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Habitat Selection and Modification by the Gopher Tortoise, *Gopherus polyphemus*, in Georgia Longleaf Pine Forest

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Abstract. – Gopher tortoise burrows in longleaf pine forest in an ecological reserve in Georgia were associated with sparse overstory canopy cover (30%), low shrub density, and positive slope. Gopher tortoises modified the habitat surrounding their burrows by compacting soils and by selective foraging. Wiregrass was equally abundant at burrows and control points, but the abundance of (fleshy) fruit-bearing plants and non-*Aristida* grasses (Poaceae), two documented food items, was significantly lower near active tortoise burrows. Fabaceae (legumes), another preferred food, were 3 times more abundant near burrows. Seeds of many native legumes in the study area have extremely thick seed coats that may benefit from scarification for successful germination. The dispersion pattern of all burrows in the study area was clumped, whereas active burrows were randomly dispersed. The random distribution of active burrows is likely related to the distribution of optimal habitat patches, whereas the clumped pattern for all burrows probably reflects use of multiple burrows by single tortoises. Our data suggest that gopher tortoises play an important role in shaping the structure of longleaf pine forests. Because adult tortoises can occupy burrows for decades, soil compaction and alteration of vegetation composition around burrows are likely to have lasting impacts on the vegetation community.

Key Words. – Reptilia; Testudines; Testudinidae; *Gopherus polyphemus*; tortoise; ecology; foraging; habitat requirements; Georgia; USA

The gopher tortoise, *Gopherus polyphemus*, is a medium-sized chelonian (15–39 cm carapace length) that inhabits upland communities throughout the southeastern U.S. Coastal Plain from southern South Carolina to southeastern Louisiana (Auffenberg and Franz, 1982; Dodd, 1986). These animals dig and inhabit long (up to 14.3 m, average 4.5–4.6 m) and deep burrows (up to 3.7 m, average 2 m) that offer protection from extreme temperatures, desiccation, and predation (Hallinan, 1923; Hansen, 1963; Diemer, 1986). Burrows are utilized by numerous vertebrate and invertebrate species (Young and Goff, 1939; Woodruff, 1982; Milstrey, 1986; Jackson, 1987; Witz et al., 1991). Jackson and Milstrey (1989), for example, documented 60 vertebrate and 302 invertebrate species that use gopher tortoise burrows. In addition to supporting a diverse animal community, gopher tortoises may also play an important role in seed dispersal (Auffenberg, 1969; Macdonald and Mushinsky, 1988), and the bare mounds of soil (aprons) associated with burrows may enhance plant biodiversity in the forest understory by providing sites for early successional species (Kaczor and Hartnett, 1990). For these reasons, the gopher tortoise is a keystone species (*sensu* Paine, 1969) in the habitats where it occurs (Eisenberg, 1983).

Because of significant declines in gopher tortoise populations the species warrants protection throughout its entire geographic range (Auffenberg and Franz, 1982; Means, 1985; Ernst et al., 1994). Population declines have been related to habitat destruction and degradation, vehicular traffic, and human predation (Landers and Buckner, 1981; Garner and Landers, 1981; Auffenberg and Franz, 1982; Wright, 1982; Diemer, 1986). Loss and alteration (e.g., fire exclusion and suppression) of the longleaf pine (*Pinus palustris*) ecosystem have likely had a significant impact on survival and persistence of the gopher tortoise. For example, there is significant overlap between the distribution of the gopher tortoise and the pre-European settlement range of the longleaf pine ecosystem (Auffenberg and Franz, 1982). Longleaf pine forests formerly covered over 28 million ha and were the dominant habitat type of the Coastal Plain (Burke, 1989). By 1993, however, the amount of longleaf pine declined to less than 1.3 million ha (Outcalt and Sheffield, 1996), including 600 ha or less of small, isolated old-growth stands (Simberloff, 1993). Low reproductive rates, high longevity, and delayed maturation may make it particularly difficult for gopher tortoises to recover from declines in population and changes in habitat (Garner and Landers, 1981), but on the positive side, human-modified habitats like old fields or orange groves can support tortoise populations.

General habitat requirements for gopher tortoises are reported to include well-drained loose soils in which to burrow and a relatively open canopy that permits light to reach the ground, supporting a herbaceous ground cover layer and egg incubation (Hallinan, 1923; Landers, 1980; Landers and Speake, 1980; Auffenberg and Franz, 1982; Cox et al., 1987). However, despite decades-long declines in longleaf pine and gopher tortoise populations, relatively few studies of gopher tortoise ecology have been conducted in the longleaf pine ecosystem. Detailed knowledge of tortoise ecology, including habitat requirements and the processes that govern burrow dispersion and occupancy, are essential for the successful conservation and restoration of gopher tortoise populations in longleaf pine ecosystems. For example, a comprehensive understanding of how gopher tortoises select burrow sites is necessary for the development of successful tortoise relocation, restocking, and repatriation strategies (Lohoefener and Lohmeier, 1986).

A primary objective of this study was to assess tortoise burrow dispersion patterns and burrow placement in relation to habitat characteristics (overstory density, vegetation composition, slope, and soils) within a longleaf pine forest. Previous studies have indicated that tortoises forage almost exclusively within a short distance (30 m or less) of their burrow (McRae et al., 1981). Furthermore, most tortoise activity has been reported to occur in front and to the sides of a burrow; little or no activity occurs behind a burrow entrance (Auffenberg, 1969; McRae et al., 1981). For a long-lived species like the gopher tortoise, it might be expected that individuals have the potential to modify their surrounding habitat, especially because most of their foraging activities occur in a relatively small area. Thus, a second objective of this study was to examine vegetation composition and soil compaction in habitats adjacent to burrows in comparison to sites that would be expected to be minimally affected by tortoise activities.

MATERIALS AND METHODS

Study Area. — This study was conducted from May to August 1996 on Ichauway, an 11,765 ha ecological reserve located in Baker County in southwestern Georgia (31°14'N, 84°28'W). The reserve is contained within the Dougherty Plain District, an 18,000 km^2 region of low, gently rolling Karst topography underlain with limestone (Lynch et al., 1986). Elevation ranges from 27–61 m (90–200 ft). Climate is typified by long, hot summers and short, cool winters. Average summer and winter temperatures are 26 and 11°C, respectively, and mean annual precipitation is 131 cm (Lynch et al., 1986).

Longleaf pine (*Pinus palustris*) upland forests dominate 60% of the landscape (Lynch et al., 1986). A relatively sparse canopy of longleaf pine overstory and a ground cover of dense wiregrass (*Aristida stricta*) characterize these forests. Several scrub oak species (*Quercus laevis, Q. incana, Q. margaretta*) are found scattered throughout the forest. Other common ground cover species include *Sporobolus junceus, Andropogon virginicus, Pityopsis graminifolia, Tephrosia virginiana, Lechea sessiliflora, Dyschoriste oblongifolia, Vaccinium myrsinites, Croton argyranthemus, Asimina longifolia,* and *Rhus copallina.* Soils are typically well drained and are composed of fine-loamy, siliceous thermic Arenic and Typic Paleudults in the Norfolk, Wagram, Suffolk, Orangeburg, Lucy, and Bonneau series (Stoner, 1986). Prescribed burning in late winter or early spring on a 2–4 year schedule maintains the savanna-like conditions and diverse understory of the longleaf pine forests on Ichauway (J. Atkinson, *pers. comm.*).

Green Grove, a 49 ha mesic area located in the northeastern section of the reserve, was utilized for this study. Land cover was dominated by longleaf pine forest with a wiregrass understory (40 ha), but also included patches of hardwood and mixed pine/hardwood (4 ha) and abandoned agricultural fields and wildlife food plots (5 ha).

Burrow Dispersion. — Burrow locations were permanently marked, surveyed with a Trimble Global Positioning System (± 2 m), and incorporated into an Arc/Info Geographic Information System (GIS) database (Fig. 1). In early May, burrow activity status (active, inactive, or abandoned) was classified according to criteria defined by Auffenberg and Franz (1982). Recent signs of tortoise activity including footprints, plastral slide marks, freshly disturbed soil, and/or feces characterized active burrows. Inactive burrows were identified as burrows with no fresh signs of a tortoise but with an intact entrance requiring minimal modification prior to occupation by a tortoise. Abandoned burrows had entrances that were heavily eroded, blocked by debris, or collapsed.

Habitat Parameters. — A random sample of 50 active burrows in Green Grove was selected for habitat evaluation (Fig. 1). Of these, 48 active burrows were subsequently determined (by examination with a camera device) to be occupied by adult tortoises. Two burrows occupied by juveniles were not retained for analysis due to their ephemeral nature (Wilson et al., 1994; Butler et al., 1995) and known differences in foraging ranges and habitat use by adults and juveniles (McRae et al., 1981). Habitat immediately surrounding active adult burrows was assumed to be representative of conditions that initially made the location suitable for burrowing.

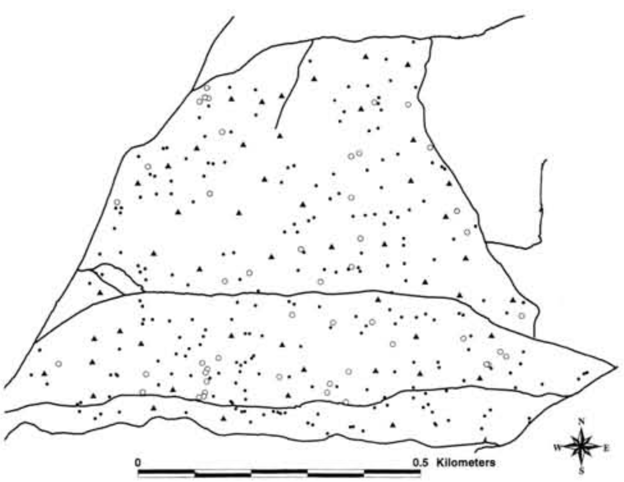

Figure 1. Distribution of gopher tortoise burrows (dots) and the 48 active burrows (circles) and 50 control points (triangles) used for habitat characterization in Green Grove, Ichauway ecological reserve, Baker Co., southwestern Georgia.

Fifty control points, assumed to represent areas minimally affected by tortoises, were randomly selected in Green Grove according to the following protocol. First, 5000 random points within the Green Grove study site were generated and incorporated into an Arc/Info GIS database. Second, points less than 20 m from a burrow or less than 10 m from roads, firebreaks, and food plots were eliminated to minimize overlap with tortoise foraging areas and anthropogenic disturbances. Finally, a subset of 50 of the remaining points (> 3000) was randomly selected as control points (Fig. 1).

For measurement purposes, the direction leading out of each burrow entrance was considered the front subplot; the back, left, and right subplots were determined accordingly. Subplots for control points were assigned by first randomly designating the front direction; back, left, and right were then determined as indicated above.

Canopy cover, basal area, soil compaction, slope, ground cover vegetation (including the herb and shrub layers) and woody vegetation were examined at burrows and control points to determine if burrow placement was related to microhabitat differences. These variables were believed to reflect specific habitat needs of gopher tortoises including open areas for basking and nesting, suitable soil and microtopography for digging, and adequate forage (Diemer, 1986) or, in some cases, to reflect microhabitat modification by the tortoises.

Canopy cover (% above each burrow and control point) was measured with a spherical crown densiometer (Lemmon, 1956). Basal area (m^2/ha) was measured for pine and hardwood trees using a JIM-GEM prism (Basal Area Factor 10) at each burrow and control point (Bonham, 1989). Soil compaction (kg/cm^2) was measured with a pocket soil penetrometer (Bradford, 1986) in each of the four subplots, 3 m away from each burrow and control point to avoid the burrow apron. A 3-m long aluminum frame with a floating-needle protractor fastened to the center was constructed to measure microtopographical slope (± 0.5°) at burrows and control points (Fig. 2). The central frame stake was placed at a point immediately behind the burrow entrance or control point and the measurement arm extended 3 m in front of the burrow. A second measurement was then taken 3 m behind each burrow and control point. The two measurements were then averaged to obtain the mean slope for a 6-m long transect (3 m in front to 3 m behind each burrow and control point).

A 1 m^2 grid divided into 100 intersections, each 10 cm apart, was used to assess ground cover vegetation. The grid was placed in each of the four subplots 3 m away from each burrow and control point. A point-intercept method was used to quantify frequencies of pre-assigned groups (Mueller-Dombois and Ellenberg, 1974). These groups included *Aristida stricta*, *Dyschoriste oblongifolia*, *Quercus* spp., non-*Aristida* Poaceae and grass-like plants, Fabaceae, fruit-bearing plants, miscellaneous herbaceous plants (not known to be eaten by gopher tortoises), and bare ground.

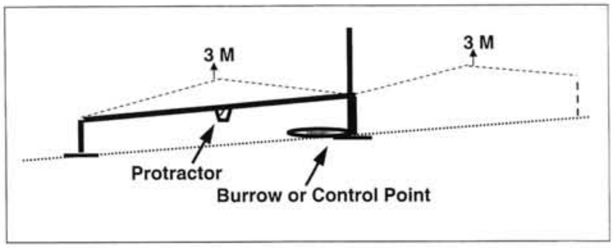

Figure 2. Device used to measure slope. Dark lines are a 3-m long aluminum frame with a floating needle protractor attached to the center. Dashed lines indicate placement of frame 3 m in front and 3 m in back of each burrow and control point to create a 6-m long transect.

Woody vegetation was measured by a point-centered quarter method (Bonham, 1989) that documented woody species within two radii (≤ 2 m and ≤ 10 m) in each subplot at burrows and control points. For the ≤ 2 m and ≤ 10 m radii, the distance to each woody plant in each subplot was measured. Every woody plant was identified within the smaller radius. Within the large radius, each woody plant at least 2 m tall and with a diameter at breast height (DBH) of at least 1 cm was identified.

Statistical Analyses. — A Clark and Evans nearest neighbor analysis with boundary strip modification was used to examine spatial patterning of all burrows and active burrows (Krebs, 1989). Habitat data were analyzed using the SAS statistical package (SAS Institute, Inc., 1989). Soil and woody vegetation data were log-transformed and groundcover vegetation data (proportions) were arcsine-transformed to induce normality and homoscedasticity (Sokal and Rohlf, 1995). One soil subplot at two burrows fell within either a road or a firebreak. To avoid bias due to this anthropogenic disturbance, these two burrows were not included in subsequent analyses.

Analysis of variance (ANOVA) was used to compare canopy cover and basal area at burrows and control sites. Least squares linear regression analysis was used to assess the relationship between canopy cover and basal area. ANOVA was also used to compare soil compaction at burrows and control sites, as well as within subplots. Multivariate analysis of variance (MANOVA) was used to assess slope and ground cover at burrows, control sites, and subplots. Woody vegetation was compared at burrows and control sites, and analyzed separately for each radius (≤ 2 m vs. ≤ 10 m) using MANOVA. Overall model significance was judged at $\alpha \leq 0.05$.

Four *a priori* tests were performed to examine differences in soil compaction, ground cover vegetation, and woody vegetation among burrows and control sites. First, differences among subplots at control points were examined. The absence of systematic statistically significant differences among the four control point subplots served as the basis for subsequent tests. Second, backs of burrows were compared with control points to determine whether specific habitat features were selected by tortoises during burrow establishment. Finally, the fronts and sides of burrows were each compared with the control points to examine potential microhabitat

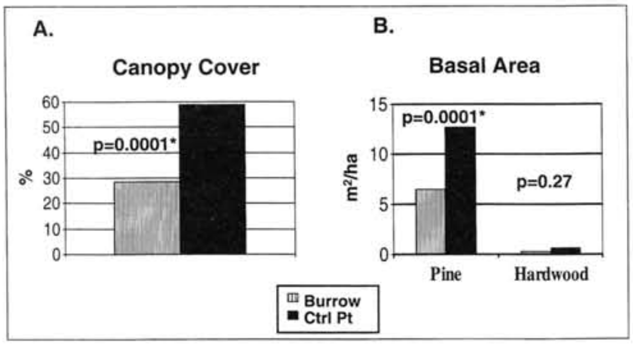

Figure 3. **(A)** Canopy cover (%) and **(B)** basal area (m^2/ha) of pine and hardwood species at 48 burrows and 50 control points within 49 ha area of Green Grove. * indicates significance.

modification by tortoises. Type I error rate in the four tests was controlled by the Bonferroni correction method (Scheiner, 1993); significance was established at $\alpha \leq 0.0125$ for the Tukey's studentized range test.

RESULTS

Burrow Dispersion. — We surveyed 274 burrows in Green Grove (127 active, 54 inactive, 93 abandoned). The dispersion pattern for all burrows was clumped (Z = 2.602). However, the 127 active burrows were randomly dispersed (Z = 1.225).

Habitat Parameters. — Canopy cover and pine basal area were twice as large at control points (60%, 12 m^2/ha) compared to burrows (30%, 6 m^2/ha) (F = 37.9, p = 0.0001; F = 75.1, p = 0.0001, respectively; Fig. 3); hardwood basal area was low (< 1 m^2/ha) and did not differ between burrows and control points (F = 1.2, p = 0.27; Fig. 3). Canopy cover and total basal area were positively correlated (r^2 = 0.39).

There were no differences in mean soil compaction between the backs of burrows and control points (Fig. 4). However, soil was more compact (1.3 times) at burrow fronts (p = 0.002) and sides (p = 0.001) than at control points (Fig. 4). No differences in slope were observed between burrows and control points for 3 m in front, but slopes behind burrows were slightly (30%) steeper than at control points (p = 0.08) (Table 1a).

No significant differences were observed in the frequency of wiregrass, *Dyschoriste oblongifolia, Quercus* spp., miscellaneous herbaceous plants, or bare ground at burrows or control points (Table 1b). However, three ground cover vegetation groups (Fabaceae, non-*Aristida* Poaceae and grass-like plants, and fruit-bearing plants) differed in abundance between burrows and control points. For example, Fabaceae were 4.5 times more frequent, non-*Aristida* Poaceae and grass-like plants were 30% less abundant, and fruit-bearing plants were 10 times less abundant in front of burrows than at control points (Tables 2 and 3). Ground cover vegetation of the three groups did not differ among the four subplots at control points.

Data for woody vegetation were grouped according to genus and species prior to analysis. For a radius of ≤ 2 m,

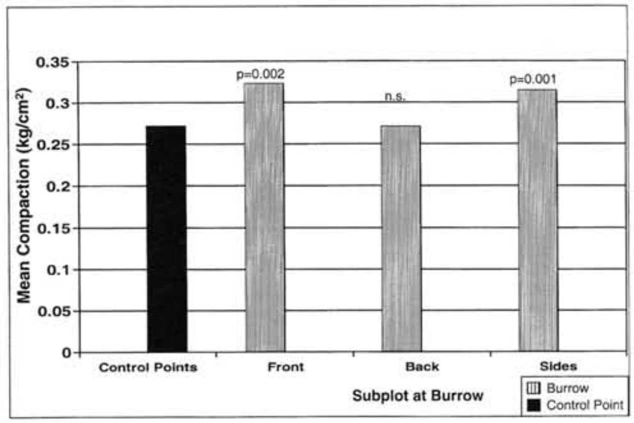

Figure 4. Comparisons of soil compaction between control points and burrow subplots.

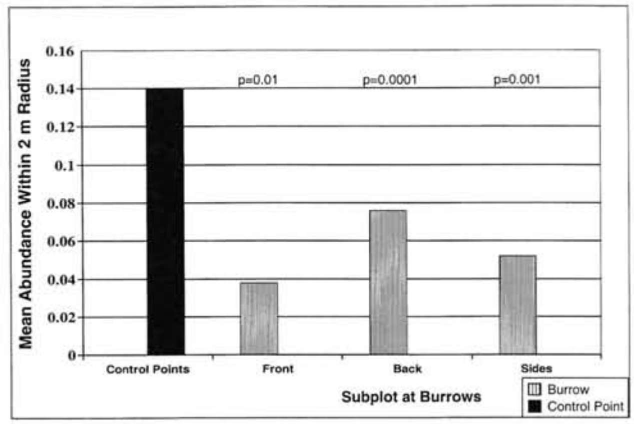

Figure 5. Comparisons of *Asimina longifolia* abundance between control points and burrow subplots.

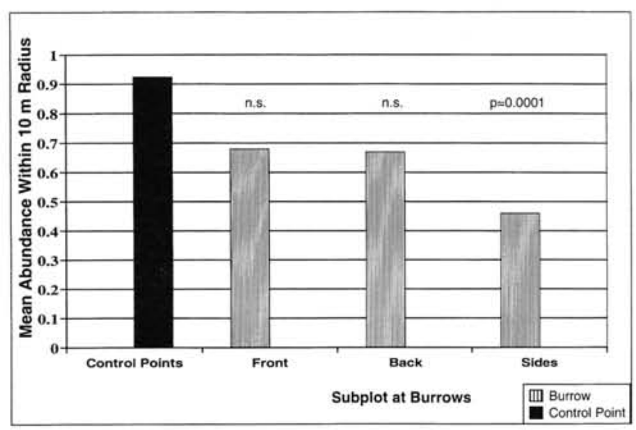

Figure 6. Comparisons of *Pinus palustris* abundance between control points and burrow subplots.

Asimina longifolia was almost 3 times more abundant at control points than at burrows (Table 1c) and was consistently (2–3 times) more abundant at control points than at any subplot at burrows (Fig. 5). No differences were observed at burrows and control points in the abundance of *Dyosporus virginiana, Pinus palustris, Quercus* spp., and *Rhus copallina.*

For a radius of 0 ≤ 10 m, one species, *Pinus palustris,* differed between burrows and control points; it was 25% more abundant at control points than at burrows (Table 1d)

Table 1. Habitat characteristics of burrows and control points in Green Grove. Means, one standard deviation, and ANOVA results (F, p) are included.

Habitat Variable	Burrow	Control Point	F	p
A. Slope (degrees)				
0-3 m (front of burrow)	0.95 ± 1.73	0.99 ± 1.51	n.s.	n.s.
3-6 m (back of burrow)	1.29 ± 1.29	0.76 ± 1.65	3.09	0.08
Average	1.07 ± 1.14	0.87 ± 1.37	n.s.	n.s.
B. Groundcover Type (frequency; number/m²)				
Aristida stricta	3.60 ± 3.78	3.21 ± 3.79	n.s.	n.s.
Dyschoriste oblongifolia	0.22 ± 0.58	0.38 ± 0.73	n.s.	n.s.
Quercus sp.	0.03 ± 0.20	0.07 ± 0.33	n.s.	n.s.
Non-*Aristida* Poaceae	4.68 ± 3.93	6.33 ± 5.74	10.90	0.001
Fabaceae	0.12 ± 0.36	0.04 ± 0.20	7.64	0.006
Fruit-bearing plants	0.10 ± 0.38	0.31 ± 0.67	13.85	0.0002
Misc. herbaceous plants	0.22 ± 0.52	0.27 ± 0.61	n.s.	n.s.
Bare ground	89.47 ± 12.29	86.41 ± 16.34	n.s.	n.s.
C. Woody Vegetation (abundance; number within 2 m radius)				
Asimina longifolia	1.12 ± 1.35	1.38 ± 1.62	24.19	0.0001
Dyosporus virginiana	1.12 ± 1.41	1.26 ± 1.66	n.s.	n.s.
Pinus palustris	1.29 ± 1.82	1.45 ± 2.19	n.s.	n.s.
Quercus sp.	1.23 ± 1.70	1.48 ± 2.09	n.s.	n.s.
Rhus copallina	2.00 ± 2.14	2.57 ± 2.51	n.s.	n.s.
D. Woody Vegetation (abundance; number within 10 m radius)				
Pinus palustris	1.36 ± 1.60	1.72 ± 1.61	4.45	0.0001
Quercus sp.	1.14 ± 1.41	1.10 ± 1.39	n.s.	n.s.

and more than 2 times as abundant at control points compared to the sides of burrows (Fig. 6). No differences were observed in the abundance of *Quercus* spp. at burrows and control points.

DISCUSSION

Gopher tortoise burrows in the longleaf pine forest that comprised the study area were associated with particular habitat features, including percent canopy cover, basal area, and density of woody vegetation. The average canopy cover at control points was 60%, a value that is within the range recommended for Florida gopher tortoises (0–80%; Cox et al., 1987) and at the upper limit recommended by Landers et al. (1981). If tortoises established their burrows without regard to canopy cover, one would expect average canopy cover at burrows to approximate that observed at control points. However, burrows observed in this study were located in areas with an average of 30% canopy cover, half that of control points. Similarly, longleaf pine basal area was 2 times higher at control points than at burrows. Aresco and Guyer (1999) also observed pine basal area at random points to be twice that at active burrows; however, overall pine density at their south Alabama site was ca. 4.4 times higher than at Green Grove.

Woody vegetation data also supported the observation that tortoises establish burrows in areas with a low abundance of *Pinus palustris,* as well as avoiding areas with dense shrubs, such as *Asimina longifolia.* Avoidance of areas with a dense overstory canopy and dense shrub layer might be expected to facilitate light penetration to groundcover vegetation, increase basking efficiency for tortoises, and provide more suitable burrowing conditions (i.e., reduced root density). These results also support prior observations that gopher tortoises require a relatively open canopy that permits light to reach the ground, supporting a herbaceous ground cover layer and egg incubation (Hallinan, 1923; Landers, 1980; Landers and Speake, 1980; Auffenberg and Franz, 1982; Cox et al., 1987).

Topography may also play a role in the establishment of burrows at particular sites. The difference in slope behind the burrow entrance or control point was nearly significant; burrows had a 30% steeper slope than control points. Thus, tortoises may select areas with a more positive slope when establishing burrows. Burrows constructed at sites with positive slope might be expected to experience less runoff into the burrow, possibly facilitating burrow construction and reducing burrow maintenance costs. In addition, these burrows may be less likely to experience prolonged flooding.

In addition to selecting particular habitat features for burrow excavation, gopher tortoises modify the habitat surrounding their burrows. Direct effects are indicated by the increased soil compaction and altered groundcover vegetation at the front and sides of burrows compared with the backs of burrows. These results support observations by others that most tortoise activity occurs in front and to the sides of a burrow (Auffenberg, 1969; McRae et al., 1981). Foraging activities are likely responsible for the increased soil compaction and altered groundcover at the front and sides of burrows. Repeated travel to and from burrows results in trampled soil and vegetation, leading to a series of well-defined trails that radiate outward from the burrow entrance (Auffenberg, 1969; McRae et al., 1981).

Tortoises do not appear to forage in a random manner. Instead, they select among available plants (Macdonald and Mushinsky, 1988). In many cases, selective foraging will result in decreased abundance of the target species. In other cases, by preferentially ingesting certain plant species, tortoises may affect the reproductive success of plants differentially, either by creating openings that can be colonized by new seedlings or by scarification of ingested seeds (Rick and Bowman, 1961; Baskin and Baskin, 1998), or other mechanisms that facilitate seed dispersal (Auffenberg, 1969).

Wiregrass, a species that was observed to be consumed, was equally abundant at burrows and control points. In contrast, selective foraging was likely responsible for many of the density differences in plant species that were observed

Table 2. Mean abundance (number/m²) in each subplot of significant groups of groundcover vegetation.

	Burrows				Control Points			
Groundcover Vegetation	Fronts	Backs	Lefts	Rights	Fronts	Backs	Lefts	Rights
Non-*Aristida* Poaceae	3.50 ± 2.86	5.23 ± 4.43	5.10 ± 4.16	4.88 ± 3.95	6.30 ± 5.94	6.16 ± 5.57	6.58 ± 6.66	6.26 ± 4.78
Fabaceae	0.19 ± 0.45	0.10 ± 0.37	0.04 ± 0.20	0.15 ± 0.36	0.04 ± 0.20	0.02 ± 0.14	0.04 ± 0.20	0.06 ± 0.24
Fruit-bearing plants	0.02 ± 0.14	0.06 ± 0.35	0.10 ± 0.63	0.21 ± 1.06	0.20 ± 0.77	0.26 ± 1.00	0.40 ± 0.13	0.36 ± 1.22

Table 3. Test results of *a priori* hypotheses concerning groundcover vegetation.

	Control Points vs. Burrow (F, *p*)		
Groundcover Vegetation	Backs	Fronts	Sides
Non-*Aristida* Poaceae	n.s.	12.62, 0.0004	n.s.
Fabaceae	n.s.	10.32, 0.001	n.s.
Fruit-bearing plants	7.58, 0.01	10.41, 0.001	n.s.

between control points and burrows. For instance, both fruit-bearing plants and the non-*Aristida* Poaceae and grass-like plant groups are preferred food items of gopher tortoises (Garner and Landers, 1981). The abundance of both groups was significantly lower near active tortoise burrows. In contrast, Fabaceae (legumes), another preferred food item of gopher tortoises (Garner and Landers, 1981), were 3 times more abundant near burrows. Seeds of many native legumes in the study area have extremely thick seed coats that may benefit from scarification for successful germination (Baskin and Baskin, 1998; Mark Hainds, *pers. comm.*). Consequently, tortoises may play an important role in nitrogen cycling in the longleaf pine ecosystem by enhancing legume abundance.

The dispersion pattern of all burrows in the study area was clumped, whereas active burrows were randomly dispersed. A similar pattern was noted by Kushlan and Mazzotti (1984) for an island population in south Florida. Green Grove represents a relatively flat mesic habitat containing numerous patches of relatively open canopy that are scattered throughout the area. The random distribution of active burrows is likely related to the distribution of optimal habitat patches, whereas the clumped pattern for all burrows probably reflects creation and eventual abandonment of multiple burrows by single tortoises.

Other studies have reported clumped (Auffenberg and Iverson, 1979; McRae et al., 1981; Auffenberg and Franz, 1982) or regular (Stewart et al., 1993) dispersion of tortoise burrows. In habitats where tortoises are forced into marginal areas, burrow dispersion may become clumped. Likewise, regularly distributed patches of open canopy could presumably result in a regular dispersion of burrows. Furthermore, Mushinsky and McCoy (1994) observed higher tortoise density in smaller habitat patches than in larger ones, which may also affect dispersion patterns in different sized areas.

The temporal and spatial dynamics of tortoise burrows are likely to be key variables in understanding maintenance of species richness in old-growth longleaf pine forests and, therefore, in restoration of such habitat. Because Green Grove retains old trees and a relatively undisturbed ground cover, habitat use at this site may indicate how tortoises are affected by processes associated with ancestral longleaf pine forests. Gaps in such forests are thought to result from periodic mortality of adult trees by lightning, windthrow, and fire scars (Platt et al., 1988) and are of a size (Platt et al., 1993) sufficient to accommodate foraging movements of a single tortoise (McRae et al., 1981). The dispersion pattern of active burrows observed in this study suggests that gaps are distributed in a random spatial pattern. Because adult tortoises can occupy burrows for 1–2 decades at relatively pristine sites (Guyer and Hermann, 1997), soil compaction and foraging by tortoises around burrows are likely to have lasting impacts on ground cover vegetation.

LITERATURE CITED

ARESCO, M.J. AND GUYER, C. 1999. Burrow abandonment by gopher tortoises in slash pine plantations of the Conecuh National Forest. J. Wildl. Manage. 63:26-35.

AUFFENBERG, W. 1969. Tortoise behavior and survival. Rand McNally, Chicago, IL, 38 pp.

AUFFENBERG, W. AND FRANZ, R. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). In: Bury, R.B. (Ed.). North American Tortoises: Conservation and Ecology. U.S. Dept. Int. Fish Wildl. Serv. Wildl. Res. Rep. No.12, pp. 95-126.

AUFFENBERG, W. AND IVERSON, J.B. 1979. Demography of terrestrial turtles. In: Harless, M. and Morlock, H. (Eds.). Turtles: Perspectives and Research. New York: John Wiley and Sons, pp. 541-569.

BASKIN, C.C. AND BASKIN, J.M. 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. San Diego, California: Academic Press, 666 pp.

BONHAM, C.D. 1989. Measurements for Terrestrial Vegetation. New York: John Wiley & Sons, 338 pp.

BRADFORD, J.M. 1986. Penetrability. In: Klute, A. (Ed.). Methods of Soil Analysis, Part 1. Physical and Mineralogical Methods, 2nd Edition. Madison, Wisconsin: American Society of Agronomy Inc. & Soil Science Society of America, Inc.

BURKE, R.L. 1989. Florida gopher tortoise relocation: overview and case study. Biological Conservation 48:295-309.

BUTLER, J.A., BOWMAN, R.D., HULL, T.W., AND SOWELL, S. 1995. Movements and home range of hatchling and yearling gopher tortoises, *Gopherus polyphemus*. Chelonian Conservation and Biology 1:173-180.

COX, J., INKLEY, D., AND KAUTZ, R. 1987. Ecology and habitat protection needs of gopher tortoise (*Gopherus polyphemus*) populations found on lands slated for large-scale development in Florida. Tallahassee: Florida Game and Fresh Water Fish Commission. Nongame Wildl. Program Tech. Rep. No. 4, 69 pp.

DIEMER, J.E. 1986. The ecology and management of the gopher tortoise in the southeastern United States. Herpetologica 42:125-133.

DODD, C.K., JR. 1986. Desert and gopher tortoises: Perspectives on conservation approaches. In: Jackson, D.R. and Bryant, R.H. (Eds.). The Gopher Tortoise and its Community. Proc. 5th Ann. Mtg., Gopher Tortoise Council. Gainesville, Florida: Florida Mus. Nat. Hist., pp. 54-72.

EISENBERG, J.F. 1983. The gopher tortoise as a keystone species. In: Bryant, R.J. and Franz, R. (Eds.). The Gopher Tortoise: A Keystone Species. Proc. 4th Ann. Mtg. Gopher Tortoise Council. Gainesville, Florida: Florida State Museum, pp. 1-4.

ERNST, C.H., LOVICH, J.E., AND BARBOUR, R.W. 1994. Turtles of the United States and Canada. Washington: Smithsonian Institution Press, 578 pp.

GARNER, J.A. AND LANDERS, J.L. 1981. Foods and habitat of the gopher tortoise in southwestern Georgia. Proc. Ann. Conf. Southeast. Assoc. Fish and Wildl. Agencies 35:120-133.

GUYER, C. AND HERMANN, S.M. 1997. Patterns of size and longevity for gopher tortoise (*Gopherus polyphemus*) burrows: implications for the longleaf pine-wiregrass ecosystem. Chelonian Conservation and Biology 2:507-513.

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

HANSEN, K. L. 1963. The burrow of the gopher tortoise. Quart. J. Florida Acad. Sci. 26:353-360.

JACKSON, D.R. 1987. The vertebrate commensals of the gopher tortoise burrow. Proc. 6th Ann. Mtg., Gopher Tortoise Council. Gainesville: Florida State Museum.

JACKSON, D.R., AND MILSTREY, E.G. 1989. The fauna of gopher tortoise burrows. In: Diemer, J., D. Jackson, Landers, L., Layne, J., and Wood, D. (Eds.). Proc. of the Gopher Tortoise Relocation Symposium. Tallahassee: Florida Game Fresh Water Fish Comm., Nongame Wildl. Prog. Tech Rep. No. 5, pp. 86-98.

KACZOR, S.A. AND HARTNETT, D.C. 1990. Gopher tortoise (*Gopherus polyphemus*) effects on soils and vegetation in a Florida sandhill community. Am. Midl. Nat. 123:100-111.

KREBS, C.J. 1989. Ecological Methodology. New York: Harper and Row, 654 pp.

KUSHLAN, J.A. AND MAZZOTTI, F.J. 1984. Environmental effects on a coastal population of gopher tortoises. J. Herpetol. 18:231-239.

LANDERS, J.L. 1980. Recent research on the gopher tortoise and its implications. In: Franz, R. and Bryant, R.J. (Eds.). The Dilemma of the Gopher Tortoise-Is There a Solution? Proc. 1st Ann. Mtg., Gopher Tortoise Council. Gainesville: Florida State Museum, pp. 8-14.

LANDERS, J.L. AND BUCKNER, J.L. 1981. The gopher tortoise: effects of forest management and critical aspects of its ecology. Southlands Exp. For. Tech. Note 56:1-7.

LANDERS, J.L. AND SPEAKE, D.W. 1980. Management needs of sandhill reptiles in southern Georgia. Proc. Ann. Conf. Southeast. Assoc. Fish Wildl. Agen. 34:515-529.

LANDERS, J.L., GARNER, J.A., MCRAE, W.A., AND BUCKNER, J.L. 1981. The gopher tortoise: distribution, ecology, and effects of forest management. Endangered Species Investigations E-1 Southlands Experimental Forest. Bainbridge, Georgia: International Paper Company.

LEMMON, P.E. 1956. A spherical densiometer for estimating forest overstory density. For. Sci. 2:314-320.

LOHOEFENER, R. AND LOHMEIER, L. 1986. Experiments with gopher tortoise (*Gopherus polyphemus*) relocation in southern Mississippi. Herp. Review 17:37-40.

LYNCH, J.M., GHOLSON, A.K., JR., AND BAKER, W.W. 1986. Natural Features Inventory of Ichauway Plantation, Georgia. Chapel Hill, NC: Southeast Regional Office, The Nature Conservancy, 307 pp.

MACDONALD, L.A. AND MUSHINSKY, H.R. 1988. Foraging ecology of the gopher tortoise, *Gopherus polyphemus*, in a sandhill habitat. Herpetologica 44:345-353.

MCRAE, W.A., LANDERS, J.L., AND GARNER, J.A. 1981. Movement patterns and home range of the gopher tortoise. Am. Midl. Nat. 106:165-179.

MEANS, D.B. 1985. Management recomendations for the gopher tortoise in longleaf pine ecosystems. In: Dodd, C.K. (Ed.). Gopher Habitat Management - Strategies and Options. Proc. 6th Ann. Mtg., Gopher Tortoise Council. Gainesville: Florida State Museum, pp. 41-56.

MILSTREY, E.G. 1986. Ticks and invertebrate commensals in gopher tortoise burrows : implications and importance. In: Jackson, D.R. and Bryant, R.H. (Eds.). The Gopher Tortoise and its Community. Proc. 5th Ann. Mtg., Gopher Tortoise Council. Gainesville, Florida: Florida Mus. Nat. Hist., pp. 4-15.

MUELLER-DOMBOIS, D. AND ELLENBERG, H. 1974. Aims and Methods of Vegetation Ecology. New York: John Wiley and Sons, 547 pp.

MUSHINSKY, H.R. AND MCCOY, E.D. 1994. Comparison of gopher tortoise populations on islands and on the mainland in Florida. In: Bury, R.B. and Germano, D.J. (Eds.). Biology of North American Tortoises. National Biological Survey, Fish and Wildlife Research 13, pp. 39-47.

OUTCALT, K.W. AND SHEFFIELD, R.M. 1996. The longleaf pine forest: trends and current conditions. Resource Bulletin SRS-9. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station, 23 pp.

PAINE, R.T. 1969. A note on trophic complexity and community stability. Am. Nat. 103:91-93.

PLATT, W.J. AND RATHBUN, S.L. 1993. Dynamics of an old-growth longleaf pine plantation. In: Hermann, S.M. (Ed.). Proc. 18th Tall Timbers Fire Ecology Conference. Tallahassee, Florida: Tall Timbers Res., Inc., pp. 275-297.

PLATT, W.J., EVANS, G.W., AND RATHBUN, S.L. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). Amer. Nat. 131:491-525.

RICK, C.M. AND BOWMAN, R.I. 1961. Galapagos tomatoes and tortoises. Evolution 15:407-417.

SAS INSTITUTE, INC. 1989. SAS/STAT User's Guide, Version 6, Fourth Edition, Volume 2, Cary, NC, 846 pp.

SCHEINER, S.M. 1993. MANOVA: multiple response variables and multispecies interactions. In: Scheiner, S.M. and Gurevitch, J. (Eds.). Design and Analysis of Ecological Experiments. New York: Chapman & Hall, pp. 94-112.

SIMBERLOFF, D. 1993. Species-area fragmentation effects on old-growth forests: prospects for longleaf pine communities. In: Hermann, S.M. (Ed.). Proc. 18th Tall Timbers Fire Ecology Conference. Tallahassee, Florida: Tall Timbers Res., Inc., pp. 1-13.

SOKAL, R.R. AND ROHLF, F.J. 1995. Biometry. New York: W.H. Freeman and Company, 887 pp.

STEWART, M.C., AUSTIN, D.F., AND BOURNE, G.R. 1993. Habitat structure and the dispersion of gopher tortoises on a nature preserve. Florida Scientist 56:70-81.

STONER, H.T. 1986. Soil survey of Baker and Mitchell Counties, Georgia. United States Department of Agriculture, Soil Conservation Service, 121 pp.

WILSON, D.S., MUSHINSKY, H.R., AND MCCOY, E.D. 1994. Home range, activity, and use of burrows of juvenile gopher tortoises in central Florida. In: Bury, R.B. and Germano, D.J. (Eds.). Biology of North American Tortoises. National Biological Survey, Fish and Wildlife Research 13, pp. 147-160.

WITZ, B.W., WILSON, D.S., AND PALMER, M.D. 1991. Distribution of *Gopherus polyphemus* and its vertebrate symbionts in three burrow categories. Am. Midl. Nat. 126:152-158.

WOODRUFF, R.E. 1982. Arthropods of gopher burrows. In: Franz, R. and Bryant, R.J. (Eds). The Gopher Tortoise and its Sandhill Habitat. Proc. 3rd Ann. Mtg., Gopher Tortoise Council. Gainesville: Florida State Museum, pp. 25-48.

WRIGHT, J.S. 1982. Distribution and population biology of the gopher tortoise, *Gopherus polyphemus*, in South Carolina. M.S. Thesis, Clemson University.

YOUNG, F. N. AND GOFF, C.C. 1939. An annotated list of the arthropods found in the burrows of the Florida gopher tortoise, *Gopherus polyphemus* (Daudlin). Florida Entomologist 22:53-62.

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