prairie-tree island habitat of the southwestern Everglades system during 1988–91. Microhistological analysis of rumen contents revealed that a single plant, swamp lily (*Crinum americanum* L.), constituted 40.4% of the annual diet by dry weight and occurred in the rumens of 87.7% of 39 adults (≥ 1 yr in age) and 18 fawns (< 6 mo in age). No other food among the 35 plant items identified in the rumens constituted more than 6.6% dry weight. Swamp lily was the top-ranked food by dry weight for adult females (53.3%), adult males (29.6%), fawn females (27.1%), and fawn males (31.6%). Diet, by food category (e.g., aquatic herbs, woody plants) did not differ between the winter dry season and the summer wet season. Adult females consumed more aquatic herbs (69.8% dry weight) than adult males (38.2%), and, conversely, adult males consumed more woody plants (31.9%) than adult females (18.3%). These dietary differences between adult females and males resulted from the differential use of habitats by the sexes, likely to maximize reproductive success. The diet of fawns did not mirror that of adult females. Fawns consumed more woody plants than did adult females, which probably reflected the use of tree islands by fawns for concealment to avoid predation during their first months of life.

INTRODUCTION

The oft-stated adage, "An army runs on its stomach," is directly applicable to wild animals. Each wild species must exploit its given resources to survive. Thus, an understanding of the use of habitat and food resources is prerequisite to developing management strategies for any wild species.

The only major study of food habits of white-tailed deer in the Everglades was conducted more than 40 years ago by Loveless (1959), who examined the rumen contents of 43 male and 6 female deer collected during the fall and winter months of 1955–58. Of the 51 plant species he identified from rumens, only 4 had a wet volume > 10%; they were, in descending order: white water-lily *(Nymphaea*

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odorata Ait.), royal fern (*Osmunda regalis* L.), Carolina willow (*Salix caroliniana* Michx.), and swamp lily. These 4 species occurred in > 65% of the rumens and constituted 65% of the total diet of deer by wet volume.

The Everglades system has been wrought with many changes over the past 4 decades, particularly with respect to hydrology and vegetational composition (Davis et al. 1994). Thus, this study of food habits of deer was conducted in the Everglades system in the late 1980s and early 1990s to compare differences in the diets of deer between the hunted Big Cypress National Preserve (BCNP) and the non-hunted Everglades National Park (ENP), between the wet and the dry season, and among different sex and age classes. The goal of the study was to document important plant foods of deer for the purpose of ensuring that these species receive consideration in management regimes that are being proposed for the restoration of the Everglades.

STUDY AREA

The study area, located in the westernmost portion of the "Tree Islands Everglades" system (Craighead 1971, 1984), encompasses approximately 250 km^2 in the Tamiami Ranger District of ENP and the Stairsteps Unit of BCNP. The climate is subtropical with alternating dry winter (Nov–Apr) and wet summer (May–Oct) seasons. Mean annual temperature is 23 °C, with mean monthly temperatures ranging from 14 °C in January to 28 °C in August; mean precipitation is 136 cm, two-thirds of which falls between May and October (Duever et al. 1986). Topographic relief is approximately 1.5 m; the surface water flow is southwesterly over a gradient of 9 cm/km (Duever et al. 1986).

The landscape is a mosaic of intergrading patches that result from localized variation in soil depth, topography, hydroperiod, and fire (Duever et al. 1986). The primary plant communities are wet prairie (87%), which is typified by a hydroperiod of 5–150 days, and hardwood tree islands (7%) (Duever et al. 1986, Miller 1993). Wet prairie is characterized by a complex of grasses and sedges, including sawgrass (*Cladium jamaicensis* Crantz), maidencane (*Panicum hemitomon* Schult.), sand cordgrass (*Spartina bakeri* Merr.), muhly grass (*Muhlenbergia filipes* M.A. Curtis), spike rush (*Eleocharis* spp. R.Br.), and numerous aquatic herbs such as white water-lily, swamp lily, and flag (*Sagittaria lancifolia L.*). Tree islands are characterized by both temperate and tropical hardwoods, including swampbay (*Persea palustris* [Raf.] Sarg.), sweet bay (*Magnolia virginiana* L.), gumbo limbo (*Bursea simaruba* [L.] Sarg.), live oak (*Quercus virginiania* Mill.), cabbage palm (*Sabal palmetto* [Walt.] Lodd), cocoplum (*Chrysobalanus icaco* L.) and ferns. The density of deer on the study

area approximated 3.5–4.0 deer/km^2 in BCNP and 4.5–5.0 deer/km^2 in ENP (Labisky et al. 1999).

METHODS

Rumens were collected from 57 adult (≥1yr in age) and fawn (2–6 mo in age) deer that had been sacrificed for health studies, harvested by hunters, or killed by Florida panthers *(Puma concolor coryi* L.*)* or bobcats *(Lynx rufus* Kerr*)* during 1988–91. The sample, which included ≥ 2 rumens from each calendar month except February, represented 35 deer from BCNP and 22 from ENP, and 29 from the wet season (May–Oct) and 28 from the dry season (Nov–Apr). The age and sex distribution of the sample was: adult males, 13; adult females, 26; fawn males, 10; and fawn females, 8. Rumen samples were stored in plastic containers and frozen until microhistological preparation and analysis as described by Johnson et al. (1983a). Rumen samples were oven-dried, weighed, and then ground in a Wiley mill using a 1-mm mesh sieve to obtain plant fragments that were relatively uniform in size; uniform fragments reduce error that might result from differential fragmentation (Johnson et al. 1983a). The ground samples were soaked in sodium hypochlorite for 5 minutes to remove pigments, and then rinsed in cold water to remove the bleach (Reynolds et al. 1978). Five slides were prepared for each sample, using about 0.01 g of wet plant material. Twenty microscopic fields per slide (100 fields per sample) were examined at 125X magnification. Plant fragments in dicots were identified to genus on the basis of micro-anatomical characteristics such as cell walls, cell shapes, silica bodies, trichomes, and stomates and companion cells. Fragments of monocots are more similar among species than those of dicots, thereby making species identification more difficult; thus, grasses were not identified to species. Many plants were further identifiable to species from numerous on-site collections and descriptions of Everglades flora. Frequency of occurrence was based on the presence or absence of a species in each of the 100 fields for each rumen sample. Because fragments were relatively uniform in size, the average relative frequency of occurrence represents the relative abundance of the different species in the rumen sample. Given the relative uniformity in fragment size and similar dry weight bulk densities among species, the mean fragment size is equivalent to the percentage dry weight in the rumen. The conversion formula from relative frequency to mean fragment (particle) size is: $F = 1\text{-}e^{-d}$, where F = relative frequency, e = base of the natural logarithm, and d = mean fragment size (Johnson 1982).

Mean percentages of dry weights for food categories were compared among age and sex classes using a binomial test of difference between two proportions (Zar 1974). The α *priori* a level was 0.05.

RESULTS

Thirty-five different species of plants were identified from the 57 rumen samples, and were grouped into 6 food categories: woody plants (n = 17), terrestrial herbs (n = 7), aquatic herbs (n = 6), ferns (n = 2), berries/seeds (n = 2), and grasses (n = 1). Initial analyses indicated that the proportional dry weight of food categories did not differ ($P > 0.05$) between deer collected from BCNP (n = 35) or ENP (n = 22), or between deer collected during the wet season (n = 29) and the dry season (n = 28). Thus, data were pooled to evaluate overall food habits, and to investigate food habits by age and sex classes.

Swamp lily accounted for 40.4% of the dry weight of food consumed by deer, age and sex ignored, and occurred in 87.7 % of all rumens (Table 1). Another aquatic herb, floating hearts (*Nymphoides aquatica* [G.F. Gmel.] Kuntze) was the second-ranked food, constituting 6.6 % of dry weight and occurring in 40.4 % of all rumens. Greenbriar (*Smilax* spp. L.), wild sage (*Lantana involucrata* L.), and grasses comprised 6.4%, 6.3%, and 4.0% of dry weight, respectively. Collectively, these 5 top-ranked plants constituted 63.7% of the dry weight of the rumen contents of deer from ENP and BCNP.

Among age and sex classes, swamp lily was the top-ranked food with respect to dry weight and frequency of occurrence (Table 2). Notably, swamp lily constituted over half of the dry weight of foods

Table 1. Plants comprising > 2% of dry weight in rumens of 57 (39 adults and 18 fawns) deer from ENP and BCNP, 1988–91.

Plants[1]	Percentage dry weight (SE)	Percentage frequency of occurrence
Swamp lily (*Crinum americanum* L.)	40.40 (3.66)	87.7
Floating hearts (*Nymphoides aquatica)*	6.57(1.62)	40.4
Greenbriar (*Smilax* spp.)	6.37 (1.57)	40.4
Wild sage (*Lantana involucrata*)	6.27 (1.61)	29.8
Grasses	4.01 (0.93)	35.1
Primrose willow (*Ludwigia repens* J.R. Forst)	3.87 (1.56)	28.0
Cabbage palm berries (*Sabal palmetto)*	2.98 (1.77)	8.8
Oak (*Quercus* L.spp.)	2.88 (1.13)	22.8
Arrowhead (*Sagittaria lancifolia*)	2.78 (0.66)	35.1
Bracken fern (*Pteridium aquilinum* L. Kuhn)	2.76 (1.30)	17.5
Elderberry (*Sambucus canadensis* L.)	2.73 (1.01)	17.5
Blueberry (*Vaccinium* spp. L)	2.31 (0.91)	15.8
Elderberry (*Sambucus canadensis* L.)	2.73 (1.01)	17.5
Bloodberry (*Rivina humilis* L.)	2.20 (0.76)	19.3

[1]Plants comprising < 2% of dry weight, in descending order: winged sumac (*Rhus copallina* L.), white waterlily (*Nymphaea odorata* Ait.), sea myrtle (*Baccharis halimifolia* L.), bald cypress (*Taxodium distichum* L. Rich), red mangrove (*Rhizophora mangle* L.), hemp vine (*Mikania* spp. Wildl.), royal fern (*Osmunda regalis* L.), wax myrtle (*Myrica cerifera L.)*, beggarticks (*Bidens* L. spp.), grape (*Vitis* spp. L.), musky mint (*Hyptis* spp. Jacq., water hyssop (*Bacopa* spp. Aubl.), Carolina willow (*Salix caroliniana* Michx.), key lime (*Citris aurantifolia* [Christm.] Swingle), dahoon holly (*Ilex cassine* L.), unidentified herb, unidentified seed, slash pine (*Pinus elliottii var. densa* Little & Dorman), blackberry (*Rubus trivialis* Michx.), spider lily (*Hymenocallis palmeri S.Wats.*), Brazilian pepper (*Schinus terebinthifolius* Raddi)), and aster (*Aster* spp. L.).

consumed by adult females. For fawns, the second most prevalent food plant was wild sage, accounting for 22.4% and 15.1% of the dry weight diet of females and males, respectively. The percentage dry weight of the 5 top-ranked foods by age and sex cohort was: adult females, 75.0%; adult males, 64.2%; fawn females, 76.9%; and fawn males, 68.0% (Table 2).

Among age and sex classes, the consumption of different categories of plants differed ($P < 0.05$) only for aquatic herbs and woody plants (Table 3). Adult females consumed more aquatic herbs

Table 2. The 5 top-ranked plants by dry weight in rumens of deer by age and sex class, ENP and BCNP, 1988–91.

Plants [1]	Percentage dry weight (SE)	Percentage frequency of occurrence
Adult females (n = 26)		
Swamp lily	53.3 (5.1)	92.3
Floating hearts	10.4 (3.2)	50.0
Greenbriar	4.5 (2.1)	35.0
Grasses	3.7 (1.3)	35.0
Primrose willow	3.1 (1.2)	35.0
Total	75.0	
Adult males (n = 13)		
Swamp lily	29.6 (7.7)	76.9
Cabbage palm (berries)	12.4 (7.4)	23.1
Bracken fern	7.9 (5.3)	30.8
Oak spp.	7.4 (4.4)	38.5
Floating hearts	6.9 (2.5)	53.8
Total	64.2	
Fawn females (n = 8)		
Swamp lily	27.1 (7.4)	87.5
Wild sage	22.4 (5.7)	75.0
Greenbriar	15.0 (7.2)	50.0
Arrowhead	7.7 (2.9)	75.0
Primrose willow	4.7 (3.2)	25.0
Total	76.9	
Fawn males (n = 10)		
Swamp lily	31.6 (7.9)	90.0
Wild sage	15.1 (7.2)	50.0
Blueberry	8.5 (4.4)	40.0
Grasses	6.8 (3.1)	50.0
Bloodberry	6.0 (3.2)	40.0
Total	68.0	

[1] See Table 1 for scientific names.

Table 3. Percentage dry weight of plant categories in rumens of deer by age and sex class, ENP and BCNP, 1988–91. Standard errors are within parentheses. Percentages in rows followed by the same letter differed in paired comparisons ($P < 0.05$).

Plant category	Adult females (n = 26	Adult males (n = 13	Fawn females (n = 8)	Fawn males (n = 10)
Aquatic herbs	69.8 (9.0)[a]	38.2 (13.5)[a]	36.3 (17.0)	34.8 (15.1)
Woody plants	18.3 (7.6)[a,b,c]	31.9 (12.9)[a,d,e]	47.5 (17.7)[b,d]	39.7 (15.4)[c,e]
Terrestrial herbs	7.5 (5.2)	7.2 (7.2)	9.9 (10.5)	14.3 (11.1)
Berries and seeds	0.8 (1.8)	12.4 (9.1)	0.0 0.0	
Ferns	1.6 (2.4)	8.3 (7.6)	1.3 (4.1)	4.4 (6.6)
Grasses	3.7 (3.7)	2.0 (3.9)	4.9 (6.8)	6.8 (8.0)
Total	101.7	100.0	100.0	100.0

(69.8% dry weight) than adult males (38.2%). However, adult females consumed a fewer woody plants (18.3% dry weight) than adult males (31.9%), fawn females (47.5%), and fawn males (39.7%). The percentage dry weight consumption of woody plants by adult males was less than that of either fawn females or fawn males. Consumption of different food categories by female and male fawns was similar ($P > 0.05$).

DISCUSSION

The white-tailed deer, a keystone herbivore (Waller and Alverson 1997), is considered a concentrate-selector in that it selectively forages on high-quality and easily digestible plant parts (Demarais et al. 2000). Yet, throughout their range, white-tailed deer are "nibblers" in that they consume small quantities of hundreds of plant species. To illustrate, white-tailed deer consumed > 100 different species in West Virginia (DeGarmo and Gill 1958), Missouri (Robb 1951), Louisiana (Matthews and Glasgow 1981), and Florida (Harlow 1965). However, their mainstay diet consists principally of a few species, whether the scope of study is seasonal or annual. In Florida, Loveless (1959) reported that only 4 plant species comprised > 10% by volume of the diets of deer in the north central Everglades during fall and winter, and Harlow (1965) found that only 2 to 4 species constituted > 10% by volume of the diet of deer from several pine flatwoods habitats in northern and central Florida during late fall and winter. This study revealed that diet selection was even more restricted in the wet prairie-tree island habitat in the Everglades, where a single plant, swamp lily, comprised 40.4% of dry weight of the rumen contents of deer year-round; no other plant exceeded 7%. It is notable that over half the forage consumed by adult females was swamp lily. Furthermore, swamp lily was the top-ranked plant consumed annually by all sex-age classes.

The importance of swamp lily for deer in this Everglades system likely is due to its availability and high nutritional quality. In more northern latitudes, diet selection changes in response to seasonal changes in forage abundance and nutritional quality (Crawford 1982; Vangilder et al. 1982). The lack of difference in the consumption of food categories between the wet season and dry season in the wet prairie-tree island habitat of the Everglades suggests a relatively "steady state" with respect to availability of plant species on a year-round basis, which is probably a product of the subtropical climate. Futhermore, Loveless (1959) found that swamp lily was among the 3 top-ranked forages with respect to nutritional quality and palatability in all seasons, especially during the late gestation and lactation periods of females. In all seasons, the levels of crude protein and phosphorus in swamp lily

reported by Loveless fell within or exceeded the ranges required for optimum growth and lactation, 14–24% for crude protein (Ullrey et al. 1967) and 0.11–0.19% for phosphorus (Grasman and Hellgren 1993).

Although the 5 top-ranked plants consumed by the different age and sex classes constituted ≤ 64% of their respective diets, there was, except for swamp lily, little commonality among the plants. Interestingly, wild sage, a woody species, comprised 22.4% and 15.1% of the dry weight diet of female and male fawns, respectively, but < 1% of the diet of adults.

Adult females consumed greater quantities of aquatic herbs than adult males, and, conversely, adult males consumed greater quantities of woody plants than adult females. These observations are consistent with previous findings that male white-tailed deer use poorer-quality habitat than females (Bier 1987, McCullough 1979). These observed differences in diet support the "sexual dimorphism-body size" hypothesis for sexual segregation, which is common among polygynous ungulates (Main and Coblentz 1990; Main et al. 1996). This hypothesis predicts that larger-bodied males can meet their nutritional needs by exploiting abundant, low-quality forages, whereas females must exploit high-quality forages to meet the energy demands associated with gestation and lactation. Alternative explanations for the difference in diet between ungulate sexes include differences in forage preference (Beier 1987; Oakes et al. 1992), habitat selection, and, thus, forage availability (Beier 1987; Shank 1982), and bite size and rumen capacity (Bowyer 1984; Clutton-Brock et al. 1987).

Dietary differences between sexes in this study relate to differences in habitat use. Miller (1993) found that adult male white-tailed deer in this Everglades system used tree islands more than adult females, and had a higher density of tree islands in their core home range than did females. He also found that adult females used wet prairies more than males. Thus, the higher proportion of woody plants and aquatic herbs in the rumens of adult males and females, respectively, reflects the availability and consumption of these plants within the different habitats.

Differential habitat use can be attributed to efforts by each sex to maximize reproductive success (Main et al. 1996). For males, enhancing reproductive success involves maximizing physical size, strength, and endurance, whereas for females it involves strategies to ensure the survival of offspring. In this Everglades system, males optimize foraging opportunities on tree islands, which may support a greater forage biomass than other habitats (Miller 1993). The use of wet prairie habitat and its high quality aquatic herbage by females may increase reproductive success by enhancing their physical condition and by decreasing the risk of predation of their offspring (Miller 1993). Thus, the observed dietary differences between adult males and females likely result from

the differential use of habitats by the sexes in order to maximize reproductive success. This finding, therefore, supports the predictions of the reproductive-strategy hypothesis for ungulates (Main et al. 1996).

Previous studies have indicated that the diet of fawns mimics that of their dams (Oakes et al.1991; Shank 1982). However, in this study, the diets of neither female nor male fawns, which consumed higher proportions of woody plants, mimicked the diet of their dams. This difference between the diets of fawns and adult females may be related to habitat use. Fawns may use tree islands for concealment as a deterrent to predation, principally from bobcats (Boulay 1992, Labisky and Boulay 1998), during their early months of life because tree islands represent the major overstory cover in the expanse of wet prairie (Zultowsky 1992). Field observations indicated that as the fawns grew and their mobility increased, they increasingly accompanied their mothers in foraging forays onto the wet prairie, which is reflected in their substantial consumption of aquatic herbs.

In conclusion, white-tailed deer, throughout their range, forage on many plant species. Usually, however, a small number of plant species constitute the bulk of their seasonal diet, particularly in temperate zones. In the Everglades, the diet is similar year-round because of the sustained availability of major plant species resulting from the subtropical climate. However, that a single species, swamp lily, dominated the annual diet of both adults and fawns is noteworthy, and, to our knowledge, unprecedented for white-tailed deer. Given that white-tailed deer in the Everglades are important both recreationally and as a primary prey base for the endangered Florida panther, hydrologic management regimes designed for restoration of the Everglades must ensure the continued availability of the aquatic herb, *C. americanum*.

ACKNOWLEDGMENTS

M.C. Boulay, K.E. Miller, R.A. Sargent, Jr., and J.M. Zultowsky collected the rumen samples. We are indebted to M.K. Johnson for performing the microhistological analysis of plants from the rumen samples of deer. D.M. Long performed a preliminary analysis of the microhistological data. M.B. Main, K.E. Miller, and J.R. Snyder provided helpful comments on the paper. The research was supported by the National Park Service (Big Cypress National Preserve) and the Florida Agricultural Experiment Station (FAES), and approved for publication as FAES Journal Series No. R-08932.

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