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DIET AND DIETARY PREFERENCE OF THE JUVENILE GOPHER TORTOISE (*GOPHERUS POLYPHEMUS*)

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ABSTRACT: We documented both the diet and dietary preference of free-ranging juvenile gopher tortoises (*Gopherus polyphemus*) by direct observation. All observations were conducted on a 1-ha plot of sandhill habitat that has been maintained on a 1-yr fire periodicity by controlled burning for more than 25 yr. Seventeen foraging observations of juvenile gopher tortoises were included in our analyses. Juvenile gopher tortoises ate 26 plant genera. To determine if juvenile gopher tortoises were selecting particular genera, either positively or negatively, we used Resampling Stats. Plants of 16 genera were selected positively by at least one juvenile gopher tortoise. The most abundant plant genus along the foraging paths, *Aristida*, was selected negatively. Other grasses (Poaceae) were consumed mostly during the cool months when forbs, several of which were selected positively, were in decline. Grasses mostly were eaten in proportion to their availability. Juvenile gopher tortoises foraged only for brief time periods and traveled short distances during a foraging bout. Individuals may satiate quickly and/or may be predisposed to remain near their burrow because they are vulnerable to thermal stress and/or predation. Turtles residing in habitats with high quality and abundant forage grow rapidly to sexual maturity, which, in turn, can increase population growth rate. Understanding the biology of the juvenile gopher tortoise can help shape management practices that prevent declines of gopher tortoise populations.

Key words: Conservation; Demographic health; Diet; Foraging; Gopher tortoise; *Gopherus polyphemus*; Herbivory

THE GOPHER tortoise (*Gopherus polyphemus*) is most commonly found in sparsely canopied upland habitats that occur on deep, well drained, sandy substrate suitable for construction of its extensive burrows. The habitats most often occupied by the gopher tortoise include sandhill (high pine), scrub, xeric hammock, pine flatwoods, dry prairie, coastal grasslands and dunes, and mixed hardwood pine communities (Auffenberg and Franz, 1982; Diemer, 1986, 1992; Kushlan and Mazzotti, 1984; Landers and Speake, 1980; Myers and Ewel, 1990). The habitat most densely populated by the gopher tortoise is sandhill, an upland habitat maintained by frequent fires (Diemer, 1986; Mushinsky and Gibson, 1991; Mushinsky and McCoy, 1994; Mushinsky et al., 1997; Myers and Ewel, 1990). A strong preference for relatively open areas causes the gopher tortoise to aggregate in relatively high densities in patches that have been cleared by wild fires and other “disturbances.”

The gopher tortoise is known to feed principally on herbaceous plants (Carr, 1952;

Garner and Landers, 1981). In central Florida, 68 genera of plants from 26 families, identified by direct observation and/or scat analysis, were included in the diet of a sample of mixed age gopher tortoises (Macdonald and Mushinsky, 1988). The most common families of plants consumed were Poaceae, Asteraceae, Fabaceae, Pinaceae, and Fagaceae (Macdonald and Mushinsky, 1988). The most common species consumed was wire grass (*Aristida beyrichiana*).

In general, knowledge of the biology of neonatal (Morafka, 1994; Morafka et al., 2000) and juvenile (Douglass, 1978) tortoises is incomplete. The limited information that is available on foraging habits of juvenile gopher tortoises suggests that they tend to ingest fewer grasses and plants with external defense mechanisms and more plants with high nitrogen content, such as legumes, than adults (Garner and Landers, 1981; Macdonald and Mushinsky, 1988). Our research was designed to document both the diet and dietary preference of free-ranging juvenile gopher tortoises by direct observation.

METHODS

Our study was conducted at the Ecological Research Area (ERA) of the University of

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South Florida, using the same gopher tortoise population studied by Macdonald and Mushinsky (1988), Mushinsky et al. (1994), and Wilson et al. (1994). To facilitate observation of foraging juvenile gopher tortoises, all of our research was conducted on a 1-ha plot of sandhill habitat that has been maintained on a 1-yr fire periodicity by controlled burning for more than 25 yr (Mushinsky, 1985; Mushinsky and Gibson, 1991). Although the gopher tortoise is distributed widely in the upland habitats of the ERA, juveniles are most abundant under the sparse tree canopy of the 1-yr plot. A fire lane separates the 1-yr plot from surrounding plots that are maintained on other burn frequencies. Although resident gopher tortoises are free to cross fire lanes to move among plots, the juveniles we studied did not do so during our study. The 1-yr plot has a sparse tree canopy consisting of longleaf pine (*Pinus palustris*), slash pine (*P. elliotii*), turkey oak (*Quercus laevis*), and sand live oak (*Q. geminata*). Ground vegetation includes a variety of grasses (e.g., *Aristida beyrichiana*, *Andropogon* spp.) and herbs (e.g., *Aster tortifolius*, *Baptisia* spp., *Liatris* spp., *Pityopsis* spp.). Saw palmetto (*Serona repens*) is the most abundant species in the shrub layer.

To initiate our study, we surveyed the 1-yr plot to locate all burrows that might be used by gopher tortoises seven or fewer years old. Previous research at this site established that burrow width was correlated with the carapace length of the resident tortoises (Wilson et al., 1992) and that individuals <7-yr old have carapace lengths <200 mm (Mushinsky et al., 1994); therefore, all burrows <200 mm wide were marked with a numbered metal rod. The gopher tortoises we observed foraging were between the ages of 2–6 yr (72–154 mm carapace length). Age was determined by counting plastral scute annuli (Mushinsky et al., 1994).

We collected dietary data by direct observation of foraging gopher tortoises. Opportunity for direct observation of free-ranging individuals is limited by the above ground behavior of the gopher tortoise. If the minimum behavior of an "active" gopher tortoise is defined as moving to the mouth of the burrow, then adults (Auffenberg and Iverson, 1979) and juveniles (Wilson et al., 1994) are active only about 10% of the time. Foraging and

other activity away from the burrow is even less common. Because of the limited opportunity for direct observation of foraging, we visited the study site 1–3 times per week for 21 mo from July 1998 through March 2000 to make foraging observations. Observation periods began between 1000–1100 h, prior to emergence of resident tortoises, and lasted until 1300–1600 h, after cessation of most activity. Observation stations were established to permit more than one active burrow to be visible and were located opposite to the orientation of the burrow openings. We positioned the observation stations so that shrubs were between the observer and the tortoise burrows.

During a foraging bout, we made every effort to minimize the amount of disturbance to the gopher tortoise. Foraging individuals were followed from a distance (approximately 3–5 m) and angle that was inconspicuous to them, but allowed us to identify plants as they were eaten. While following a foraging gopher tortoise, we placed a stake wire flag in the ground at the location of each directional change and every 1 m along straight paths. We recorded the amount of time spent during each foraging bout. Just before an observed gopher tortoise entered a burrow, it was captured for identification and the length of the carapace was measured. If an individual had been marked previously, it was released immediately; otherwise, it was returned to the laboratory for marking.

After completing a foraging observation, we retraced the foraging path (guided by the stake wire flags). We counted and identified all plant genera present along the entire foraging path. The width of the foraging path was approximately equal to the carapace length of the gopher tortoise we had just observed (Wilson et al., 1992). With the exception of some long, low vines, such as *Rhynchosia* spp. and *Shrankia microphylla*, which were counted as many times as they intersected a foraging path, each individual plant was counted as a single encounter. Our plant taxonomic nomenclature follows Taylor (1992) and Wunderlin (1998). With the exception of *Aristida beyrichiana*, grasses were identified only to family (Poaceae). With the exception of seedlings, all plants were identified to genus. Seedlings, most measuring only a few centimeters in height,

often were eaten completely before they could be identified and were recorded, therefore, only as "seedling." Hereafter, "seedlings" and Poaceae will be referred to as "genera." The distances between successive pairs of flags along a foraging pathway were measured to determine the total distance traveled and the maximum straight-line distance the tortoise had moved from its burrow.

The diet of the juvenile gopher tortoise was documented by direct observation and its dietary selection, either positive or negative, was established by comparing plants eaten to plants available along the foraging paths. The phrases "positive selection" and "negative selection" indicate that a plant genus was eaten disproportionately more or less, respectively, than expected based upon the availability of the genus. Because virtually all the plant genera identified along the foraging paths are known to be eaten by the gopher tortoise (Macdonald and Mushinsky, 1988), all plants along the foraging paths were considered to be available. Foraging data for each observation were of three kinds: (1) number of bites/genus, (2) number of plants partially or completely consumed/genus, (3) number of plants available/genus. Because the number of bites and number of plants consumed were correlated strongly ($r_s = 0.88$, $P < 0.01$, $n = 17$), we used number of plants consumed for all analyses.

To determine if juvenile gopher tortoises were selecting particular genera, we used the computer software program Resampling Stats. For each foraging observation, we created a distribution of the number of plants per genus available along a foraging path and then randomly drew the total number of plants consumed from the distribution 1000 times. The probability that a particular genus was selected positively or negatively was calculated from the resulting distribution of the expected number of plants. The generality of any selection, either positive or negative, for a particular genus was determined by a G-Test of independence at $P = 0.05$. Cluster analysis was used to examine relationships among the separate foraging observations (McInnis et al., 1990).

The diet of juvenile gopher tortoises was compared with the composite diet of mixed age (1–15+ yr old) individuals documented previously at the same location (Macdonald

and Mushinsky, 1988) using Spearman Rank Correlation. First, we compared the proportions of the plant genera in the two diet studies using only plants consumed by individuals in both studies. Second, we compared the proportions of the plant genera in the two diets using plants that were consumed by individuals in either of the studies and also were known to be available to the juveniles in our study.

The total nitrogen content of many of the plant genera eaten and/or available to juvenile gopher tortoises was measured. One to seven specimens of 24 plant genera were collected in October 1999 for analysis. Seventeen of the 24 genera analyzed for nitrogen content were eaten by juvenile gopher tortoises; the remaining seven were available along the foraging paths and known to be ingested by older conspecifics (Macdonald and Mushinsky, 1988). Although the absolute content of nitrogen and crude protein is greatest in spring (Garner and Landers, 1981) and plant parts (e.g., flowers) differ in nutritional value (Jennings, 2002), we assumed that the relative rankings of total nitrogen should remain constant. Whole specimens were dried to constant weight in a 60 C oven and ground in a Wiley Mill to uniform size particles. Total nitrogen was measured with a NC2100 Soil Analyzer (CE Instruments, Chicago, IL). The soil analyzer was calibrated and tested for leaks each time it was started. The ash trap was changed every 100 runs, and the water trap was changed every 100–150 runs to ensure accurate readings. Atropine was used as the known standard. The Eager 200 program was used to record the output in Excel format. Spearman Rank Correlation was used to determine the relationship between total nitrogen content and the degree of selection of the ingested genera.

RESULTS

Direct observation of foraging juvenile gopher tortoises proved to be challenging. Most individuals did not forage far from their burrows, and disturbed individuals tended to return immediately to their burrows. These individuals had to be excluded from our analyses. Seventeen foraging observations of 11 juvenile gopher tortoises were included in our analyses. We found no difference in the rank orders of ingested plants using either 11

TABLE 1.—List of plant taxa (with several grasses grouped as Poaceae, and unidentified seedlings) listed in descending order of number of individuals encountered by foraging gopher tortoises. Plants eaten by juveniles are indicated by an *.

Taxon
<i>Aristida beyrichiana</i> (Poaceae)
Poaceae*
<i>Liatris gracilis</i> (Asteraceae)*
<i>L. tenuifolia</i>
<i>Dyschoriste oblongifolia</i> (Acanthaceae)*
<i>Balduina angustifolia</i> (Asteraceae)*
<i>Quercus</i> spp. (Fagaceae)
<i>Elephantopus elatus</i> (Asteraceae)*
Seedling*
<i>Hedyotis procumbens</i> (Rubiaceae)*
<i>Berlandiera</i> spp. (Asteraceae)*
<i>Ruellia carolinensis</i> (Acanthaceae)*
<i>Crotalaria fasciculata</i> (Fabaceae)*
<i>Helianthemum corymbosum</i> (Cistaceae)*
<i>Carphophorus</i> spp. (Asteraceae)
<i>Eupatorium capillifolium</i> (Asteraceae)*
<i>Eriogonum</i> spp. (Polygonaceae)
<i>Richardia brasiliensis</i> (Rubiaceae)*
<i>R. scabra</i>
<i>Plantago</i> spp. (Plantaginaceae)
<i>Pheobanthus grandiflora</i> (Asteraceae)*
<i>Scutellaria arenicola</i> (Lamiaceae)*
<i>Tephrosia</i> spp. (Fabaceae)
<i>Cnidiosculus stimulosus</i> (Euphorbiaceae)*
<i>Pinus</i> spp. (Pinaceae)*
<i>Tillandsia</i> spp. (Bromeliaceae)
<i>Rhyncosia</i> spp. (Fabaceae)
<i>Cyperus</i> spp. (Cyperaceae)
<i>Aster tortifolius</i> (Asteraceae)*
<i>Stillingia</i> spp. (Euphorbiaceae)
<i>Evolvulus sericeus</i> (Convolvulaceae)*
<i>Shrankia microphylla</i> (Fabaceae)*
<i>Polygala grandiflora</i> (Polygalaceae)*
<i>Gnaphalium</i> spp. (Asteraceae)
<i>Pityopsis</i> spp. (Asteraceae)
<i>Polypremum</i> sp. (Tetrachondraceae)
<i>Dahlia pinnata</i> (Fabaceae)*
<i>Croton linearis</i> (Euphorbiaceae)*
<i>Solidago fistulosa</i> (Asteraceae)*
<i>S. stricta</i> (Asteraceae)
<i>Asimina</i> spp. (Annonaceae)
<i>Chamaeriste fasciculata</i> (Fabaceae)*
<i>Diospyros virginiana</i> (Ebenaceae)
<i>Baptisia</i> spp. (Fabaceae)
<i>Yucca aloifolia</i> (Agavaceae)*
<i>Stylosanthes biflora</i> (Fabaceae)
<i>Clitoria</i> spp. (Fabaceae)
<i>Serenoa repens</i> (Arecaceae)
<i>Physalis</i> spp. (Solanaceae)

or 17 observations; therefore, we used all 17 observations for all analyses.

Juvenile gopher tortoises ate 26 plant genera (Table 1) from a total of 46 genera identified along the foraging pathways. During an aver-

age foraging bout, a juvenile gopher tortoise encountered 13.7 (\pm SE 1.3, range 6–22) plant genera and ingested 5.9 (\pm SE 0.6, 3–11) of them. In terms of cumulative availability, *Aristida* was the most frequently encountered genus along the foraging paths, followed by Poaceae, *Liatris*, and *Dyschoriste* (Table 1). The rate of accumulation of new genera reached an asymptote, indicating that continued observations of foraging juvenile gopher tortoises (at the same location) would have added few new genera (Fig. 1).

The use of Resampling Stats enabled us to compute a probability to establish positive and negative selection of plant genera. Sixteen genera were selected positively by at least one juvenile gopher tortoise (Table 2). Three of these genera (*Dyschoriste*, *Liatris*, and seedling) were generally selected positively. Other genera (e.g., *Hedyotis*, *Ruellia*, *Richardia*, *Helianthemum*, *Crotalaria*, and *Elephantopus*) might also be generally selected positively, but we lacked the power to decide. Three genera (*Aristida*, Poaceae, and *Quercus*) were selected negatively by at least one juvenile gopher tortoise. Only one genus, the widely distributed and frequently encountered *Aristida*, was generally selected negatively. Poaceae mostly was eaten in proportion to its availability, but sometimes it was selected negatively and, on one occasion, it was selected positively. Juvenile gopher tortoises selected only Poaceae both positively and negatively.

Comparison of the diet of juvenile gopher tortoises to that of mixed age individuals from a previous study at the same location (Macdonald and Mushinsky, 1988) revealed both similarities and differences. The rank orders of genera eaten by individuals in both studies were correlated positively ($r_s = 0.64$, $P < 0.01$, $n = 15$). The rank order of genera eaten by mixed age individuals (Macdonald and Mushinsky, 1988) and either eaten or known to be available to juveniles in the current study were not correlated, however ($r_s = 0.11$, $P > 0.50$, $n = 29$). Several genera available to juvenile gopher tortoises, but not eaten, were eaten by mixed age individuals. For example, *Aristida* and *Pityopsis* composed 11.8% and 15.0%, respectively, of the diet of mixed age individuals, but neither genus was included in the diet of the juveniles we observed. Note, however, that *Pityopsis* was not very abundant along the

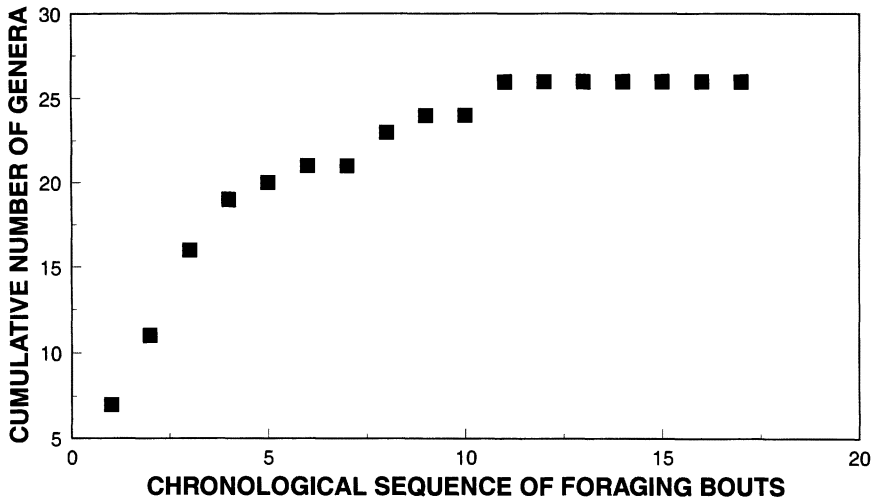


FIG. 1.—Cumulative number of plants consumed during 17 foraging bouts of juvenile gopher tortoises.

foraging paths of the juveniles we observed (Table 1). In contrast, two positively selected genera, *Liatris* and *Dyschoriste*, comprised 27% and 19%, respectively, of the diet of juvenile gopher tortoises, compared to 5% and 7%, respectively, in mixed age individuals. Macdonald and Mushinsky (1988) found *Liatris* and *Dyschoriste* each represented only about 4% of the available plants, however.

In central Florida, where the gopher tortoise can be active throughout much of the year, the juvenile gopher tortoise diet was influenced by seasonal availability of plant genera. For example, while Poaceae often was selected negatively during the months when forbs were readily available, it was consumed in proportion to its availability, or even occasionally selected positively, by juveniles when forbs were not readily available (Table 2). Cluster analysis of foraging observations corroborated the seasonal pattern. Five foraging observations that were made during the months of October–December form a distinct cluster characterized by the inclusion of Poaceae and the near absence of otherwise commonly ingested genera, such as *Liatris*, from the diet (Fig. 2).

Nitrogen content is one of many indicators of food quality. Total nitrogen content of the 17 ingested plant genera (from a total of 24 genera tested) was not correlated with the respective probability of selection ($r_s = -0.24$, $P = 0.34$, $n = 17$). If only the plant genera selected, either positively or negatively, by two

or more individuals were considered, then the correlation was improved ($r_s = -0.47$, $P = 0.19$, $n = 9$). Finally, if only the genera generally selected were considered, then the correlation was improved further ($r_s = -1.00$, $P = 0.08$, $n = 4$).

Our observations of juvenile gopher tortoises indicate that they tend to minimize the time spent out of their burrows. The individuals that we observed moved more or less continuously while foraging. A foraging bout averaged $19.4 (\pm \text{SE } 10.3)$ min, and individuals traveled an average of $26.8 (\pm \text{SE } 41.5)$ m round trip during that time. Time and distance were positively related ($r_s = 0.66$, $P < 0.05$, $n = 17$). As the number of available plants (individuals) increased, which was a seasonal occurrence, juvenile gopher tortoises spent more time foraging, ($r_s = 0.58$, $P < 0.02$, $n = 17$), traveled farther ($r_s = 0.57$, $P < 0.02$, $n = 17$), and ate more plants ($r_s = 0.76$, $P < 0.01$, $n = 17$). Neither the relative time spent foraging nor the number of plants consumed was linearly related to the number of plants available; however, both relationships were strongly asymptotic (Fig. 3).

DISCUSSION

Juvenile gopher tortoises in central Florida consumed a relatively wide array of plant genera and showed distinct selection for some of them. Of the 26 genera that we observed eaten by the juveniles, resampling procedures

TABLE 2.—Number (n) of foraging observations during which a genus was selected positively or negatively or was sampled in proportion to its availability (not selected) by juvenile gopher tortoises and the probability that the observed distribution does not differ from random (based on Resampling Stats).

Taxon	n	Positive	Not selected	Negative	Probability
<i>Aristida</i>	17	0	2	15	0.0001
<i>Liatrix</i>	13	10	3	0	0.0003
<i>Dyschoriste</i>	14	7	7	0	0.006
Seedling	8	6	2	0	0.007
Poaceae	17	1	10	6	0.103
<i>Ruellia</i>	8	3	5	0	0.2
<i>Hedyotis</i>	12	3	9	0	0.217
<i>Richardia</i>	3	2	1	0	0.4
<i>Helianthemum</i>	4	2	2	0	0.429
<i>Crotalaria</i>	8	2	6	0	0.467
<i>Elephantopus</i>	9	2	7	0	0.471
<i>Quercus</i>	13	0	11	2	0.48
<i>Balduina</i>	4	1	3	0	1.0
<i>Evolvulus</i>	2	1	1	0	1.0
<i>Pinus</i>	3	1	2	0	1.0
<i>Polygala</i>	4	1	3	0	1.0
<i>Yucca</i>	1	1	0	0	1.0
<i>Cnidoscopus</i>	1	1	0	0	1.0
<i>Chamaecriste</i>	1	0	1	0	1.0
<i>Phoebanthus</i>	2	0	2	0	1.0
<i>Shrankia</i>	3	0	3	0	1.0
<i>Aster</i>	2	0	2	0	1.0
<i>Scutellaria</i>	1	0	1	0	1.0
<i>Berlandiera</i>	3	0	3	0	1.0
<i>Dahlia</i>	1	0	1	0	1.0
<i>Croton</i>	1	0	1	0	1.0
<i>Solidago</i>	1	0	1	0	1.0
<i>Eupatorium</i>	1	0	1	0	1.0

indicated that 16 were selected positively by at least one individual and five were selected positively by three or more individuals. A very common genus of grass, *Aristida*, was not eaten at any time of the year and, in most cases, was selected negatively. Other grasses (Poaceae) were included in the diet of juvenile gopher tortoises only during fall and winter months, when forbs were in decline. The rank order of plant genera eaten by juvenile gopher tortoises was not different from the rank order of plant genera eaten by mixed age tortoises at the same location (Macdonald and Mushinsky, 1988). Overall, total nitrogen content of available plants alone could not account for the rank order of preference of ingested plants. Individuals did not move far from their burrows to forage, and foraging bouts lasted only for brief periods of time, regardless of the availability of plants. We were unable to link positive selection with any distinct benefit

derived by the gopher tortoise, just as we are unable to know exactly why some genera were negatively selected.

When our findings are added to those of other studies, a fundamental picture of the differences in diet between juvenile and adult gopher tortoises begins to emerge. Grasses (Poaceae), which contain relatively little protein or other nutrients and have a high crude fiber content (Garner and Landers, 1981), are eaten less by juveniles than adults (Macdonald and Mushinsky, 1988; present study). During fall and winter months, however, grasses can constitute a substantial part of the diet of the juvenile gopher tortoise (Garner and Landers, 1981; present study). Although forbs, such as *Liatrix* and *Dyschoriste*, are important components of the diet of adult gopher tortoises, they are especially important to juveniles (Garner and Landers, 1981; Macdonald and Mushinsky, 1988; present study). Positively selected genera may contain relatively high amounts of nitrogen (e.g., *Liatrix*) (Garner and Landers, 1981; present study), and/or they may contain relatively high amounts of some other equally (or more) important nutrients, such as calcium and magnesium (e.g., *Dyschoriste*) (Garner and Landers, 1981).

Although the juvenile gopher tortoises we studied consumed fewer plant genera than the mixed age group at the same location (Macdonald and Mushinsky, 1988), we suspect that at least part of the difference likely reflects the larger sample size taken by Macdonald and Mushinsky (1988); 38 foraging observations made over nearly 30 ha, compared to 17 foraging observations made over only 1 ha in the present study. Many more genera of plants were available to the gopher tortoises on 30 ha than on the 1 ha we studied. Furthermore, we observed only juvenile gopher tortoises, which have small home ranges and a mass that is two orders of magnitude less than adults. Once beyond the juvenile stage of its life, a gopher tortoise uses a relatively large home range (Diemer, 1992) and, therefore, can sample a broader array of available plants.

Number of plants (individuals) eaten by juvenile gopher tortoises was not a linear function of availability. At least three, not mutually exclusive, explanations may account for this observation. The first explanation is that juvenile gopher tortoises became satiated during

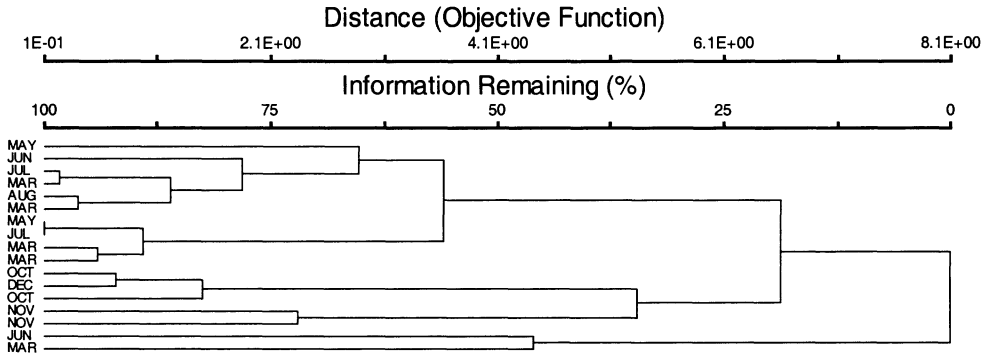


FIG. 2.— Cluster analysis of foraging bouts by month. Distance measure = Relative Euclidean, Linkage method = Flexible Beta (−0.25).

the 20–30 min foraging bout and returned to the burrow to digest the meal. We know of no studies to support or refute this idea. In contrast, our general observations of (mostly adult) gopher tortoises indicate that, when an individual is out of its burrow and not involved in some other activity (e.g., courtship), it is likely to be foraging. The second possible explanation is that juvenile gopher tortoises were able to forage for only a short time and travel only a short distance because of thermal constraints. Ambient temperatures influence daily and seasonal activity patterns of the gopher tortoise (Diemer, 1992; Douglass and Layne, 1978; Wilson et al., 1994). In sunlight

on a sandy substrate, an adult gopher tortoise increases body temperature at 0.14 C/min (Douglas and Layne, 1978). The small size of a juvenile would accelerate the rate of increase. If temperature was the factor limiting the activity of juvenile tortoises, then it would be most limiting during warm summer months, when many of the positively selected plants are most abundant, and would contribute to the non-linear relation between number of plants available and number eaten that we observed. The third possible explanation is that juvenile gopher tortoises were able to forage for only a short time and travel a short distance because of predation. A variety of

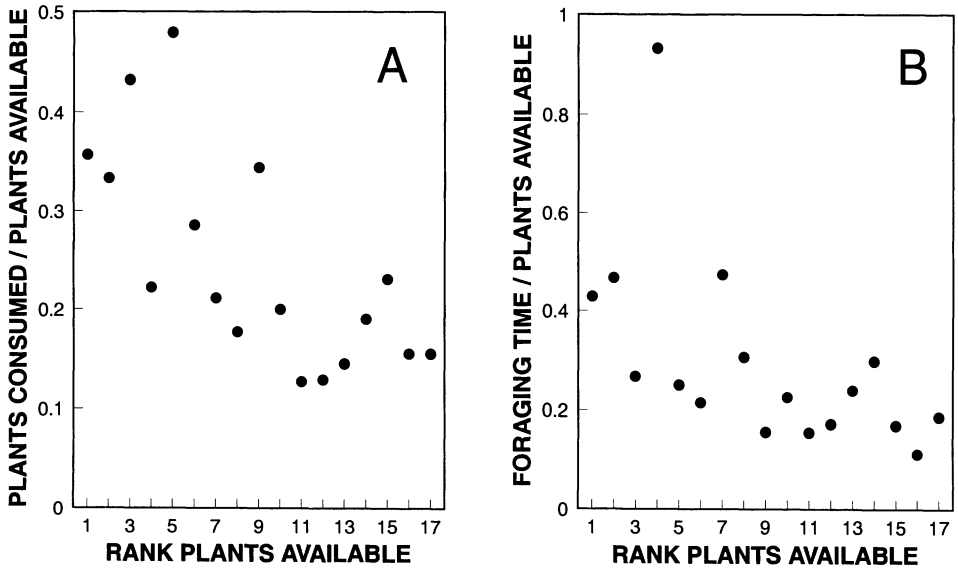


FIG. 3.—Relationship between the plants consumed (A) and time (minutes) spent foraging (B) to the number of plants available. (A) $r_s = -0.74$, $P < 0.01$, $n = 17$, (B) $r_s = -0.67$, $P < 0.01$, $n = 17$.

predators are known to prey on juvenile gopher tortoises (Fitzpatrick and Woolfenden, 1978; Mushinsky and McCoy, 1994; Wilson et al., 1994). Annual gopher tortoise mortality from egg to 1 yr of age was 94.2% in north Florida (Alford, 1980) and 92.3% in central Florida (Witz et al., 1992). During 1 yr of a previous study at the ERA, 11 of 32 radiotagged juvenile tortoises were killed by raptors or mammalian predators (Wilson, 1991). Consistent predation pressure on juvenile gopher tortoises may be a force that selects for wariness, which, in turn, is expressed as time and distance constraints.

Selecting high quality diets may be important in accelerating the growth rate of chelonians (Okamoto, 2002). The desert tortoise (*Gopherus agassizii*), like the congeneric gopher tortoise, exhibits selective foraging (which, in turn, is influenced by the seasonal availability of plants), preferring native species, especially relatively uncommon species that grow only in hill areas or in washes (Jennings, 1997; Jennings and Fontenot, 1992). Individuals residing in habitats with a high diversity of high quality plants increase in mass and body size at a faster rate than those residing in habitats with a lower diversity and quality of plants (Barboza, 1995). Gopher tortoises at the ERA, where frequent controlled burning has promoted a high diversity and abundance of herbaceous plants (Mushinsky and Gibson, 1991), grow to sexual maturity at 9–10 yr (Mushinsky et al., 1994), whereas individuals at a nearby location that has a sparse herbaceous ground cover because of fire exclusion grow to sexually maturity in 14–16 yr (Godley, 1989). Juvenile slider turtles (*Trachemys scripta*) and green turtles (*Chelonia mydas*) maintained on high protein, low fiber diets grew more rapidly than individuals maintained on reduced protein and/or increased fiber content (Avery et al., 1993). Accelerated individual growth rates may promote earlier sexual maturity and increased population growth rates (Auffenberg and Iverson, 1979; Germano, 1994; Mushinsky et al., 1994).

Although studying juvenile gopher tortoises presents a unique set of challenges, the effort required to understand their biology can provide the information needed to establish land management practices that promote healthy populations (Morafka et al., 2000). Florida is

the mainstay of the gopher tortoise, yet, because of the increase of the human population, the distribution of the species soon will be limited to publicly owned lands. Management of the public lands, such as by controlled burning, will be essential to maintain or increase the sizes of gopher tortoise populations. Adults can and do persist in relatively poor quality locations because they can travel long distances to find food (McCoy and Mushinsky, 1992; Mushinsky et al., 1997). In contrast, as we have demonstrated, juveniles tend to travel short distances and forage for short periods of time; therefore, they would seem to be able to persist only in relatively good quality locations. Successful management will require a comprehensive understanding of the different habitat requirements of adult and juvenile gopher tortoises.

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LITERATURE CITED

- ALFORD, R. 1980. Population structure of *Gopherus polyphemus* in northern Florida. *Journal of Herpetology* 14:177–182.
- AUFFENBERG, W., AND R. FRANZ. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). Pp. 95–126. In R. B. Bury (Ed.), *North American Tortoises: Conservation and Ecology*. United States Fish and Wildlife Service, Wildlife Research Report 12, Washington, D.C., U.S.A.
- AUFFENBERG, W., AND J. B. IVERSON. 1979. Demography of terrestrial turtles. Pp. 541–569. In M. Harless and H. Morlock (Eds.), *Turtles: Perspectives and Research*. John Wiley & Sons, New York, New York, U.S.A.
- AVERY, H. W., J. R. SPOTILA, J. D. CONGDON, R. U. FISCHER, JR., H. A. STANDORA, AND S. B. AVERY. 1993. Roles of diet protein and temperature in the growth and nutritional energetics of juvenile slider turtles, *Trachemys scripta*. *Physiological Zoology* 66:902–925.
- BARBOZA, P. S. 1995. Nutrient balances and maintenance requirements for nitrogen and energy in desert tortoises (*Xerobates agassizii*) consuming forages. *Comparative Biochemistry and Physiology* 112A:537–545.
- CARR, A. F. 1952. *Handbook of Turtles*. Cornell University Press, Ithaca, New York, U.S.A.
- DIEMER, J. E. 1986. The ecology and management of the gopher tortoise in the southeastern United States. *Herpetologica* 42:125–133.
- . 1992. Home range and movements of the tortoise *Gopherus polyphemus* in Northern Florida. *Journal of Herpetology* 26:158–165.

- DOUGLASS, J. F. 1978. Refugia of juvenile gopher tortoises, *Gopherus polyphemus* (Reptilia, Testudines, Testudinae). *Journal of Herpetology* 12:413–415.
- DOUGLASS, J. F., AND J. N. LAYNE. 1978. Activity and thermoregulation of the gopher tortoise (*Gopherus polyphemus*) in southern Florida. *Herpetologica* 34: 359–373.
- FITZPATRICK, J. W., AND G. E. WOOLFENDEN. 1978. Red-tailed hawk preys on juvenile gopher tortoise. *Florida Field Naturalist* 6:49.
- GARNER, J., AND J. LANDERS. 1981. Foods and habitat of the gopher tortoise in southwestern Georgia. *Proceeding of the Annual Conference of Southeastern Association Fish Wildlife Agencies* 35:120–134.
- GERMANO, D. J. 1994. Comparative life histories of North American tortoises. Pp. 175–185. *In* R. B. Bury and D. J. Germano (Eds.), *Biology of North American Tortoises*. United States Department of the Interior, National Biological Survey, Fish and Wildlife Research Report 13, Washington, D.C., U.S.A.
- GODLEY, J. S. 1989. A comparison of gopher tortoise populations relocated onto reclaimed phosphate-mined sites in Florida. Pp. 43–58. *In* J. E. Diemer, D. R. Jackson, J. L. Landers, J. N. Layne, and D. A. Wood (Eds.), *Gopher Tortoise Relocation Symposium*. Florida Game and Fresh Water Fish Commission, Non-game Wildlife Program Technical Report 5, Tallahassee, Florida, U.S.A.
- JENNINGS, W. B. 1997. Habitat use and food preferences of the desert tortoise, *Gopherus agassizii*, in the Western Mojave and impacts of off-road vehicles. Pp. 42–45. *In* *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—an International Conference*. Joint Publication of the New York Turtle and Tortoise Society and WCS Turtle Recovery Program Purchase, New York, New York, U.S.A.
- . 2002. Diet selection by the desert tortoise in relation to the flowering phenology of ephemeral plants. *Chelonian Conservation and Biology* 4:353–358.
- JENNINGS, W. B., AND C. L. FONTENOT, JR. 1992. Observations on the feeding behavior of desert tortoises (*Gopherus agassizii*) at the Desert Tortoise Research Natural Area, Kern Co. CA. Pp. 69–81. *In* *Proceedings: the Desert Tortoise Council 1992 Symposium*. Las Vegas, Nevada, U.S.A.
- KUSHLAN, J. A., AND F. J. MAZZOTTI. 1984. Environmental effects on a coastal population of gopher tortoises. *Journal of Herpetology* 18:231–239.
- LANDERS, J. L., AND D. W. SPEAKE. 1980. Management needs of sandhill reptiles in southern Georgia. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 34:515–529.
- MACDONALD, L. A., AND H. R. MUSHINSKY. 1988. Foraging ecology of the gopher tortoise, *Gopherus polyphemus*, in a sandhill habitat. *Herpetologica* 44:345–353.
- MCCOY, E. D., AND H. R. MUSHINSKY. 1992. Studying a species in decline: changes in populations of the gopher tortoise on federal lands in Florida. *Florida Scientist* 55:116–125.
- MCINNIS, M. L., L. I. LARSON, AND M. VAVRA. 1990. Classifying herbivore diets using hierarchical cluster analysis. *Journal of Range Management* 43:271–274.
- MORAFKA, D. J. 1994. Neonates: missing links in the life histories of North American tortoises. Pp. 161–174. *In* R. B. Bury and D. J. Germano (Eds.), *Biology of North American Tortoises*. United States Department of the Interior, National Biological Survey, Fish and Wildlife Research Report 13, Washington, D. C., U.S.A.
- MORAFKA, D. J., E. K. SPANGENBERG, AND V. A. LANCE. 2000. Neonatology of reptiles. *Herpetological Monographs* 14:353–370.
- MYERS, R. L., AND J. J. EWEL. 1990. *Ecosystems of Florida*. University of Central Florida Press, Orlando, Florida, U.S.A.
- MUSHINSKY, H. R. 1985. Fire and the Florida sandhill herpetofaunal community: with special attention to responses of *Cnemidophorus sexlineatus*. *Herpetologica* 41:333–341.
- MUSHINSKY, H. R., AND D. J. GIBSON. 1991. The influence of fire periodicity on habitat structure. Pp. 237–259. *In* S. E. Bell, E. D. McCoy, and H. R. Mushinsky (Eds.), *Habitat Structure: the Physical Arrangement of Objects in Space*. Chapman and Hall Ltd, New York, New York, U.S.A.
- MUSHINSKY, H. R., AND E. D. MCCOY. 1994. Comparison of gopher tortoise populations on islands and on the mainland in Florida. Pp. 39–47. *In* R. B. Bury and D. J. Germano (Eds.), *Biology of North American Tortoises*. United States Department of the Interior, National Biological Survey, Fish and Wildlife Research Report 13, Washington, D.C., U.S.A.
- MUSHINSKY, H. R., D. S. WILSON, AND E. D. MCCOY. 1994. Growth and sexual dimorphism of *Gopherus polyphemus* in central Florida. *Herpetologica* 50:119–128.
- MUSHINSKY, H. R., E. D. MCCOY, AND D. S. WILSON. 1997. Patterns of gopher tortoise demography in Florida. Pp. 252–258. *In* *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference*. Joint Publication of the New York Turtle and Tortoise Society and WCS Turtle Recovery Program, Purchase, New York, U.S.A.
- OKAMOTO, C. L. 2002. An experimental assessment of color, calcium, and insect dietary preferences of captive juvenile desert tortoises (*Gopherus agassizii*). *Chelonian Conservation and Biology* 4:359–365.
- TAYLOR, W. K. 1992. *The Guide to Florida Wildflowers*. Taylor Publishing Co., Dallas, Texas, U.S.A.
- WILSON, D. S. 1991. Estimates of survival for juvenile gopher tortoises, *Gopherus polyphemus*. *Journal of Herpetology* 25:376–379.
- WILSON, D. S., H. R. MUSHINSKY, AND E. D. MCCOY. 1992. Relationship between gopher tortoise body size and burrow width. *Herpetological Review* 22:122–124.
- . 1994. Home range, activity and use of burrows of juvenile gopher tortoises in central Florida. Pp. 147–160. *In* R. B. Bury and D. J. Germano (Eds.), *Biology of North American Tortoises*. United States Department of the Interior, National Biological Survey, Fish and Wildlife Research Report 13, Washington, D.C., U.S.A.
- WITZ, B. W., D. S. WILSON, AND M. D. PALMER. 1992. Estimating population size and hatchling mortality of *Gopherus polyphemus*. *Florida Scientist* 55:14–19.
- WUNDERLIN, R. P. 1998. *Guide to the Vascular Plants of Florida*. University Press of Florida, Gainesville, Florida, U.S.A.

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