FOODS AND HABITAT OF THE GOPHER TORTOISE IN SOUTHWESTERN GEORGIA

JAMES A. GARNER, International Paper Company, Southlands Experiment Forest, Bainbridge, GA 31717
J. LARRY LANDERS, International Paper Company, Southlands Experiment Forest, Bainbridge, GA 31717

Abstract: Broad-leaved grasses (Poaceae) were staple foods of gopher tortoises *(Gopherus polyphemus),* while wiregrass *(Aristida stricta)* was taken mainly in early spring and late fall. These plants were relatively high in fiber and were partially replaced in the diet by more nutritious forbs when available. Wild legumes (Fabaceae), which were very high in protein, were used extensively, especially by juveniles. Individuals near agricultural areas fed heavily on Florida pussley *(Richardia scabra),* and poor-Joe *(Diodia teres)* was taken frequently in areas of past soil disturbance. Vegetation in ruderal areas generally contained more minerals than food plants on natural sand ridges. Forage production (161 - 683 kg/ha) was positively correlated (r^2 = 0.88) with tortoise density and largely determined carrying capacity. However, occasional ingestion of animal matter (especially by females) may be a significant source of protein and minerals which are limited in xeric tortoise habitat.

Proc. Ann. Conf. S.E. Assoc. Fish & Wildl. Agencies 35:120-134

Wild gopher tortoises are thought to feed predominately on herbaceous plants. Grasses are reported to be the main component of the diet (Hallinan 1923, Braddock 1962, Black 1965, Bramble 1974). Fletcher (1899) specified wiregrass as the primary food resource, but other common grasses (e.g. *Andropogon* spp.) that grow on sand ridges are taken (Auffenberg and Franz 1975). Leaves of succulent, naturally occurring forbs are also important foods (Allen and Neill 1951). Conant (1975) reported a mixed diet of grasses, leaves, and wild fruits. Carr (1952) examined digestive tracts and found similar items plus small quantities of bones, charcoal, and insect chitin. However, none of the aforementioned accounts were based on quantitative analysis of the diet. In light of recent efforts to protect *G. polyphemus* populatons and the sand ridge community (Auffenberg and Franz 1975), detailed information is needed on requirements of the species to maintain quality habitat. The objectives of this study were to determine the primary constituents of the diet, to chemically analyze composition of major foods, and to estimate the production of food plants within natural and certain ruderal habitats used by tortoises.

This work was conducted by personnel of International Paper Company and partially funded under Section 6 of the Endangered Species Act of 1973 (PL93-205) administered through the Georgia Dept. Nat. Res. (Project No. 8-933). We sincerely appreciate the assistance in the field by W. McRae and A. K. Gholson, the chemical analysis work by the Soils Research Section at Southlands Experiment Forest, and the review of this manuscript by A. S. Johnson.

METHODS

Study Area

This study was conducted on the 1,400-ha Silver Lake Station of International Paper Company's Southlands Experiment Forest (SEF) near Bainbridge, Georgia. The Station is adjacent to Lake Seminole and has many permanent ponds and seasonally wet limestone depressions, which formed or enlarged upon closing of the Jim Woodruff Dam in the late 1950's. Elevation ranges from 24 to 31 m above mean sea level. Average maximum temperature for the summer is 32 C, and annual rainfall averages 127 cm.

Longleaf pine *(Pinus palustris)* in natural stands is the predominant forest type. Groundstory vegetation is dominated by grasses, bracken fern *(Pteridium aquilinum),* and running oak *(Quercus pumila).* The topography is flat to gently rolling with occasional sand ridges (depth of coarse sand surface layer = 0.5 - 2 m or more) where the longleaf pine-scrub oak *(Quercus* spp.) forest type occurs.

The area is managed for bobwhites *(Colinus virginianus).* Annual, late winter burning has maintained open habitat conditions for approximately 20 years. Intensive forest management has been applied to a small portion of the area. The clear-cutting and replanting schedule, along with large agricultural fields, and an extensive system of small plots of crops in the forest have established a variety of habitat types used by tortoises.

Seven colonies were chosen for habitat analysis: 1 on a chopped area, 1 in each of 4 slash pine *(Pinus elliottii)* plantations, and 2 in natural forest on sand ridges. The chopped area had been site-prepared 1 growing season prior to plant sampling. Site preparation included pushing down trees and shrubs on the area with a bulldozer which pulled 2 rolling drum choppers to crush woody plants and break up the ground surface. The oldest plantation studied had been established after similar site preparation 16 years prior to the study. Also sampled were a 3- and 2 6-year-old plantations which were established after less intense site preparaton but with similar equipment. The longleaf pine-scrub oak study sites had regenerated naturally with no site preparation after timber harvesting approximately 60 years prior to the study.

Habitat Analysis

In each of the 7 colony areas, a 30 × 60 m plot was established where the density of tortoise burrows appeared to be greatest. For each tree ($\geq$1.4 m tall) in these plots, the total height was recorded. Diameter at 1.4 m above ground also was measured in the 16-year-old plantation and the natural stands. Herbaceous vegetation was sampled (Jul - Aug 1979) at 20 grid positions in each large colony plot by a wooden frame with inside dimensions of 0.71 × 1.41 m. Above ground portions of all herbs were clipped, separated by species, oven-dried at 70 C, and weighed to the nearest 0.1 g.

Tortoise density in each of the 6 established colonies under study (the chopped area was excluded because the colony was temporarily disrupted) was estimated using the technique developed by Auffenberg and Franz (1975). This involved counting active burrows within the plot and applying a correction factor of 0.61 for number of individuals per number of burrows.

Food Habits Analysis

Gopher tortoises were captured during the activity seasons of 1978-80. Food items were recorded when feeding tortoises (n = 94 occurrences) were observed or captured outside their burrows. On other occasions tortoises were captured at their burrows in pit-fall traps (containers buried flush with the floor of the burrow). Trapped specimens were confined until at least 1 fecal dropping per tortoise could be collected for examination. Additional information was obtained from digestive tracts taken from necropsied tortoises. Stomachs of adults usually contained 1 to 3 boluses which were analyzed as separate specimens.

Each fecal or stomach sample was stirred in a container of water, and floating items were removed. The remainder was washed through 1.00 mm and 0.42 mm sieves. Materials in the larger sieve were separated to species when possible. Contents of the smaller sieve were checked under magnification for seeds, insect fragments, etc. which were separated when measurable quantities occurred, and the finely digested material was discarded. Food items were measured by water displacement to the nearest 0.01 cc. The aggregate percent method (Martin et al. 1946) was used to calculate volumetric percentages of food items.

Data on fecal dropping contents were summarized by month of collection and age of the tortoise as determined by Landers et al. (1981). Sixty-seven fecal samples from juveniles (ages 8 months to 15 years) and 87 from adults ($\geq$18 years) were analyzed. Data from stomach contents of juveniles (n = 6) and adults (n = 32) were combined and analyzed by season of collection.

Nutritional Analysis

Samples of major food items were collected in 1980 during the season of greatest use, as determined from food habits analyses. Samples were oven-dried at 70 C, ground with a Wiley mill to pass through a 1 mm screen, and stored in air-tight containers. Proximate chemical analysis of plants was conducted according to procedures of Horwitz (1980). Crude fat and crude fiber compositions were determined utilizing extraction and digestion apparatuses from Labconco Corporation, Kansas City, Missouri. Calcium, magnesium, and potassium levels were determined using the atomic absorption spectrophotometer model No. 372 from Perkin-Elmer Corporation, Norwalk, Connecticut. Nitrogen and phosphorus were determined using the Technicon BD-40 block digestor and the autoanalyzer II, both manufactured by Technicon Industrial Systems, Tarrytown, New York.

RESULTS AND DISCUSSION

Habitat

In this area, tortoises occupied droughty habitats where low-growing herbaceous vegetation was abundant. It previously has been shown that density of gopher tortoises in southern Georgia was closely related to biomass of herbaceous food plants (Landers and Speake 1980). Roadsides and edges of fields and pastures were common burrowing sites. Although some used burrows were found throughout the activity season, feeding ranges seemed to be only temporarily established in

such areas as indicated by a high frequency of unused burrows. Also, movements associated with breeding and nesting behavior resulted in many tortoises temporarily using these areas (McRae et al. 1981). Others relocated to these sites when large acreages of habitat were cleared. Colonies with tortoises of all ages were not only found in the natural longleaf pine-scrub oak forest type, but also in planted stands where the canopies were sufficiently open. Auffenberg and Franz (1975) reported similar findings in other portions of the gopher tortoises' range.

The most extensively used habitat type on our study area was the natural pine-oak forest on well- to excessively-drained soils. Deep, coarse sands (Lakeland series) occurred predominately on upper slopes of ridges where rapid internal drainage quickened the leaching of nutrients and lowered fertility. Herbaceous vegetation (Table 1) was less abundant on those sites (583 kg/ha) than on shallower, loamy sands (Wagram series) of the toe slopes (907 kg/ha).

Light intensity at the ground was high on the chopped area and the 3-year-old plantation which had not reached the crown closure stage (Table 2). Two other sites were on deep sands where tree survival was low and light penetration was much greater than in typical plantations of those ages (6 and 16 years). Herbs were abundant, and tortoises colonized those sites. In contrast, the survival and growth of pines in the 6-year-old plantation on shallower sands were greater; consequently, light intensity at the ground was lower and tortoise burrowing was limited to plantation edges where low-growing herbs were more abundant. Herbs were most abundant on the chopped area (1,779 kg/ha) and tended to decrease with time.

Groundstory composition was a function of successional stage. The chopped area (1-year fallow) was essentially covered by pioneer species such as blue-curls (*Trichostema* sp.) (37% of total herbaceous biomass), pineweed *(Hypericum gentianoides)* (13%), and poor-Joe (10%). These plants, though significant components of the 3-year-old plantation, were less abundant than in the fallow area and were essentially absent in older plantations. Composites (Asteraceae) and rock-roses (Cistaceae) were important on the deep sands in the 3- and 6-year-old plantations where they comprised 40 and 18% of the biomass, respectively. Shallower sands in the 6-year-old plantation supported an abundance of blackberry (*Rubus* spp.) (35%) and pennyroyal (*Hedeoma* sp.) (14%) as well as grasses. Silkgrass *(Heterotheca graminifolia)* was present in all habitats but dominated the 16-year-old plantation where wiregrass had been eliminated. Herbaceous vegetation was dominated by grasses in 3 of the tortoise colony areas. Wiregrass comprised over half of total biomass on both natural pine-oak sites. The 6-year-old plantation on excessively-drained soils was dominated by a mixture of wiregrass and broad-leaved grasses. Panic grasses (*Panicum* spp.) were the major broad-leaved grasses on the chopped site (130 kg/ha). These species steadily declined through subsequent successional stages, and were lowest on natural sand ridges (1-2 kg/ha) where bluestems (*Andropogon* spp.) and indian grass *(Sorghastrum secundum)* were the most abundant broad-leaved grasses.

Food Habits

Grasses and grass-like plants (certain species of Cyperaceae and Asteraceae) were the principal foods throughout the season of activity. This group includes

Table 1. Dry-matter yields of herbaceous vegetation in gopher tortoise habitats on Silver Lake Station.

	% Composition						
	1st yr.	3rd yr.	6th yr. plantation		16th yr.	Natural Sand Ridge	
Food item	fallow (1779)[a]	plant. (1040)	Upper Slope (835)	Toe Slope (696)	plant. (800)	Upper Slope (583)	Toe Slope (907)
Grasses & grass-likes							
Broad-leaved grasses	11.5	22.8	38.8	18.8	11.5	9.0	22.7
Wiregrass	2.0	11.9	24.6	14.5	0.0	52.0	51.7
Silkgrass	2.5	0.2	5.1	3.2	70.5	14.3	9.5
Nutrush	0.7	0.0	0.3	0.1	0.4	3.8	4.0
Legumes							
Hoary pea	3.1	0.0	0.9	0.5	0.5	0.5	2.8
Sensitive brier	0.8	0.0	0.0	0.0	0.0	4.0	0.0
Milk pea	0.0	0.0	0.3	0.1	1.4	0.2	0.3
Butterfly pea	0.0	0.0	0.2	0.1	0.7	0.3	0.3

[a] Numbers in parantheses are total herbaceous biomass (kg/ha).

Table 2. Overstory characteristics in gopher tortoise colony areas on Silver Lake Station.

Species	3rd yr. Plant.	6th yr. Plantation Upper Slope	6th yr. Plantation Toe Slope	16th yr. Plant.	Natural Sand Ridge Upper Slope	Natural Sand Ridge Toe Slope
Longleaf pine						
No./ha					317	67
$\bar{x}$ ht. (m)					9.9	10.9
$\bar{x}$ dbh (cm)					12.0	19.3
Slash pine						
No./ha	1128	615	1478	722		
$\bar{x}$ ht. (m)	1.8	5.0	4.7	8.8		
$\bar{x}$ dbh (cm)				10.7		
Oaks						
No./ha	1692	1784	5788	211	372	378
$\bar{x}$ ht. (m)	1.6	4.1	3.9	7.4	6.2	6.8
$\bar{x}$ dbh (cm)				8.2	10.5	11.0
Total No./ha	2820	2399	7266	933	689	445

several species from different habitats. Carpet grass *(Axonopus affinis)* and goose grass *(Eleusine indica)* occurred only along woods roads in conjunction with side-seed grasses (*Paspalum* spp.). Bahia *(Paspalum notatum)* was the principal grass available along pasture and highway edges. Crab grass *(Digitaria sanguinalis)* and nutgrass *(Cyperus esculentus)* were found only around agricultural fields. Silkgrass was prolific in ruderal as well as natural areas. Nutrush *(Scleria ciliata)* and wiregrass occurred mostly in the natural forest type. Greatest use was evident for this group of plants by the season average of 80% of the fecal contents of adults. These foods were especially important during early spring and late fall when leafy forbs were least available. Mean monthly content of grasses in fecal samples peaked in spring and fall (Tables 3 and 4). Maximum values during those seasons were near 90%, while summer months averaged 70 - 80% for adults and 31 - 58% for juveniles. Stomach analysis depicted this same pattern with 90% in early spring followed by a low of 49% in late spring, whereas stomachs collected in summer showed the increasing trend to a value of 87% in fall (Table 5).

Broad-leaved grasses were favored, and very little use of wiregrass was shown on our area. Although notable quantities were found in feces from adults in some months, volume and occurrence dropped sharply when forbs became more available during late spring and summer. Fecal analysis values may exaggerate the actual use of wiregrass because it is tough and fibrous and appeared to be less digestible than other foods. This plant was apparently unpalatable to juveniles, since none of the 31 samples analyzed from tortoises less than 6 years old contained wiregrass. Considering the large quantity available in relation to other food plants (see

Table 3. Foods of adult gopher tortoises on Silver Lake Station as revealed by analysis of feces collected during 1978-80.

Food item[a]	Aggregate percentage[b]								
	Mar (7)[c]	Apr (15)	May (13)	Jun (10)	Jul (10)	Aug (10)	Sep (10)	Oct (6)	Nov (6)
Grasses & grass-likes	91	87	81	70	80	77	75	91	69
Broad-leaved	90	81	77	69	78	76	72	75	67
Wiregrass	1	6	4	1	2	1	3	16	2
Legumes	1	2	11	19	11	11	4	1	
Sensitive brier		1	2						
Hoary pea		1	4	14	1	5	1		
Milk pea			1	2	1				
Butterfly pea			4	3	9	4	2	1	
Others — veg. & fl.	1					2	1		
Pawpaw — veg. & sd.		3	2				6		5
Prickly-pear — veg. & sd.					2				
Fleshy fruits — sd.					1	1			
Poor-Joe — veg. & sd.							3	4	19
Florida pussley — veg. & sd.									4
Minor plant foods		1	1	2	1	1			
Unidentified forbs		2	1	3	1	3	4		1
Dead leaves									
Pine	7	4	3	5	3	6	6	2	1
Other		2	1	1				1	

[a] Food items consisted of leaves and stems (veg.) unless otherwise designated as seeds (sd.) or flowers (fl.).
[b] Percentage values were rounded to the nearest whole number, and those less than 0.51 were omitted.
[c] Numbers in parentheses are sample sizes.

Table 4. Foods of juvenile gopher tortoises on Silver Lake Station as revealed by analysis of feces collected during 1978 - 80.

Food item[a]	Aggregate percentage[b]							
	Apr (11)[c]	May (8)	Jun (6)	Jul (9)	Aug (16)	Sep (11)	Oct (4)	Nov (2)
Grasses & grass-likes	85	40	55	58	34	31	69	92
Broad-leaved	84	39	50	58	34	30	69	92
Wiregrass	1	1	5			1		
Legumes	10	37	32	30	54	50	26	
Sensitive brier	9	12	17	14	7			
Hoary pea		14	6		7	1	25	
Milk pea		7	9	13	36	39	1	
Butterfly pea		1		3	4	7		
Others	1	3				3		
Flowers (unid.)		4						
Bracken Fern			6					
Fleshy fruits — sd.				1	1			
Poor-Joe — veg. & sd.				1			1	1
Minor plant foods — veg. & sd.	1	1	2			8		
Unidentified forbs		13	1	8	7	11	2	6
Dead leaves								
Pine	1	2	1				1	
Other	2	2	1					2
Insects		2		1	3			

[a] Food items consisted of leaves and stems (veg.) unless otherwise designated as seeds (sd.) or flowers.
[b] Percentage values were rounded to the nearest whole number, and those less than 0.51 were omitted.
[c] Numbers in parentheses are sample sizes.

Table 5. Foods[a] of gopher tortoises on Silver Lake Station and vicinity as revealed by analysis of stomachs collected during 1978-80.

Food item	Aggregate percentage[b] April to mid-May (9)[c]	mid-May to June (15)	July-Sep (9)	Oct-Dec (5)
Grasses & grass-likes	49	67	87	
Broad-leaved	90	48	66	86
Wiregrass		1	1	1
Legumes	5	14	5	
Sensitive brier		8	1	
Hoary pea	1	3	1	
Milk pea	1			
Butterfly pea		3	1	
Others — veg., fl. & fr.	3		2	
Morning-glory — veg. & fl.		16	1	
Dyschoriste		6	5	
Poor-Joe — veg. & sd.		3	3	9
Fleshy fruit — fr.		1	5	
Florida pussley			7	
Pawpaw				1
Minor plant foods — veg. & sd.	3	8	4	
Dead leaves				
Pine	1	3	1	1

[a] Food items consisted of leaves and stems (veg.) unless otherwise designated as seeds (sd.), flowers (fl.) or fruit (fr.).

[b] Percentage values were rounded to the nearest whole number, and those less than 0.51 were omitted.

[c] Numbers in parentheses are sample sizes.

Habitat), wiregrass apparently was not a choice food, but was taken when preferred foods were depleted.

Fisher (1917) observed tortoises in the pine-barren regions of Florida eating wiregrass, and stomachs from that region contained chiefly wiregrass. Forb production on our area was greatly enhanced by prescribed burning and other management practices (Buckner and Landers 1979) and appeared to be higher than in any of several tortoise colonies visited in southern Georgia during the course of this study. Tortoises on those areas where forbs are less available may be forced to depend more heavily on wiregrass.

Forbs became increasingly important in the diet as the growing season progressed. Juveniles consumed a greater percentage of this forage type than did adults. In southern Florida forbs along with grasses were the principal foods as indicated by feeding observations and contents of digestive tracts of 2 juveniles (Douglass 1978).

Legumes were the most important forbs in tortoise diets in our study. In early spring, their leaves and stems were taken, and use peaked with vegetative

development. Sensitive brier *(Schrankia microphylla)* and hoary pea *(Tephrosia* spp.) were earlier maturing species and were the most important legumes in the spring. They were followed predominately in the summer by milk pea *(Galactia* spp.) and butterfly pea *(Clitoria mariana),* which emerged in the habitat later in the growing season. Adult use of legumes peaked in late spring. Juveniles depended most heavily on legumes, which comprised 26 - 54% of mean monthly percent volumes of feces collected in May - October. The fact that juveniles typically disperse from adult activity centers and live solitarily until adulthood (McRae et al. 1981) may be related to depletion of preferred forbs in colony areas.

Grasses, grass-like plants, and legumes were by far the most important forage plants in the habitat and evidently determined carrying capacity. Adult tortoise density (n/ha = y), as estimated from counts of burrows $\geq$18.0 cm wide, was most strongly correlated ($r^2 = 0.88$, $y = 6.41 + 0.45x$) with the production (kg/ha x $10^{-1} = x$) of these food plants. Landers and Speake (1980) also found that tortoise density was directly related to herbaceous biomass. These findings parallel those of Auffenberg and Iverson (1979) who found that tortoise home range was inversely related to the coverage of key herbaceous plants.

Another important forb in the diet of tortoises was poor-Joe, which occurred in abundance in areas with past soil disturbance. Fecal analysis showed notable percentage volumes only in autumn, but these figures underestimate the use of this plant. Leaves and stems were low in fiber content (see Nutrition) and were apparently very digestible through early fall. During that period vegetative portions were poorly represented and samples consisted primarily of seeds. Hardened stems were prevalent in poor-Joe taken from feces of adults during November, when mean monthly volume reached 19%. Stomach analysis revealed its initial use in late spring with increased use in the fall.

Other forbs were found to be important foods. One of these was Florida pussley (an associate of agriculture) which previously has been reported as a food in Florida (Hutt 1967). Narrow-leaved pawpaw *(Asimina longifolia)* also was a significant component of feces of adults collected in the fall.

Dyschoriste *(Dyschoriste oblongifolia)* and bracken fern occasionally were major components of individual fecal and stomach samples of late spring and summer when plants were generally most succulent. Seventeen other species were recorded as minor foods during this period, the majority of which were members of 3 families: Asteraceae (n = 6 species), Euphorbiaceae (n = 4), and Polygonaceae (n = 2).

Morning-glory *(Ipomoea pandurata)* leaves were major items in the stomach contents. This plant occurred only rarely in natural habitat, but was prolific along roadsides and disked areas. In observations of feeding on morning-glory, adult tortoises showed a preference for its flowers over its leaves.

Fleshy fruits were available in the summer and early fall and appeared commonly in feeding observations (Table 6) and stomachs. Their occurrence in feces was predominately of seeds, rather than the more easily digested fruit pulp, which resulted in low total volume. Gopher tortoises have previously been reported to eat berries (Allen and Neill 1951). The most heavily used fruits on our area were blackberry *(Rubus cuneifolius)* and sloe plum *(Prunus umbellata).* Fruits of blueberry (*Vaccinium* spp.), huckleberry (*Gaylussacia* spp.), prickly-pear (*Opuntia* spp.), maypop *(Passiflora incarnata),* muscadine *(Vitis rotundifolia),* and hawthorne (*Crataegus* spp.) also were taken.

Table 6. Gopher tortoise feeding observations on Silver Lake Station during 1978-80.

Food item[a]	Percent occurrence		
	Spring (47)[b]	Summer (39)	Fall (10)
Grasses & grass-likes	38	39	80
Unidentified broad-leaved	9	10	
Wiregrass	4		
Panic grass	2	5	30
Silkgrass	2		40
Nutrush	2		
Carpet grass	9	8	
Crab grass	4	3	10
Side-seed grass	4	10	
Goose grass		3	
Legumes	14	12	
Sensitive brier	2	3	
Hoary pea — veg. & fl.	6		
Other	6	9	
Flowers	4		
Florida pussley	2		
Prickley-pear	2		
Fleshy fruit	15	16	
Blackberry	2		10
Poor-Joe		13	10
Morning-glory — veg. & fl.	2	8	
Pawpaw	2		
Mushrooms	2	3	
Maypop		3	
Minor plant foods	4	12	
Raccoon feces		3	
Carrion/skeletons	15		

[a] Food items consisted of leaves and stems (veg.) unless otherwise designated as flowers (fl.) or fruit.

[b] Numbers in parentheses are sample sizes.

Seeds, spines, and epidermis of prickly-pear were found in feces, but the succulent readily digestible tissues of this plant were not, and the use of this species as a food probably was underestimated. Also, this plant was uncommon over most of the study area and it may be a more important resource in some other areas of the range.

Mushrooms (Agaricales) were found only occasionally in specimens, and volume was low. Apparently they were readily accepted, but occurred infrequently in the xeric habitat. On 2 occasions we observed tortoises eating mushrooms that had emerged in their burrows after several days of rain. Brode (1959) also observed tortoises feeding on mushrooms.

Insects, flesh, bones, and feathers occurred in 8% of the fecal droppings of adults. Adult females were observed eating carrion (n = 3 occasions), carrying bones in their mouths to their dens (n = 2), and biting fragments from a decaying turtle skeleton (n = 1) or old egg shells (n = 1).

A rabbit fecal pellet was found in a fecal sample of a 9-year-old tortoise. Also, we observed a smaller juvenile eating raccoon *(Procyon lotor)* feces composed chiefly of blackberry seeds and insects.

Nutrition

Detailed studies of nutrient requirements of the gopher tortoise evidently have not been published. Accelerated growth associated with improved nutrition has been documented by feeding captive *G. agassizi* a diet high in protein and vitamins (Jackson et al. 1976) and by monitoring growth of *G. polyphemus* on fertilized and on natural ranges (Landers et al. 1981). Requirements related to sex, age, and season of the year may be reflected in chemical composition of the major items revealed from food habits analyses.

Early spring was the period when dietary requirements may have been most critical. Body reserves had been depleted during winter dormancy as shown by cessation of growth and loss of body weight (Landers et al. 1981). Also, adult females require more of the nutrients required for egg formation (Jackson et al. 1974), which occurs at this time (Landers et al. 1980).

Content of many important nutritional components was highest in spring samples of food plants (Table 7). Protein, which was likely essential for initiation of annual growth, was at peak concentrations in actively growing plant tissues. Potassium and phosphorus peaked in spring samples of food plants; the latter element is notably deficient in southern range (Dietz 1970) and may be a limiting factor in tortoise nutrition. This factor may account for the evident selection by females for animal matter, which is a concentrated source of phosphorus as well as calcium and protein; all are needed during egg formation. The relatively low fiber content of spring foods indicated a diet high in digestibility.

As grasses became more fibrous in the summer and fall than in the spring, tortoises tended to shift to higher quality forage plants. Among these were legumes which had the highest concentrations of protein and phosphorus of all food plants sampled from the natural habitat. They were selected in late spring and summer, especially by young tortoises. Peak seasonal growth of juveniles (the life stage of most rapid development), as reported by Landers et al. (1981), corresponded to peak consumption of legumes. Phosphorus was exceptionally high in summer flowers, and prickly-pear and dyschoriste contained highest calcium and magnesium levels of food plants on sand ridges. The ingestion of protein and minerals at this time also may be important in re-conditioning females after the egg-laying period, especially since follicular enlargement for the next year begins soon after laying (Landers et al. 1980).

A lean period is indicated for autumn, as gopher tortoises returned to a diet of mature grasses (and other plants high in fiber) from which they had partially shifted during summer. This period also marks a pronounced reduction in tortoise growth (Landers et al. 1981).

Table 7. Nutrient composition of major plant foods of tortoises on Silver Lake Station.

Food item[a]		% dry weight									% wet wt
		Crude Protein	Crude Fiber	NFE	Fat	Ash	Ca	P	K	Mg	Moisture
Roadside grasses	Mar-May	9.8	29.1	51.1	2.3	7.6	0.17	0.14	0.94	0.20	76.4
(Panic & carpet grasses)	Jun-Aug	5.8	30.2	53.3	3.5	7.1	0.19	0.08	0.64	0.15	68.3
	Sep-Nov	6.9	27.9	54.1	3.3	7.8	0.18	0.08	0.51	0.16	69.7
Field grasses & grass-likes (Bahia, crab & nut grasses)	July	9.7	27.3	52.5	2.4	8.0	0.33	0.19	1.43	0.28	70.7
Natural broad-leaved grasses	Mar-May	10.8	28.8	53.0	2.0	6.0	0.22	0.15	1.00	0.10	74.2
(Bluestems & indian grass)	Jun-Aug	4.5	32.8	56.2	2.7	3.9	0.19	0.05	0.43	0.10	64.9
	Sep-Nov	4.0	34.3	56.2	2.0	3.5	0.17	0.04	0.31	0.09	60.3
Wiregrass	Mar-May	8.9	35.7	49.3	1.5	4.6	0.12	0.12	0.83	0.08	69.0
	Jun-Aug	4.6	39.4	51.9	1.1	3.0	0.10	0.03	0.30	0.06	55.4
	Sep-Nov	3.1	35.4	56.7	1.5	3.2	0.13	0.03	0.15	0.06	51.7
Silkgrass	Mar-May	9.3	32.1	46.4	2.0	10.1	0.62	0.16	1.98	0.16	78.4
	Jun-Aug	5.4	35.0	48.4	3.9	7.3	0.80	0.06	1.07	0.20	73.1
	Sep-Nov	5.5	32.6	52.2	3.8	5.9	0.80	0.07	0.71	0.20	66.9
Legumes											
Hoary pea	May-Jul	17.2	24.5	51.2	3.7	3.4	0.46	0.13	0.51	0.22	64.1
	Aug-Oct	13.8	25.6	51.2	4.4	5.0	0.75	0.10	0.32	0.27	59.8
Sensitive brier	Apr-May	31.3	11.0	49.1	3.4	5.2	0.66	0.25	1.10	0.26	77.8
	Jun-Aug	13.3	17.0	59.5	4.0	6.1	1.31	0.13	0.50	0.43	70.1
Butterfly pea	May-Jul	17.3	24.5	51.2	3.2	3.9	0.60	0.14	0.60	0.18	68.9
Milk pea	Jul-Sep	14.5	19.9	57.5	2.5	5.6	0.91	0.11	0.51	0.33	64.6
Partridge pea	Jul-Sep	15.6	20.8	55.6	4.2	3.8	0.61	0.10	0.46	0.20	69.7
Prickly-pear	Apr	5.4	8.5	71.7	1.2	13.3	3.27	0.12	1.75	0.90	87.7
Morning-glory	May-Jul	12.6	14.9	57.5	2.0	12.9	0.95	0.13	1.13	0.54	75.9
Flowers	Jun	9.0	10.2	68.2	4.9	7.8	0.18	0.26	2.12	0.18	89.1
Pawpaw	Jun-Sep	8.4	26.1	52.2	7.0	6.4	1.28	0.11	0.66	0.32	68.6
Dyschoriste	Jun-Jul	8.0	14.1	58.2	4.2	15.4	2.80	0.10	0.84	0.81	72.0
Poor-Joe	Jul-Aug	10.4	18.8	59.5	2.2	9.1	1.38	0.16	0.90	0.42	82.2
	Sep-Oct	8.8	28.6	51.1	5.8	5.8	0.86	0.18	0.38	0.19	68.0
Florida pussley	Jul-Oct	9.8	14.8	53.2	5.9	16.3	2.60	0.20	1.30	0.48	86.3

[a] Percentages are averages of 2-5 samples of current vegetative growth unless otherwise designated.

Moisture levels in foods were also thought to be important because tortoises were never observed near water, even though many lived on sand ridges bordering ponds or rivers. Minnich and Ziegler (1976) reported that this species acquires most of its moisture requirements through a succulent diet of mostly cactus and grasses. Cacti (*Opuntia* spp.) on our area contained 88% moisture in April while broad-leaved grasses ranged from 60 - 70% throughout the activity season. Moisture content in foliage exceeded 80% only in species sampled from ruderal areas. A notable drop in moisture content of most plants occurred during the summer months. During this same time, there was a pronounced reduction in tortoise movement, possibly to avoid the extreme summer heat (McRae et al. 1981) and conserve body moisture.

CONCLUSIONS

Gopher tortoises inhabit the most xeric areas in southern Georgia, but thrive in a variety of natural and ruderal habitats with sufficient herbaceous vegetation. The species is selective; it avoids certain coarse plants that may be abundant (e.g. rock-roses, pineweed, wiregrass) in favor of broad-leaved grasses and certain forbs. Critical periods appear to be early spring, a time of recovery from hibernation, and fall when food plants have become fibrous. Seasonal shifts in forage help to maintain intake of protein and minerals. Legumes are particularly high in these food fractions; their more constant use (when available) by juveniles evidently satisfies requirements during the rapid growth stage. The emigration of young tortoises from colony areas may be related in part to a heightened need for succulent plants that became depleted in colonies.

Tortoises readily take other high quality plant foods (e.g. fleshy fruits and mushrooms) that usually occur infrequently on natural sand ridges. Animal matter is consumed only occasionally, but may be an important resource, especially for conditioning females prior to and shortly after egg laying. Conservation of nutrients and moisture appears to be the key for maintaining the large biomass in typical tortoise colonies on infertile, droughty soils. For this reason, fire is important in recycling nutrients, perpetuating herbs, and supporting tortoises and (indirectly) their burrow associates.

LITERATURE CITED

Allen, R., and W. T. Neill. 1951. The gopher. Fla. Wildl. 5(7):10, 32.

Auffenberg, W., and R. Franz. 1975. The status and distribution of *Gopherus polyphemus*. USDI Fish and Wildl. Serv. Rep. 48pp.

_____, and J. B. Iverson. 1979. Demography of terrestrial turtles. Pages 541-569 *in* M. Harless and H. Morlock, eds. Turtles: research and perspectives. Wiley-Interscience, New York.

Black, J. D. 1965. Gopher tortoise. Encycl. Amer. 13:61.

Braddock, J. E. 1962. A gopher named "Tuffy." Fla. Nat. 35:46.

Bramble, D. M. 1974. Occurrence and significance of the Os transiliens in gopher tortoises. Copeia 1974:102-109.

Brode, W. E. 1959. Notes on behavior of *Gopherus polyphemus*. Herpetologica 15:101-102.

Buckner, J. L., and J. L. Landers. 1979. Fire and disking effects on herbaceous food plants and seed supplies. J. Wildl. Manage. 43:807-811.

Carr, A. 1952. Handbook of turtles. Cornell Univ. Press, Ithaca. 542pp.

Conant, R. 1975. A field guide to reptiles and amphibians of eastern and central North America, 2nd ed. Houghton Mifflin Company, Boston. 429pp.

Dietz, D. R. 1970. Definition and components of forage quality. Pages 1-9 *in* Range and wildlife habitat evaluation — a research symposium. USDA For. Serv. Misc. Publ. No. 1147.

Douglass, J. F. 1978. Refugia of juvenile gopher tortoises, *Gopherus polyphemus* (Reptilia, Testudines, Tustudinidae). J. Herp. 12:413-415.

Fisher, G. C. 1917. "Gopher pulling" in Florida. Am. Mus. J. 17:291-293.

Fletcher, W. B. 1899. The Florida gopher. Proc. Indiana Acad. Sci. 1899:46-52.

Hallinan, T. 1923. Observations made in Duval County, northern Florida, on the gopher tortoise *(Gopherus polyphemus).* Copeia 1923:11-20.

Horwitz, W., ed. 1980. Methods of analysis, 13th ed. Association of Official Analytical Chemists, Washington D.C. 1018pp.

Hutt, A. 1967. The gopher tortoise, a versatile vegetarian. Fla. Wildl. 21(7):20-24.

Jackson, C. G., Jr., C. M. Holcomb, and M. M. Jackson. 1974. Aortic calcification, serum calcium, magnesium, sodium and cholesterol in *Gopherus polyphemus.* Comp. Biochem. Physiol. 49A:603-605.

_____, J. A. Trotter, T. H. Trotter, and M. W. Trotter. 1976. Accelerated growth rate and early maturity in *Gopherus agassizi* (Reptilia:Testudines). Herpetologica 32:139-145.

Landers, J. L., and D. W. Speake. 1980. Management needs of sandhill reptiles in southern Georgia. Proc. Ann. Conf. S.E. Assoc. Fish and Wildl. Agencies 34:515-529.

_____, J. A. Garner, and W. A. McRae. 1980. Reproduction of gopher tortoises *(Gopherus polyphemus)* in southwestern Georgia. Herpetologica 36:353-361.

_____, W. A. McRae, and J. A. Garner. 1981. Growth and maturity of the gopher tortoise in southwestern Georgia. Bull. Florida State Mus. Biol. Ser. 27(2): 81-110.

Martin, A. C., R. H. Gensch, and C. P. Brown. 1946. Alternative methods in upland game bird food analysis. J. Wildl. Manage. 10:8-12.

McRae, W. A., J. L. Landers, and J. A. Garner. 1981. Movement patterns and home range of the gopher tortoise. Am. Midl. Nat. 106(1):165-179.

Minnich, J. E., and M. R. Ziegler. 1976. Comparison of field water budgets in the tortoises, *Gopherus agassizi* and *G. polyphemus.* Am. Zool. 16:219. (Abstr.)