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THE DIET OF THE GOPHER TORTOISE, *Gopherus polyphemus*, IN A SANDHILL HABITAT IN CENTRAL FLORIDA

by

Laurie Ann Macdonald

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology at
the University of South Florida

May 1986

Major Professor: Henry R. Mushinsky, Ph.D.

Graduate Council
University of South Florida
Tampa, Florida

CERTIFICATE OF APPROVAL

MASTER'S THESIS

This is to certify that the Master's Thesis of
Laurie Ann Macdonald
with a major in Zoology
has been approved by the Examining Committee
on April 15, 1986 as satisfactory for the
Thesis requirement for the Master of Science degree.

Thesis Committee: ______________________________
Major Professor: Henry R. Mushinsky, Ph.D

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Member: Earl D. McCoy, Ph.D

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Member: Glen E. Woolfenden, Ph.D

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Member: Richard P. Wunderlin, Ph.D

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THE DIET OF THE GOPHER TORTOISE, *Gopherus polyphemus*,
IN A SANDHILL HABITAT IN CENTRAL FLORIDA

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An Abstract

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Scat analysis and foraging observations were used to determine the diet of a gopher tortoise, *Gopherus polyphemus*, population in a sandhill community in west central Florida. Live vegetation was assessed to determine plant availability. The bulk of the gopher tortoise diet was composed of the dominant plant species in the habitat while the tortoises were selective with respect to most plant genera. Tortoises ingested many plant taxa with Poaceae, Asteraceae, Fabaceae, Pinaceae and Fagaceae being the most frequent components of the diet. Sixty-eight genera from 26 families were identified in the tortoise diet. In the scat the most common genus identified was *Aristida* and the most common family was Poaceae. Other common genera were *Pinus*, *Quercus*, *Galactia*, *Cnidoscolus*, *Tillandsia*, *Pityopsis*, and *Richardia*. Insects and charcoal were often present in scats. Although plant availability differed between seasons, the gopher tortoise diet did not change significantly. The proportions of plants in the diet differed from the proportions of plants available in the spring but no significant difference was indicated between diet and availability in the fall. Comparing the overall diet indicated no difference between sexes or age groups. Comparing diet with respect to individual plant taxa indicated young tortoises ingested significantly less Poaceae and some plants with external defense mechanisms (*Rubus*, *Cnidoscolus*) than did adults. Nonplant items may be a significant source of nutrients. Jacobs Electivity Index indicated the tortoises preferred *Galactia*, *Cnidoscolus*, *Pinus*, *Quercus*, and the Rubiaceae. Poaceae, *Aristida*, Asteraceae, and *Pityopsis*, the most common plants in the habitat, were selected at or below the proportions at which they were available.

Feinsinger's Proportional Similarity Index indicated gopher tortoise foraging behavior lies midway between a specialist and generalist.

Abstract Approved:________________________________

Major Prof: Henry R. Mushinsky, Ph.D.

Assistant Professor of Biology

____

Date of Approval

INTRODUCTION

The gopher tortoise, *Gopherus polyphemus*, is a major herbivore in xeric habitats in southeastern United States, such as, pine-oak uplands, xeric hammock, sand pine scrub, and ruderal successional types (Auffenberg and Franz 1982). Tortoises have a disjunct distribution within the coastal plain, ranging from South Carolina to Louisiana with their greatest abundance in Florida. Auffenberg and Franz (1982) estimated gopher tortoise populations have been reduced by about 80% in the last 100 years. The gopher tortoises' status as a keystone species (Eisenberg 1983) is based upon the its excavation of burrows that are used as living quarters, foraging grounds, and refuge from fires by over thirty vertebrate species and numerous arthropods (Hallinan 1923; Auffenberg 1969; Landers and Speake 1980; Landers and Buckner 1981; Woodruff 1982; Eisenberg 1983). Burrow excavation by tortoises recycles nutrients which have been leached from the surface of the sandhills (Auffenberg 1969; Landers 1980).

The interactions between the gopher tortoise and the plants in its community are not as well known as the commensal faunal relationships. Auffenberg (1969) suggested gopher tortoises contribute to the maintenance of the southeast's extensive fire subclimax pine forests by dispersing the seeds of *Aristida* (wiregrass), an important ground fuel for spreading fires. As the major herbivore in the sandhill (Landers and Buckner 1981) gopher tortoises may help maintain the openness and composition of the vegetation. Understanding the animal's food habits is a first step in answering questions concerning the components of suitable habitat for this declining species, the energetics of a large, herbivorous reptile, and the dependency of sandhill plant species (seed dispersal and germination) upon the gopher tortoise.

The literature on gopher tortoise diet consists primarily of short, descriptive lists of plants, such as grasses, leaves, and berries (Hallinan 1923; Hutt 1967). Carr (1952) examined the stomach contents of 40-50 tortoises and found grasses or leaves in every case. He found occasional bits of hard fruits, bones, charcoal and on one occasion, insect chitin. Auffenberg (1969) found tortoises fed on native grasses, including Aristida, have a preference for Opuntia (prickly pear cactus) and other plants with red fruits, and were a major factor in the dispersal of grass and Licania (gopher apple) seeds. Through feeding observations Wright (1982) concluded South Carolina gopher tortoises ate vegetation exclusively. He found the bulk of the tortoise diet consisted of Aristida but they consumed small amounts of almost any available plant or fruit. Wright observed tortoises eating woody twigs of low growing Quercus laevis (turkey oak) during extreme droughts. The South Carolina populations frequently ingested readily available Opuntia, Andropogon (beardgrass or bluestemgrass) and Eupatorium (dog fennel).

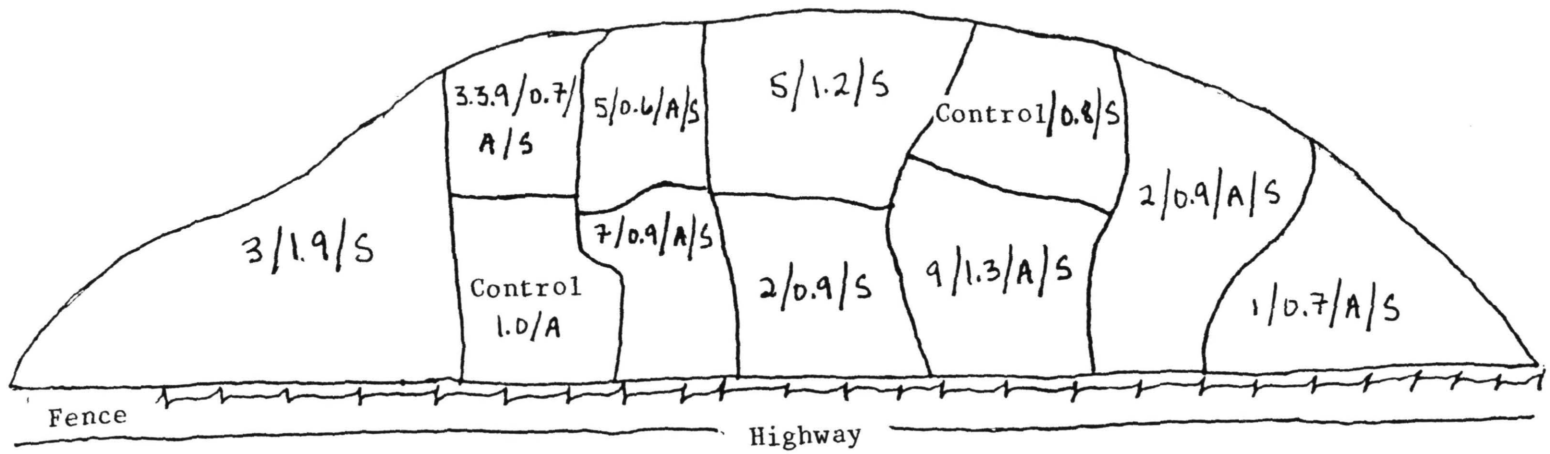
Garner and Landers (1981) in a quantitative study based on scat analyses, foraging observations and stomach contents, found grasses, grasslike plants (some Asteraceae and Cyperaceae) and the Fabaceae to be the most important tortoise forage plants in southwest Georgia. They suggested that those same plants determined gopher tortoise carrying capacity. Garner and Landers found that broad-leaved grasses were the staple food of the southwestern Georgia population. Aristida was ingested when more preferred foods were unavailable. More nutritious forbs, such as Richardia (Florida pussley) and Diodia (poor-Joe), partially replaced the grasses in the diet when available. Legumes were used extensively, especially by juveniles (aged 0-15 years). Garner and Landers suggested that occasional ingestion of animal matter, especially by females, could be a significant source of protein and minerals.

This study was designed to determine the diet of a gopher tortoise population in a sandhill community in west central Florida. This research first addresses the broad questions 1) what foods are included in the gopher tortoise diet, and 2) what is the percent composition of each of these foods in the diet. Scat contents are compared to plant availability to determine which plants the tortoises select, avoid, or eat in a random manner. Additional aspects of gopher tortoise foraging are considered: similarity of young, juvenile and adult tortoise diets, similarity of male and female tortoise diets, nonplant items ingested by tortoises, and gopher tortoise foraging behavior with respect to generalist and specialist strategies.

MATERIALS AND METHODS

The study was conducted on the 200 ha Ecological Research Area of the University of South Florida, Hillsborough County, in west central Florida, U.S.A. (lat.:28.05N;long.:82.20W). The study site was approximately 11 ha of xeric uplands divided into approximately 1 ha plots that were subjected to periodic controlled burning. The soils of the area are well drained, yellowish sands (Lakeland series) with a limestone base (Laessle 1958). Sandhills are characterized by Pinus palustris (longleaf pine), Pinus elliottii (slash pine), Quercus laevis (turkey oak) and Quercus geminata (sandhill live oak), stands of Serenoa repens (saw palmetto), extensive grasses, Aristida spp., Andropogon spp. and panicoids, and diverse herbaceous growth that includes numerous asters and legumes, Pityopsis graminifolia (silkgrass), Liatris gracilis (blazing star), Galactia spp. (milk pea), and Tephrosia spp. (hoary pea). Vegetation composition and structure differed among plots depending upon their burn periodicity. Figure 1 is a map of the study site; the burn history of the plots is presented in Table 1. Appendix 1 is a list of vascular plant species that have been identified on the USF Ecological Research Area with asterisks marking those found on the sandhills.

Characterization of the gopher tortoise diet was based primarily on analysis of 63 fecal samples (scats) collected between November 1982 and December 1983 from 50 tortoises for whom life history data and date of scat collection were known. Sample size was considered adequate and representative of the total gopher tortoise population based on the



LEGEND

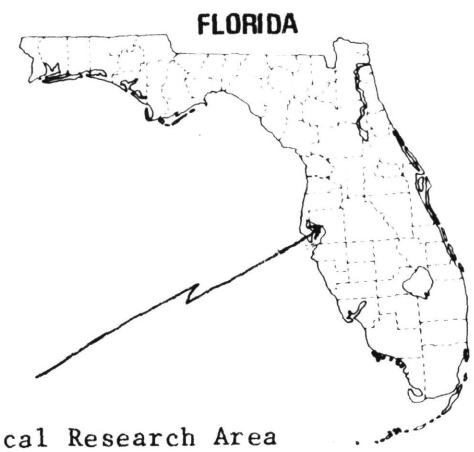
Number of years between burns/

Area in hectares/

A=vegetation transects were taken on this plot to determine plant availability/

S=scat was collected from a tortoise captured on this plot

Firelines divide the plots



USF Ecological Research Area
Study site

Figure 1. Study site at USF Ecological Research Area and its location within the state of Florida.

Table 1. Burn schedule at USF Ecological Research Area. The presence of an x means the plot was burned in the year indicated.

Year	Plot					
	1	2	3	5	7	9	3.3.9
1968							X
1971							X
1974							X
1976				X	X		
1979	X	X					
1980	X						
1981	X	X		X		X	
1982	X						
1983	X	X	X		X		X
1984	X						
1985	X	X					
1986	X		X	X			X

infrequency of finding new plant taxa in the later scat samples analyzed. Scats were categorized by the age and sex of the tortoises from which they were obtained (Table 2) and by date of collection. Gopher tortoises are sexually dimorphic with some degree of overlap in the range of measurements for any single sexual characteristic (McRae et al. 1981). The sex of each gopher tortoise was determined by a combination of three factors; abdominal cavity depth, anal notch width and gular projection length. Annuli on one plastron scute were counted to determine the age of tortoises; each annulus represented one year of growth. Age categories were chosen to represent stages in tortoises' life history during which potential differences in the nutritional needs or digestive capabilities exist. Individuals aged 0 to 7 years were rapidly growing, prereproductive tortoises and were classified as "young", 8 to 15 year old tortoises whose growth rate slows as they enter the reproductive age were classified as "juveniles", and the mature tortoises over 15 years of age were considered "adults" (Landers et al. 1982).

For comparing seasonal data, the scats collected in 1983 were separated into two time periods, late spring-early summer (May-July), referred to as early summer, and autumn-early winter (September-November), referred to as autumn. Scats collected in August were excluded from the seasonal comparisons.

Tortoises were hand captured or caught in pitfall traps. Each trap was a 25 l bucket with a cheese cloth and sand cover that was buried flush with the surface of the soil mounded at the mouth of the burrow. Tortoises generally defecated within minutes of capture. Additional scats were obtained from captive tortoises that had not eaten

Table 2. Categorization of scats (n=63) by sex and age of tortoises.

Age (years)		Sex			TOTAL
		Female	Male	Unknown	
Young	0-7	0	0	24	24
Juvenile	8-15	8	13	1	22
Adult	15+	5	6	0	11
Unknown		0	1	5	6
TOTAL		13	20	30	63

subsequent to capture. Scats were kept frozen until examination. Thawed scats were soaked individually in a mixture of water, detergent, and thymol for 24 hours or until plant material could be separated easily. Depending upon the size and condition of each scat 100-500ml of water was used to soak the pellets, 1-10ml of detergent was used to cleanse and separate scat material, and 0.2-1.0g of thymol was used to preserve the material. Each scat was washed with water through four stacked sieves of mesh sizes 1.9685, 3.937, 7.874 and 15.748 squares per cm.

Representative specimens of plant pieces (e.g., blades, stems, seeds, leaves) or other items (e.g., rock, glass, insect remnants) contained in the 1.9685 mesh sieve and distinguishable without the aid of a microscope were removed, air dried and sorted. The contents of each of the other three sieves were washed into and air dried in separate petri dishes. Each scat sample, consisting of the large hand-sorted material and the contents of the three petri dishes, was examined through a dissecting microscope (50x). Scat contents were cataloged and each new specimen was described and added to a reference collection. Plants in the reference collection were identified by comparison with specimens in the University of South Florida Herbarium. Nomenclature follows Wunderlin (1982) and Wunderlin, et al (1985). Seventy-five percent of the nearly 600 reference specimens were identified. Each record of scat contents (n=63) listed every identifiable plant present named to the lowest identifiable taxon, the part of the plant that was identified (e.g., seed, leaf), and the reference collection number. Nonplant material was recorded with a description and reference collection number.

The taxon deemed appropriate for analysis of these data was the genus because it was the lowest taxon that could be identified with certainty using the methods described above. In two cases, the Poaceae and *Galactia*-*Tephrosia*, results were pooled because digested blades and leaves of these genera were difficult to distinguish to genus. All grasses except *Aristida* were summed under Poaceae to eliminate potential error. *Aristida*, a genus which could be identified from other grasses in scat, remained as a separate genus because of its importance as the most common plant on the study site and because it was considered a major food of gopher tortoises in other studies (Fletcher 1899; Fisher 1917; Auffenberg 1969; Garner and Landers 1981; Wright 1982).

Results of the scat analysis were recorded as presence or absence of each plant taxon per scat; any taxon identified in a scat was counted only once for that scat no matter how many times it may have been present. Data from the 63 scats were pooled. The pooled data were representative of the diet of the population, ranked foods as commonly to rarely ingested, and made no assumptions concerning assimilation rates. To calculate the percent composition of the pooled scats by taxon, the number of scats that contained a given taxon was divided by the total number of occurrences of all the taxa in all the scats (i.e., the sum of the numerators) and multiplied by 100:

$$\text{percent composition of taxon i} = 100 \times \frac{\text{number of scats containing taxon i}}{\text{sum of the number of scats containing taxa 1-n (the sum of the numerators)}}$$

For example, *Richardia* was present in 13 scats; summing all occurrences of taxa for all of the 63 scats equals 547. To calculate percent composition, 100 x (13 - 547) = 2.45%. Richardia represented 2.4% of the plant occurrences in the scats sampled.

Foraging observations (FO´s) were made to verify and supplement results of the analysis of scat contents. Each FO consisted of one continuous time period in which the foraging behavior of one tortoise was recorded. Observations were made at various times during daylight hours. The majority lasted between 20 and 60 minutes. Most FO´s took place during the months of September through December 1983. Observations were made either by a team consisting of one recorder and one observer who followed within three meters of the tortoise, or as unscheduled, opportunistic field observations. The data recorded during each FO included individual tortoise, date, time, and lowest identifiable taxon of each plant or nonplant material ingested.

Data from 38 FO´s were used to calculate the percent composition by taxon of the pooled FO´s. Each taxon ingested during a FO was counted once per FO:

$$\text{percent composition of taxon i} = 100 \times \frac{\text{number of FO's in which taxon i was ingested}}{\text{sum of the number of FO's in which taxa 1-n were ingested (the sum of the numerators)}}$$

This method of analysis was considered comparable to the presence/absence method used to determine percent composition in scat contents. To substantiate the above method, a second method based on the number of instances of ingestion (number of bites) was calculated in which a taxon could have been ingested from zero to several times per

FO. Both methods yielded the same frequency of occurrence rankings for the taxa.

Vegetation data were gathered to establish relative availability of live plants on the study site. In early summer of 1983 one transect was taken on each of six different burn plots on the study site (Figure 1). Transect placement was determined by randomly choosing a starting point within a plot and extending the transect 1 m by 15 m north to south. During the second sampling period, autumn of 1983, five smaller transects were taken on each of six plots. Transects were 15 cm in width by 5 m in length. The dimensions of the transects were changed to better approximate a profile of the vegetation that a gopher tortoise would encounter as it traversed an area. The starting point of each transect was determined randomly. The direction of the transect was established by randomly choosing one of sixteen possible compass points. To determine if the two methods of vegetation sampling yielded comparable results, in the summer of 1984 both methods were carried out on five of the six plots sampled previously. Results of a Kolmogorov-Smirnov two sample frequency test failed to show a difference between the frequency distributions of plants based upon the two sampling methods.

All live plants with bases within the transect area were identified and counted. Plants that grew in clumps were considered separate individuals if a 2 cm space existed between clumps. Firelanes, which were cleared of vegetation twice a year, were excluded from the sampling. Data were gathered on oaks and pines both as live plants and as leaf litter. Tillandsia was counted only among litter. Availability in leaf litter was estimated by combining information from two sources.

First, concurrent with the 1983 vegetation transects, plant biomass data were obtained by measuring dry and wet weights of vegetation collected from m^2 plots. Second, when both vegetation transect methods were tested in the summer of 1984 the amount of *Quercus* and *Pinus* in the litter was noted as dense, moderate, sparse, or nonexistent. The number of *Tillandsia* plants on the ground was counted.

To facilitate comparing plant availability with scat data, the plant counts were converted to presence/absence per m. If more than one individual of a taxon had been recorded within one of the m, that taxon was counted only once for that m. Plant availability data were maintained separately for the two seasons. Availability of each taxon was represented by percent composition:

$$\text{percent composition of taxon } i = 100 \times \frac{\text{number of meters in which taxon } i \text{ was present}}{\text{sum of the number of meters in which taxa } 1 - n \text{ were present (the sum of the numerators)}}$$

Jacobs´ Electivity Index (Jacobs 1974) was calculated using scat contents and plant availability data to examine selectivity of individual taxa by the tortoises. Jacobs "D" values range from -1 to 0 for negative selection or avoidance, and from 0 to +1 for positive selection or preference. A value of 0 indicates the animal is ingesting the food in the same proportion as it occurs in the habitat or in a random manner. The formula for Jacobs D is:

$$D = \frac{r - p}{r + p - 2rp}$$

where, r is a fraction of a given food type in the feeder´s ration, represented in this study by the percent composition of a taxon in scat;

p is the fraction of the same food in the environment, represented in this study by the percent composition of a taxon in the habitat.

Feinsinger's Proportional Similarity Index (PSI) (Feinsinger et al. 1981) was used to indicate the degree of generalism or specialism exhibited in gopher tortoise foraging behavior. The PSI ranges from minimum q to +1, where minimum q represents a forager that specializes on the rarest resource available and +1 represents the generalist forager that uses resources in the same proportions as those resources are available. The formula for the PSI is:

$$PS = 1 - 0.5 \sum_i |p_i - q_i|$$

where, p is the proportion of resource items in state i out of all items used by the population (Jacobs r or percent composition of scat) and q is the proportion of i items in the resource base available to the population (Jacobs p value or percent composition of habitat).

RESULTS

Fifty-two plant genera from 23 families were identified in the scats. Scat results include 8 genera pooled under Poaceae and 2 genera pooled under Galactia-Tephrosia. Tortoises were seen ingesting 39 genera from 14 families during foraging observations (FO's). FO results include 5 genera pooled under Poaceae and 2 genera pooled under Galactia-Tephrosia. Merging scat and FO data resulted in identification of 68 genera from 26 families in the gopher tortoise diet. The plant taxa identified in the 63 scats, the number of occurrences of each taxon, the percent composition of the total gopher tortoise diet by taxon, and the primary structure by which each taxon was identified are shown in Table 3. Summaries of data are given for FO's in Table 4. The data were pooled for the two legumes, Galactia and Tephrosia, and for all members of the Poaceae except Aristida. Galactia comprised at least 85% of the Galactia-Tephrosia group. These pooled genera were treated in the same manner as a genus and referred to as Poaceae and Galactia.

The plant taxon of most frequent occurrence in the pooled scats was Poaceae which represented 20.7% composition of taxa in scats. The most frequently identified genus was Aristida (10.6%). Following Aristida the most common taxa in scats were Pinus (9.7%), Quercus (9.1%), Galactia (7.3%), Cnidoscolus (5.5%), and Tillandsia (5.1%). Less common, between 3.8% and 1.8% composition, were Pityopsis, Richardia, Eriogonum, and Vaccinium. Each of the remaining taxa was present in fewer than ten scats (<1.8%). Summing the percent composition of the top ranked taxa showed that 75% of all occurrences of taxa in the scats

Table 3. Scat composition.

Taxa (estimated occurrences)	No. of Occurrences	Percent Composition	Primary Structure of Identification
Poaceae	113	20.7	
Andropogon(30)Axonopus(2)			blade,seed
Dichanthelium(23)Digitaria(7)			seed,seed
Eustachys(1)Panicum(7)			seed,seed
Paspalum(32)Sporobolus(11)			seed,seed
Aristida	58	10.6	blade
Pinus	53	9.7	needle
Quercus	50	9.1	leaf
Galactia-Tephrosia	40	7.3	
Galactia(30)			leaf
Tephrosia(3) Unknown(3)			leaf,leaf
Cnidoscolus	30	5.5	stinging hairs/seed
Tillandsia	28	5.1	skeletal structure
Pityopsis	21	3.8	blade
Richardia	13	2.4	seed
Eriogonum	12	2.2	leaf
Vaccinium	10	1.8	leaf
Polygonella,Aureolaria	<10 @	<1.8 @	seed,seed
Bulbostylis,Cyperus			seed,seed
Rubus; Diodia;			seed,seed
Hedyotis,Sisyrinchium			seed,blade
Balduina, Smilax;	≤5 @	≤0.9 @	seed,leaf
Chamaecrista,Opuntia			leaf,seed/spine
Ruellia, Rumex;			seed,seed
Eupatorium,Helianthemum			seed,leaf/seed
Serenoa; Berlandiera			blade,seed
Dalea,Dyschoriste			seed,seed
Liatris,Oxalis			seed
Crotalaria,Desmodium	1 @	0.18 @	seed.seed
Krigia,Lactuca			seed,seed
Lechea,Licania			seed,seed
Rhexia, Rhynchosia			seed.leaf
Scleria,Tragia			seed,seed
Xyris			seed
TOTAL = 52 genera/44 taxa	547	100.00%	

Table 4. Foraging observation composition.

Taxa (estimated occurrences)	No. of Occurrences	Percent Composition
Poaceae *Andropogon* (3) *Dichanthelium* (10) *Digitaria* (5) *Heteropogon* (1) *Paspalum* (2)	21	16.6
Pityopsis	19	15.0
Aristida	15	11.8
Dyschoriste	9	7.1
Phoebanthus	7	5.5
Liatris	6	4.7
Galactia-*Tephrosia*	5	3.9
Balduina	4	3.15
Chrysopsis, *Crotalaria*, *Richardia*	3 @	2.4 @
Ageratina, *Chamaecrista*, *Diodia*, *Elephantopus*, *Eriogonum*, *Hedyotis*, *Scutellaria*, *Stylisma*, *Tragia*	2 @	1.6 @
Asclepias, *Aster*, *Bulbostylis*, *Carphephorus*, *Centrosema*, *Croton*, *Helianthemum*, *Hieracium*, *Opuntia*, *Quercus*, *Rhynchosia*, *Solidago*, *Stylosanthes*, *Trichostema*	1 @	0.8 @
Total = 39 genera/34 taxa	127	100.00%

were represented by nine taxa from eight families. In descending order these taxa were Poaceae, Aristida, Pinus, Quercus, Galactia, Cnidoscolus, Tillandsia, Pityopsis, and Richardia. Fifty percent of all occurrences of taxa were represented by the first four taxa.

During FO′s Poaceae was the taxon ingested by tortoises most frequently (16.6%). I observed Pityopsis being eaten more frequently (15%) than Aristida (11.8%). Following Aristida in percent composition of FO′s was Dyschoriste (7.1%) and a variety of Fabaceae, Asteraceae, and Rubiaceae.

Summing the results of percent composition of occurrences of taxa by family confirms that Poaceae was the most common family in the gopher tortoise diet (31.3%). Pinaceae, Fabaceae, and Fagaceae were present at the next highest frequencies (over 9%). Tortoises ate a variety of legumes including Chamaecrista, Dalea, Desmodium, Rhynchosia, and Tephrosia; however, Fabaceae′s high percent composition was largely due to the frequent occurrence of Galactia in the scats. The pines, legumes, and oaks were followed by Asteraceae (6.4%), Euphorbiaceae (5.4%), Bromeliaceae (4.9%), Rubiaceae (4.5%), and Polygonaceae (4.4%).

Most of the grasses and rarer plants (<1.8% composition) in scat were identified by seeds, while leaves (including needles and blades) were the primary identifying structures for many of the common genera. The bulk of most scats was composed of broad leaved grasses. Some sections of pine needles up to 10 cm in length and small portions of oak and Galactia leaves were found with little sign of deterioration. Quercus and Galactia leaves comprised the bulk of several scats although epidermal layers of leaves were often digested. Over 90% of the scats contained intact seeds. Food retention time ranged from 3 days to 2.5 months.

To verify that scat contents was a valid indicator of gopher tortoise diet, the following hypothesis was tested. H_o: the percent composition of plants in scats does not differ from the percent composition of plants ingested during FO's. Results of a Kolmogorov-Smirnov test of frequency distributions indicated a failure to reject the hypothesis. Thus, no difference was found between the overall diets as indicated by what tortoises ingested and what was contained in scat. The relationship between scat and FO's was examined further by comparing individual genera through the G test of independence (Sokal and Rohlf 1973). Contingency tests indicated a difference in the ingestion of Aristida, Aureolaria, Cnidoscolus, Cyperus, Dyschoriste, Eriogonum, Galactia, Phoebanthus, Pinus, Polygonella, Quercus, Tillandsia, Vaccinium, and Poaceae. In all but one case, Phoebanthus, the difference was caused by failure to observe tortoises ingesting those plants. The availability of most of these taxa was lower in the fall which was the season when the majority of FO's were made.

Table 5 summarizes the percent of scats and FO's in which each plant family was present. The results reflect the probability of finding a family in a scat and the probability of observing its ingestion. The percentage values were based on the number of scats out of the total 63 scats that contained the family and number of FO's out of the total 38 FO's in which the family was ingested. Poaceae was present in nearly 100% of the tortoise scats. FO results show a greater probability of ingestion of Asteraceae (76.3%) than of Poaceae (68.4%). Fagaceae, Pinaceae, and Bromeliaceae exhibited a disproportionately high

Table 5. Plant families represented in the scats (n=63) and the foraging observations (n=38).

Family	% of scats in which family was present	% of FO's in which family was ingested
Acanthaceae	9.5	23.7
Arecaceae	4.8	0.0
Asclepiadaceae	0.0	2.6
Asteraceae	60.3	76.3
Bromeliaceae	44.4	0.0
Cactaceae	6.35	2.6
Chrysobalanaceae	1.6	0.0
Cistaceae	6.35	2.6
Convolvulaceae	0.0	5.3
Cyperaceae	28.6	1.0
Ericaceae	15.9	0.0
Euphorbiaceae	49.2	7.9
Fabaceae	65.1	23.7
Fagaceae	79.4	2.6
Iridaceae	9.5	0.0
Lamiaceae	0.0	7.9
Melastomataceae	1.6	0.0
Oxalidaceae	3.2	0.0
Pinaceae	84.1	0.0
Poaceae	98.4	68.4
Polygonaceae	33.3	5.3
Rosaceae	12.7	0.0
Rubiaceae	33.3	18.4
Scrophulariaceae	12.7	0.0
Smilaceae	7.9	0.0
Xyridaceae	1.6	0.0

probability of being identified in scat compared to the probability of ingestion. The reverse is true for the Acanthaceae which appeared to be frequently ingested but infrequently identified in scat. Table 5 also shows that one can expect to find the Asteraceae, Euphorbiaceae, Fabaceae, Fagaceae, Pinaceae, and Poaceae in 50% or more of the scats. Poaceae and Asteraceae were ingested at least 50% of the time during FO´s.

Sixty-eight genera from 24 families were identified in the gopher tortoise habitat (Table 6). Genera that were identified in scats or FO´s but were not present in the 1983 vegetation transects are listed in Table 7. The genera in Table 7 were subsequently found on the firelanes of the study site, in the 1984 vegetation transects or in a search of the study site for rare plant species. Most of these genera occurred in the scats or FO´s once (0.2% composition). Digitaria, Sisyrichium, Diodia, and Rumex (0.7% to 1.5% composition) grew in the disturbed, open area of the firelanes. Sporobolus (2% composition) grew among stands of Aristida.

Plant availability differed in early summer and autumn primarily in two ways, 1) the number of taxa present, and 2) the percent composition of grasses. I identified 41 taxa in early summer and 53 taxa in autumn. The most common taxa in both seasons were Poaceae, Aristida, and Pityopsis. The percent composition of Poaceae changed from a total 24% in early summer (11.3% Poaceae and 12.3% Aristida) to 55% in autumn (25.1% Poaceae and 20.1% Aristida). Pityopsis remained the third most common taxon and second most common genus during both seasons. Between early summer and autumn Pityopsis increased in percent composition from 10.0% to 12.8%. Genera that remained at or above 2% composition in both

Table 6. Plant availability as percent composition of habitat.

Taxa	Early Summer Percent Composition	Autumn Percent Composition
Aristida	12.3	20.1
Aster	4.5	2.1
Baccharis	4.4	0.15
Berlandiera	1.6	0.3
Bulbostylis	0.0	2.1
Chamaecrista	1.3	0.0
Chrysopsis	5.5	2.0
Cnidoscolus	2.1	0.3
Dalea	2.1	0.0
Dyschoriste	5.2	3.2
Eriogonum	4.8	2.7
Eupatorium	1.8	2.6
Galactia-Tephrosia	3.1	4.4
Hedyotis	1.1	0.0
Helianthemum	2.3	0.15
Heterotheca	1.6	0.0
Lechea	5.9	0.9
Liatris	2.8	4.4
Phoebanthus	4.7	1.4
Pityopsis	10.0	12.8
Poaceae	11.3	25.1
Quercus	2.8	1.7
Solidago	0.6	1.5
Ageratina, Aureolaria, Balduina, Baptisia, Carex, Carphephorus, Crotalaria, Croton, Crotonopsis, Cyperus, Diospyros, Elephantopus, Emilia, Fimbristylis, Galium, Hieracium, Indigofera, Ipomoea, Licania, Opuntia, Parthenocissus, Pinus, Polygala, Polygonella, Rhynchosia, Rhyncospora, Richardia, Rubus, Scutellaria, Serenoa, Schrankia, Smilax, Stillingia, Stylisma, Teucrium, Tragia, Trichostema, Viola, Zornia	<1.0 @	<1.0 @

Table 7. Genera identified in scat or foraging observations that were not found in 1983 vegetation transects.

Family / *Genus*	Family / *Genus*
Acanthaceae	Melastomataceae
Ruellia	*Rhexia*
Asclepiadaceae	Oxalidaceae
Asclepias	*Oxalis*
Asteraceae	Poaceae
Krigia	*Axonopus*
Lactuca	*Digitaria*
	Eustachys
Cyperaceae	*Sporobolus*
Scleria	
	Polygonaceae
Fabaceae	*Rumex*
Centrosema	
Desmodium	Rubiaceae
Stylosanthes	*Diodia*
Iridaceae	Xyridaceae
Sisyrinchium	*Xyris*

seasons included Aristida, Aster, Chrysopsis, Dyschoriste, Eriogonum, Galactia, Liatris, and Pityopsis.

A Kolmogorov-Smirnov test indicated a significant difference in plant availability between early summer and autumn but no difference in scat contents existed between the two seasons. During early summer the Kolmogorov-Smirnov test indicated a significant difference between availability and scat contents; no difference between availability and scat contents was indicated in autumn. Tables 8a and 8b list the percent composition of the top ranked plant taxa in the scat and in the habitat by season. All top ranked plant taxa in the habitat (Tables 8a and 8b) were included in the tortoise diet (Tables 3 and 4) although the number of occurrences varied from 1 to 58. Jacobs Electivity Indexes (D values) were used to examine the relationships between the scat contents and plant availability. These values are best considered as indicators of electivity, avoidance and random foraging. Results can be influenced by sampling error, differential assimilation of plants and relative difficulty of identification in scat. Jacobs D values for the top ranked taxa in scat and selected other taxa are listed in Table 9. The D values for early summer and autumn, respectively, are noted in the text following the name of each taxon. Each D value with an absolute value equal to or greater than 0.7 was considered strong preference, a value of 0.3 to 0.7 was considered moderate preference, and zero to 0.3 was considered random.

Electivity results showed that the gopher tortoises were selective foragers with respect to most plant taxa although the taxa that were ingested most frequently were selected in a random manner (Poaceae and Aristida). Less than 10% of the D values were in the random selection

Table 8. Percent composition of top ranked genera in scat and habitat by season.

a. Early summer (May-July)

Rank	Taxa	% Composition of scat	Taxa	% Composition of habitat
1	Poaceae	20.2	*Aristida*	12.3
2	*Aristida*	11.1	Poaceae	11.3
3	*Quercus*	10.5	*Pityopsis*	10.0
4	*Pinus*	9.9	*Lechea*	5.9
5	*Galactia*	7.7	*Chrysopsis*	5.5
6	*Cnidoscolus*	6.5	*Dyschoriste*	5.2
7	*Pityopsis*	4.0	*Eriogonum*	4.8
8	*Eriogonum*	3.1	*Phoebanthus*	4.7
9	*Richardia*	2.6	*Aster*	4.5
10	*Rubus*	2.0	*Balduina*	4.4
11	*Vaccinium*	2.0	*Galactia*	3.1
12	*Polygonella*	1.7	*Quercus*	2.8
13	*Sisyrinchium*	1.7	*Liatris*	2.8
14	*Aureolaria*	1.4	*Helianthemum*	2.3
15	*Balduina*	1.4	*Cnidoscolus*	2.1
16	*Cyperus*	1.4	*Dalea*	2.1
17	*Smilax*	1.4	*Eupatorium*	1.8

Table 8. (continued)

b. Autumn (September-November)

Rank	Taxa	% Composition of scat	Taxa	% Composition of habitat
1	Poaceae	25.0	Poaceae	25.1
2	Aristida	13.0	Aristida	20.1
3	Pinus	12.0	Pityopsis	12.8
4	Galactia	8.3	Galactia	4.4
5	Quercus	7.4	Liatris	4.4
6	Cnidoscolus	4.7	Dyschoriste	3.2
7	Bulbostylis	3.7	Eriogonum	2.7
8	Pityopsis	3.7	Eupatorium	2.6
9	Aureolaria	2.8	Aster	2.1
10	Vaccinium	2.8	Bulbostylis	2.1
11	Chamaecrista	1.85	Chrysopsis	2.0
12	Diodia	1.85	Quercus	1.7
13	Hedyotis	1.85	Solidago	1.5
14	Polygonella	1.85	Phoebanthus	1.4
15	Richardia	1.85	Lechea, Diospyros, Crotalaria Balduina, Ageratina	0.9 @

Table 9. Jacobs D values for top ranked and selected genera.

Taxa	Early summer	Autumn
Aristida	-0.06	-0.26
Chrysopsis	-1.00	-1.00
Cnidoscolus	0.53	0.88
Diodia	1.00	1.00
Eriogonum	-0.22	-1.00
Eupatorium	-0.74	-0.48
Hedyotis	0.00	1.00
Helianthemum	-0.78	0.00
Heterotheca	-1.00	0.00
Galactia-Tephrosia	0.44	0.33
Lechea	-0.91	0.00
Phoebanthus	-1.00	-1.00
Pinus	0.95	1.00
Pityopsis	-0.46	-0.59
Poaceae	0.33	0.00
Polygonella	0.34	0.72
Quercus	0.60	0.65
Richardia	1.00	0.85
Solidago	-1.00	-1.00

category. The D values indicated that Poaceae (.33,0) and Aristida (-.06,-.26) were selected in a random manner with moderate preference for Poaceae in early summer. Pinus (.95,1.0) was strongly preferred and Quercus (.60,.65) was moderately preferred. Pinus and Quercus D values may be misleadingly high because these genera were, respectively, moderately and highly available as leaf litter. Galactia (.44,.33) and Cnidoscolus (.53,.88) were preferred genera. Jacobs D values were also examined by family. The Asteraceae, especially Chrysopsis (-1,-1), Eupatorium (-.74,-.48), Heterotheca (-1,0), Phoebanthus (-1,-1) and Solidago (-1,-1) were avoided in both seasons, as was Pityopsis (-.46, -.59). In the Cistaceae family, Helianthemum (-.78,0) and Lechea (-.91,0) were strongly avoided though abundant in early summer. The Rubiaceae were strongly preferred; Diodia (1,1), Hedyotis (0,1), Richardia (1,.85). Fabaceae were generally avoided with the exception of Galactia. Genera with values of less than 1% composition of the habitat or less than 2% composition of the scat are not reported individually. In early summer 15 genera had values of -1 and 14 genera had values of +1. In autumn these totals were 36 and 7, respectively.

The Proportional Similarity Index (PSI) condensed scat content and availability into one value which indicated the foraging behavior of the gopher tortoise population lay midway between a specialist and generalist strategy. In early summer the PSI value was 0.4553 and in autumn the PSI value was 0.5337.

Kolmogorov-Smirnov tests indicated no differences in scat contents of tortoises by age group or sex. Contingency tests indicated significant differences in the use of some taxa by young and adult tortoises. Ranking the percent composition of taxa for each of the three age groups and for the sexes resulted in nearly identical ranks for the first eight taxa. These taxa were Poaceae, Aristida, Pinus, Quercus, Galactia, Cnidoscolus, Tillandsia, and Pityopsis. Contingency test results indicated there was significantly less ingestion of Poaceae, Cnidoscolus, and Rubus by young tortoises than by adult tortoises. Although a significant difference was not indicated, Aristida was absent from four of the young and one of the juvenile scats but was present in the scats of all adults. I identified 32 taxa in the 11 adult tortoise scats; however, I found only 26 taxa in the 24 young tortoise scats. Based on the hypothesis that young and adult tortoises had similar diets, the sample from young tortoises should have contained at least as many taxa as the adult tortoise sample. The results indicated young tortoises do not eat the same plant material as the adults. The scats of the youngest tortoises were composed of finer material than the scats of older tortoises. No difference in overall diet nor ingestion of individual taxa was indicated between the sexes.

Nonplant items identified in gopher tortoise scats included insects, charcoal, rocks, and a variety of natural and manufactured materials that ranged from animal shell to components of shotgun shell. Table 10 lists the nonplant items; percentages are based on the ratio of scats containing an item to the total number of scats (n=63). Insects were present in 75% of the gopher tortoise scats making insects the fourth most common item identified in scat compared with plant genera (Aristida 92%, Pinus 84%, Quercus 79%). Scats from tortoises of both sexes and all age groups contained insects. Charcoal, present in 67% of the scats, was the fifth most common item identified when compared to plant genera. Charcoal was found in the scats of both sexes and all age

Table 10. Nonplant items ingested by gopher tortoises.

Description	% of scats in which item is present (n=63)
Insect remnants/chitin	75.0
Charcoal	66.7
Rock	11.1
Plastic (from marker flags)	9.5
Silicon	1.3
Egg shell	0.6
Mollusc shell	0.6
Aluminum foil	0.6
Paper	0.6
Glass (length 5cm)	0.6
	# of observations
Mushroom	2
Sand/dirt	2
Rock	1
Scat (two instances of gopher tortoise scat ingestion by captive tortoises)	2

groups. Eleven percent of the scats contained rock which measured up to 18 mm by 34 mm in size (adult tortoise jaws are approximately 37 mm in width. One-third of the female scats contained rock. Sand was filtered out of all scats. Tortoises were observed licking sandy soil twice. Two instances of mushroom ingestion and reingestion of scat by two captive tortoises occurred.

DISCUSSION

Gopher tortoises ingested a large number of diverse plants (68 genera) but almost a third of the occurrences of taxa in the diet were members of the Poaceae. The most common genera in the tortoise diet were dominant or perennial plants in the sandhill. The plant families most frequently identified in the tortoise scat and foraging observations (FO's) were Poaceae, Asteraceae, Fabaceae, Pinaceae, and Fagaceae.

The Poaceae, broad leaved grasses (e.g. Andropogon, Dichanthelium, Paspalum) and Aristida that are common in the sandhill, composed a major portion of the tortoise diet. Aristida is a tough, fibrous wiregrass that may be difficult for young tortoises to masticate and digest, however the importance of Aristida in the diet of the adult gopher tortoises (Fletcher 1899; Fisher 1917; Auffenberg 1969; Wright 1982) has been confirmed for this Florida sandhill population where Aristida is the dominant plant in the habitat. Wright (1982) found that the bulk of the diet of South Carolina tortoises was primarily Aristida. However, Garner and Landers (1981) found that a southwestern Georgia population ingested little Aristida when more nutritious forbs were available.

Asteraceae were frequently identified in the tortoise diet because 1) many genera of Asteraceae occur in the sandhill and tortoises ingested small amounts of each, and 2) the grasslike aster, Pityopsis (silkgrass), the second most common genus available to the tortoises, occurred frequently in both scats and foraging observations (FO's). The 3.8% scat composition value for Pityopsis was probably underestimated because Pityopsis resembled broad leaved grasses after partial digestion. If Pityopsis had been discernible in the unidentified scat material, the percent composition values for other taxa identified in scats would have been proportionately lower.

Tortoises ingested several genera of legumes but Fabaceae's large percent composition of diet is the result of the frequent ingestion of Galactia. Galactia was the most common legume at the study site and, as a prostrate vine, it was accessible to the tortoises. Legumes are high in protein and mineral content and the genus Galactia is a source of calcium (Garner and Landers 1981). Garner and Landers (1981) considered legumes the most important forbs in the tortoise diet because of the high frequency of ingestion and the nutritional value.

Pinus and Quercus were the third and fourth most common genera in scats and are characteristic of the Florida sandhill habitat. Live pine and oak leaves were accessible to gopher tortoises only as seedlings. As dead material in ground litter, oak leaves were readily available and pine needles were moderately available to the tortoises. I could not determine if scat remnants were from live or dead material at the time of ingestion. Although Pinus and Quercus formed a high percent composition of scat, only one instance of oak ingestion and no pine ingestion by tortoises was observed. Both Pinus and Quercus may have had a disproportionately high rate of recovery and identification in scat when compared to pulpier plants. However, evidence suggests pine and oak are an important element of the tortoise diet. Wright (1982) observed gopher tortoises feeding on Quercus during extreme drought. Garner and Landers (1981) listed the presence of dead leaves (Pinus and "other") in scat during all months of their sampling period. Leaf litter is common in the diet of other tortoises (Gibson 1983; Rick and Bowman 1961). Explanations for the high frequency of Pinus and Quercus in scats are 1) they contribute nutrients despite limited digestibility, 2) they aid mechanical breakdown of other plants, 3) they hinder passage through the digestive tract thus increasing assimilation of other foods, 4) they supply moisture that adheres to the leaf surface, and 5) they are ingested inadvertantly.

Other plants that were commonly identified in scat or FO´s included Cnidoscolus, Tillandsia, Richardia, and Dyschoriste. Cnidoscolus (stinging nettle) flowered all year and was dispersed throughout the sandhill. The stinging hairs of Cnidoscolus were found frequently in tortoise scats. Scats also contained the capsular fruiting heads of Cnidoscolus and other Euphorbiaceae, for example, Stillingia and Tragia. The frequent use of euphorbs by gopher tortoises has not been reported. Richardia (Florida pussley) is commonly eaten by both Georgia and Florida tortoises (Hutt 1967; Garner and Landers 1981) and is high in moisture, fat, calcium and other minerals, and low in crude fiber (Garner and Landers 1981). This sprawling, pubescent perennial with fruits measuring 1-3 cm in diameter is characteristic of disturbed areas and may be one of the most beneficial of tortoise forage plants. Richardia and other Rubiaceae (e.g. Diodia, Hedyotis) were identified in scat by their seeds. Tillandsia usneoides and T. recurvata were common bromeliads in the trees of the sandhill community that became available to the tortoises after the plants or branches the plants were attached to had fallen to the ground. Although the presence of Tillandsia at ground level suggests they were rarely encountered by tortoises almost half of the tortoise scats contained the tough skeletal structure of these airplants. Lack of digestibility may result in a disproportionately high recovery rate of *Tillandsia*. However, its use in keeping the colon open in inactive, wintering tortoises has been proposed by Franz (unpublished) who has found bolluses of *Tillandsia* in the anterior portion of the colon in two dissected gopher tortoises. *Dyschoriste* (Acanthaceae), the fourth most common taxon identified in FO´s and a common plant in the sandhill, was found to contain the highest calcium and magnesium levels of gopher tortoise food plants on sand ridges in Garner and Landers´ southwest Georgia study (1981).

The number of intact seeds in scats suggests gopher tortoises are an agent of seed dispersal. Ingestion may enhance seed germination as has been demonstrated for Berlandier´s tortoise, *Gopherus berlandieri*, and the *Opuntia* cactus (Rose 1982), and for the Galapagos tortoise, *Testudo elephantopus porteri*, and the Galapagos tomato, *Lycopersicon esculentum* var. *minor* (Rick and Bowman 1961). The frequency of occurrence of insects and charcoal in the scats, 75% and 67%, respectively, suggests these items are sources of nutrition. These frequencies are higher than those reported elsewhere in the literature (Carr 1952; Garner and Landers 1981). Stones and sand were found frequently in scats; they may mechanically break down food in the gut (Sokal 1971) or, in the case of limestone, may serve as a source of calcium (Sokal 1971).

When changes in plant availability and food choice were compared for early summer and autumn a significant difference was indicated in the availability of plants between the two seasons while no difference was indicated in the tortoise diet. The major differences in availability between the two seasons were 1) the increase in percent composition of grasses, and 2) the increase in the number of taxa available between early summer and autumn. The tortoise diet reflected plant availability more closely in autumn when moist grasses were in greater abundance and a greater diversity of plant genera were available.

Jacobs Electivity Index (D values) indicated gopher tortoises were selective with respect to most plant genera, but the PSI value in early summer (0.4553) and in autumn (0.5377) indicated foraging behavior midway between a specialist and a generalist. These values likely represent the mixture of selective and random foraging for various plant taxa evident in electivity results. The tortoises randomly chose or avoided the dominant plants in the sandhill (Poaceae, Aristida, Asteraceae, Pityopsis) that supplied the bulk of their diet and tortoises did not exclude any common plant genus from their diet. The electivity index indicated that plant apparency was not the determining factor in frequency of food selection as most taxa were moderately to highly preferred or avoided by the tortoises. It is possible that a plant with an electivity value in the "avoided" category is an important element of the diet. This situation could occur whenever a plant supplies necessary nutrition, moisture, or other mechanical or chemical benefit, yet the plant is more than adequately abundant to fill the tortoises' needs.

Overall diet was similar among the three age groups and both sexes of gopher tortoises; however, some differences in foods existed. Scat contents of the youngest tortoises were of finer consistency than that of adults and contained fewer fibrous grasses, sedges and stems. Only scats from young tortoises did not contain Aristida. A larger sample size of young tortoises may have established a significant difference between young and adult tortoises with respect to ingestion of Aristida. Young tortoises ingested plants with external defense mechanisms, such as, Cnidoscolus (stinging hairs) and Rubus (thorns), in significantly smaller amounts than did adults. Fewer taxa were identified in scats from young tortoises possibly because 1) they foraged on fewer plant taxa, 2) they foraged on pulpier plant taxa, or 3) they foraged on the pulpier tissues of plants also eaten by adults. The data indicate the diets of young Gopherus spp. proportionately are higher in protein obtained from legumes and other herbaceous plants than the lower protein, more grassy diets of adults (Garner and Landers 1981; Morafka 1982). A high protein diet is important to growth and maturation of young tortoises (Jackson et al. 1976; Landers and Buckner 1981).

The gopher tortoise seems to exemplify the local specialist described by Fox and Morrow (1981). When studied in different geographic locations and habitat types the species may be seen as a generalist whose food choices are based on the locality in which it lives. Congeners of Gopherus polyphemus, G. agassizii, G. berlandieri, and G. flavomarginatus, are herbivorous grazers and pruners that rely on the dominant plants in their respective habitats for the staples of their diets while ingesting a variety of other plants (Burge and Bradley 1976; Carr 1952; Ernst and Barbour 1972; Hansen et al. 1976; Luckenbach 1982; Morafka 1982; Rose and Judd 1982). The degree to which the gopher tortoise, a large, herbivorous reptile, is an adaptable forager and an optimal forager will be better understood once energy and nutrient contributions of the foods in its diet are known.

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APPENDIX

APPENDIX

UNIVERSITY OF SOUTH FLORIDA ECOLOGICAL RESEARCH AREA VASCULAR PLANT SPECIES LIST

Compiled by D. Richardson, R. Wunderlin, and B. Hansen, September 1983 with additions by L. Macdonald September 1985. Species with an asterisk (*) are those occurring in the sandhill habitat. Species with a dagger (†) are unvouchered.

ACANTHACEAE
 *Dyschoriste oblongifolia
 *Ruellia caroliniensis
ACERACEAE
 Acer rubrum
AGAVACEAE
 *Yucca filamentosa
ALISMATACEAE
 Sagittaria graminea
AMARANTHACEAE
 Alternanthera philoxeroides
 Amaranthus spinosus
 *Froelichia floridana
AMARYLLIDACEAE
 *Zephyranthes atamasco
ANACARDIACEAE
 *Rhus copallina
 Schinus terebinthifolius
 *Toxicodendron radicans
ANNONACEAE
 *Asimina pygmaea
 *Asimina reticulata
APIACEAE
 Centella asiatica†
 Eryngium baldwinii
 Hydrocotyle umbellata
 Hydrocotyle verticillata
 Ptilimnium capillaceum
APOCYNACEAE
 *Catharanthus roseus†
AQUIFOLIACEAE
 Ilex ambigua
 Ilex glabra
ARECACEAE
 Sabal palmetto†
 *Serenoa repens
ASCLEPIADACEAE
 *Asclepias humistrata
 Asclepias lanceolata†
 Asclepias perennis
 *Asclepias tuberosa
 *Asclepias verticillata
ASPIDIACEAE
 Thelypteris dentata
ASPLENIACEAE
 Asplenium platyneuron
ASTERACEAE
 Acmella oppositifolia
 *Ageratina jucunda
 *Ambrosia artemisiifolia
 *Arnoglossum floridanum
 *Aster concolor
 *Aster dumosus
 *Aster tortifolius
 *Baccharis halimifolia†
 *Balduina angustifolia
 *Berlandiera subacaulis
 *Bidens alba
 *Carphephorus corymbosus
 Carphephorus odoratissimus
 *Carphephorus paniculatus
 *Chrysopsis linearifolia
 *Chrysopsis mariana
 *Chrysopsis scabrella
 *Chrysopsis subulata
 Cirsium nuttallii
 *Coreopsis leavenworthii
 Eclipta alba
 *Elephantopus elatus
 *Emilia fosbergii†
 *Erechtites hieracifolia
 *Erigeron quercifolius
 *Erigeron vernus
 *Eupatorium capillifolium
 *Eupatorium compositifolium
 *Eupatorium leptophyllum
 *Eupatorium mohrii
 *Gnaphalium pensylvanicum
 *Helenium flexuosum
 Helianthus angustifolius
 Helianthus radula
 *Heterotheca subaxillaris

*Hieracium gronovii
*Hieracium megacephalon
*Krigia virginica†
*Lactuca graminifolia
*Liatris gracilis
*Liatris tenuifolia
Mikania scandens
*Palafoxia integrifolia
*Phoebanthus grandiflorus
*Pityopsis graminifolia
Pluchea rosea
*Pyrrhopappus carolinianus
Senecio glabellus
*Solidago fistulosa
*Solidago stricta
*Youngia japonica

BIGNONIACEAE
Campsis radicans

BRASSICACEAE
*Cardamine hirsuta
*Lepidium virginicum

BROMELIACEAE
Tillandsia bartramii
Tillandsia fasciculata
*Tillandsia recurvata
Tillandsia setacea
*Tillandsia usneoides

CACTACEAE
*Opuntia humifusa

CAMPANULACEAE
Campanula floridana
Lobelia glandulosa
Lobelia paludosa

CAPRIFOLIACEAE
Sambucus canadensis
Viburnum obovatum

CARYOPHYLLACEAE
*Stipulicida setacea

CHENOPODIACEAE
*Chenopodium ambrosioides

CHRYSOBALANACEAE
*Licania michauxii

CISTACEAE
*Helianthemum corymbosum
*Lechea cernua†
*Lechea mucronata
*Lechea sessiliflora

COMMELINACEAE
*Commelina erecta

CONVOLVULACEAE
*Dichondra carolinensis
*Ipomoea cordatotriloba
*Ipomoea pandurata
*Stylisma patens
*Stylisma villosa†

CUCURBITACEAE
*Melothria pendula
*Momordica charantia

CYPERACEAE
*Bulbostylis ciliatifolia
Carex abolutescens
Carex gigantea
Carex lupulina†
Carex verrucosa
Cyperus filiculmus
Cyperus globulosus
Cyperus haspan
*Cyperus polystachyos
Cyperus retrorsus
Cyperus surinamensis
Eleocharis vivipara
*Fimbristylis puberula
Rhynchospora colorata
Rhynchospora corniculata
Rhynchospora fascicularis
Rhynchospora globularis
*Rhynchospora megalocarpa
Rhynchospora microcarpa
Rhynchospora pusilla
Scirpus validus
*Scleria reticularis
Scleria triglomerata
Scleria verticillata

DROSERACEAE
Drosera capillaris

EBENACEAE
*Diospyros virginiana

ERICACEAE
Befaria racemosa†
*Lyonia ferruginea
*Lyonia fruticosa
*Lyonia lucida
Vaccinium arboreum
*Vaccinium darrowii
*Vaccinium myrsinites
*Vaccinium stamineum

ERIOCAULACEAE
Eriocaulon decangulare
*Lachnocaulon anceps
Syngonanthus flavidulus

EUPHORBIACEAE
*Acalypha gracilens

*Chamaesyce hirta
*Chamaesyce maculata
*Cnidoscolus stimulosus
*Croton argyranthemus
*Croton glandulosus
*Crotonopsis linearis
*Stillingia sylvatica
*Tragia urens
FABACEAE
*Astragalus obcordatus
*Baptisia lecontei
*Centrosema arenicolum†
*Chamaecrista fasciculata
*Chamaecrista nictitans
*Crotalaria rotundifolia†
*Dalea carnea
*Desmodium incanum
Desmodium paniculatum
*Galactia regularis†
*Galactia volubilis
Gleditsia aquatica
*Indigofera caroliniana
*Indigofera hirsuta
*Lupinus diffusus
*Rhynchosia michauxii
*Schrankia microphylla
*Senna obtusifolia
*Sesbania emerus
*Stylosanthes biflora
*Tephrosia floridana
*Tephrosia rugelii
Vicia acutifolia
*Vignia luteola
*Zornia bracteata†
FAGACEAE
Quercus chapmanii†
*Quercus geminata
*Quercus incana
*Quercus laevis†
Quercus laurifolia†
Quercus myrtifolia
Quercus nigra
Quercus virginiana†
GENTIANACEAE
*Sabatia brevifolia
Sabatia grandiflora
HAEMADORACEAE
Lachnanthes caroliniana
HALORAGACEAE
Proserpinaca palustris
HAMEMELIDACEAE
Liquidambar styraciflua
HYDROPHYLLACEAE
Hydrolea corymbosa
HYPERICACEAE
Hypericum cistifolium
Hypericum fasciculatum
Hypericum gentianoides
Hypericum hypericoides
Hypericum mutilum
*Hypericum tetrapetalum
HYPOXIDACEAE
*Hypoxis juncea
Hypoxis leptocarpa
IRIDACEAE
*Sisyrinchium atlanticum
JUGLANDACEAE
Carya glabra
JUNCACEAE
Juncus dichotomus
Juncus effusus
Juncus elliottii
Juncus emarginatus
Juncus scirpoides
KRAMERIACEAE
*Krameria lanceolata
LAMIACEAE
Hyptis alata
*Piloblephis rigida
*Scutellaria arenicola
*Stachys floridana
*Teucrium canadense†
*Trichostema dichotomum
LAURACEAE
Cassytha filiformis†
Persea borbonia
LENTIBULARIACEAE
Pinguicula caerulea
Pinguicula pumila
Utricularia inflata
LINACEAE
Linum medium
LOGANIACEAE
Mitreola petiolata
*Polypremum procumbens
LORANTHACEAE
Phorodendron serotinum†
MALVACEAE
*Sida acuta
*Sida cordifolia
*Urena lobata†
MELASTOMATACEAE

*Rhexia mariana
MYRICACEAE
*Myrica cerifera
OLACACEAE
Ximenia americana
OLEACEAE
Chionanthus virginica
Fraxinus caroliniana
ONAGRACEAE
*Guara angustifolia
*Ludwigia maritima
Ludwigia microcarpa
Ludwigia octovalvis†
Ludwigia palustris
Ludwigia peruviana†
Ludwigia repens
*Oenothera laciniata
ORCHIDACEAE
Calopogon tuberosus
Encyclia tampensis
Epidendrum conopseum
Habenaria repens
Pteroglossaspis ecristata
*Spiranthes vernalis
Spiranthes odorata
OSMUNDACEAE
Osmunda cinnamomea
Osmunda regalis
OXALIDACEAE
*Oxalis florida
PHYTOLACCACEAE
*Phytolacca americana
PINACEAE
*Pinus clausa
*Pinus elliottii
*Pinus palustris
Pinus taeda
PLANTAGINACEAE
Plantago virginica
POACEAE
*Andropogon brachystachyus†
*Andropogon glomeratus
*Andropogon gyrans
*Andropogon longiberbis
Anthaenantia villosa
*Aristida stricta
*Axonopus affinis
Axonopus furcatus
*Dichanthelium aciculare
Dichanthelium commutatum
Dichanthelium dichotomum
*Dichanthelium ovale
*Dichanthelium sabulorum
Dichanthelium strigosum
*Digitaria serotina
*Echinochloa walteri
*Eragrostis elliottii
Eragrostis refracta
*Eustachys glauca
*Eustachys petraea
*Gymnopogon ambiguus
*Heteropogon melanocarpus†
Luziola fluitans
*Muhlenbergia capillaris
Panicum hemitomum
Panicum rigidulum
*Paspalum setaceum
*Rhynchelytrum repens
*Schizachyrium stoloniferum
*Setaria geniculata
*Sorghastrum secundum
*Sporobolus domingensis
*Sporobolus junceus†
POLYGALACEAE
*Polygala grandiflora
Polygala lutea
Polygala nana
Polygala rugelii
Polygala setacea
POLYGONACEAE
*Eriogonum tomentosum
*Polygonella gracilis
*Polygonella polygama
Polygonum densiflorum
Polygonum hydropiperoides
Polygonum punctatum
*Rumex hastatulus
POLYPODIACEAE
Phlebodium aureum
Polypodium polypodioides
PONTEDERIACEAE
Eichhornia crassipes†
Pontederia cordata
PORTULACACEAE
*Portulaca pilosa†
PSILOTACEAE
Psilotum nudum
PTERIDACEAE
*Pteridium aquilinum
ROSACEAE
Crataegus flava
Prunus serotina

Prunus umbellata
Rubus betulifolius
*Rubus trivialis†

RUBIACEAE
Cephalanthus occidentalis
*Diodia teres
*Diodia virginiana
*Galium tinctorium
*Hedyotis procumbens
*Hedyotis uniflora
Mitchellia repens
*Richardia brasiliensis
*Richardia scabra
Spermacoce assurgens

SALICACEAE
Salix caroliniana

SALVINIACEAE
Azolla caroliniana
Salvinia minima

SAPOTACEAE
Bumelia reclinata

SAURURACEAE
Saururus cernuus

SCHIZAEACEAE
Lygodium japonicum

SCROPHULARIACEAE
Agalinis fasciculata
Agalinis purpurea
Agalinis setacea
*Aureolaria pectinata
*Gratiola pilosa
Linaria canadensis
Lindernia grandiflora
Mecardonia acuminata
*Penstemon multiflorus
*Scoparia dulcis
*Seymeria cassioides
Seymeria pectinata

SMILACACEAE
*Smilax auriculata
Smilax bona-nox
Smilax laurifolia†
Smilax pumila

SOLANACEAE
*Physalis arenicola
Solanum americanum

TAXODIACEAE
Taxodium distichum

TYPHACEAE
Typha domingensis

TURNERACEAE
*Piriqueta caroliniana

ULMACEAE
Ulmus americana

URTICACEAE
Boehmeria cylindrica

VERBENACEAE
*Callicarpa americana
*Lantana camara
*Lippia nodiflora

VIOLACEAE
*Viola lanceolata
*Viola septemloba

VITACEAE
Ampelopsis arborea
*Parthenocissus quinquefolia†
Vitis aestivalis
*Vitis munsoniana
Vitis shuttleworthii

XYRIDACEAE
Xyris brevifolia
Xyris elliottii