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Patterns of Size and Longevity of Gopher Tortoise (*Gopherus polyphemus*) Burrows: Implications for the Longleaf Pine Ecosystem

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Abstract. – Burrows of gopher tortoises (*Gopherus polyphemus*) are a key resource in the longleaf pine ecosystem because they also provide shelter for other animals and interrupt understory vegetation. We compared patterns of burrow size and longevity, as well as use rates by tortoises, at two sites: the Wade Tract, a site in Georgia with clay-based soils, old-growth trees, and a relatively undisturbed understory, and the Conecuh National Forest, a site in Alabama with sandy soils impacted by forestry management practices. The Wade Tract was dominated by large burrows that retained tortoises for longer periods of time than burrows on the Conecuh National Forest. On both sites, large (width > 30 cm) burrows lasted longer and were used by tortoises longer than medium (width > 20 but ≤ 30 cm) and small (width ≤ 20 cm) burrows. No differences were observed between the two sites in the rates at which medium and large burrows filled with soil. Our observations suggest that: 1) ancestral forests were dominated by large, presumably old tortoises that created and remained faithful to burrows that were present for long time periods (half life of at least 12–24 years), 2) burrow longevity is determined primarily by factors other than soil type and root structure, and 3) patterns characteristic of ancestral forests have been altered on managed forest lands where vegetation is more sparse. On managed forest lands, tortoises create burrows that, when matched for size, have similar minimum half lives to those on areas with more vegetation. However, tortoises on these disturbed sites tend to be smaller and, therefore, create smaller burrows. These burrows and their associated aprons remain as soil disturbances for shorter periods of time and are readily abandoned, possibly as tortoises migrate to sites with better forage. Such abandoned burrows may play a role in the spread of armadillos (*Dasypus novemcinctus*) into these areas.

Key Words. – Reptilia; Testudines; Testudinidae; *Gopherus polyphemus*; tortoise; armadillo; ecology; burrows; longleaf pine; soil disturbance; Alabama; Georgia; USA

In the southeastern Coastal Plain of the United States, the gopher tortoise (*Gopherus polyphemus*) is considered a keystone species in the longleaf pine (*Pinus palustris*) ecosystem (Guyer and Bailey, 1993). This animal is an important grazer and potential dispersal agent of understory plants (Kaczor and Hartnett, 1990). Additionally, gopher tortoises dig extensive burrows that serve as hiding places, nesting sites, or overwintering dens for many animals (Jackson and Milstrey, 1989), including vulnerable species like the eastern indigo snake (*Drymarchon corais couperi*) and the dusky gopher frog (*Rana capito sevosa*). Thus, the presence or absence of gopher tortoises may have profound effects on conservation, management, and restoration efforts. Because this species is long-lived and exhibits low rates of recruitment (Alford, 1980; Landers et al., 1980, 1982), it recovers slowly following anthropogenic population reductions (Auffenberg and Franz, 1982). This slow recovery is exacerbated by the small home ranges and low migration rates of tortoises (McRae et al., 1981; Diemer, 1992a, 1992b; Butler et al., 1995).

The longleaf pine ecosystem possesses striking species richness and endemicity (Folkerts et al., 1993; Guyer and Bailey, 1993; Peet and Allard, 1993). This forest type has been subjected to prolonged and intense human impact (Means and Grow, 1985; Frost, 1993; Simberloff, 1993) that has prompted increased efforts to preserve and restore extant remnants. Tracts maintaining old-growth trees and intact understory vegetation represent as little as 0.002% of the original distribution (Simberloff, 1993). The gopher tortoise may play a pivotal role in management efforts associated with this forest type. Much of the perceived benefit of gopher tortoises to the longleaf pine ecosystem is associated with their burrows. Therefore, the life span of these physical structures is a critical factor in documenting how tortoises impact an imperiled forest type. Unfortunately, no such data are available.

Here, we estimate longevity of burrows at two sites, one on clay-based and the other on sandy soils, representing extremes of soil types occupied by gopher tortoises. Our eventual goal is to describe the time frame over which these small-scale soil disturbances impact longleaf pine ecosystems (Hermann, 1993). We are interested in inferring what this disturbance regime was like in ancestral forests and comparing it to current human-altered habitats. This paper represents the first phase of this long-term project.

At least two factors could affect burrow longevity. The first is the physics of maintaining burrow integrity in soils friable enough to allow digging. For this factor longer survival of burrows is expected in clay-based soils than in

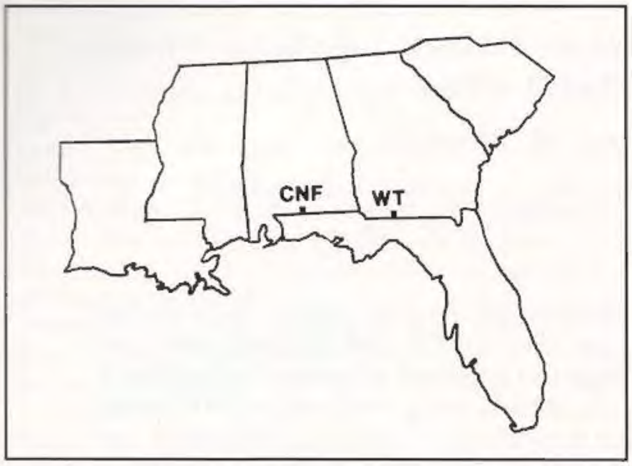

Figure 1. Map of southeastern United States showing locations of the Conecuh National Forest (CNF), Alabama, and the Wade Tract (WT), Georgia.

sandy soils and longer survival is expected of larger burrows than smaller ones. The second factor is vegetation, which also has two components. First, roots in more heavily vegetated areas might maintain burrow integrity over longer time periods than in areas with less vegetation. Second, tortoises at heavily vegetated areas might remain faithful to a burrow for longer time periods than at areas with sparse vegetation; tortoises in the latter habitat might wander in search of better forage.

From the above, we expected that survival of burrows and the residency time of tortoises associated with those burrows would differ between the two sites; burrows on clay-based soils should last longer and retain tortoises longer than those on sandy soils. To test such hypotheses, replicate sites on each soil type are needed. However, descriptions of patterns of burrow longevity are needed for current conservation and restoration decisions. Therefore, we present data in an exploratory fashion in hopes that emergent patterns of burrow survival on the two sites will lead to appropriate hypotheses that can be tested with accumulating data from other sites.

METHODS

We surveyed gopher tortoise burrows at two sites (Fig. 1). One was the Conecuh National Forest (CNF; Fig. 2) in south-central Alabama. This region has a variety of soil types, but we focused on those with deep sands (Troup and Fuquay soil types). Additionally, the CNF is heavily impacted by forestry operations. The overstory in our study area was dominated by slash pine (*Pinus elliottii*) planted in the 1970s as a replacement for the original longleaf pine forest (*Pinus palustris*). The ground cover was sparse, partly as a result of the nutrient-poor nature of sandy soils and partly because of management practices (forestry site preparation and a dormant-season fire regime). At the CNF, we marked burrows with numbered metal tags in 1991 and censused them yearly through 1995. In the initial survey, all burrows were marked at six sites used for a study on the effects of forest stand-thinning on tortoises (Herrington, 1996). These burrows included those used by tortoises (n = 490) as well as those used by armadillos (*Dasypus novemcinctus*; n = 562). The shape of the entrance was used to distinguish which animal used a burrow (see below). The width of each entrance was measured with tree calipers placed inside the mouth of a burrow.

The other study site was the Wade Tract (WT; Fig. 2), a private ecological preserve located in Thomas County, Georgia, and managed by Tall Timbers Research Station (see Platt et al., 1988). The WT was used to represent patterns characteristic of clay-based soils which are thought to be near the limit of friability for tortoise burrowing activities. Soil types on the preserve include Faceville, Lucy, Norfolk, and Orangeburg. The WT has an overstory of old-growth longleaf pine (*P. palustris*) and an understory of lush vegetation dominated by wiregrass (*Aristida stricta*). The only major human impacts to the vegetation were salvage of dead and dying large trees, dormant- season, annual fires, and a few scattered abandoned food plots which were used to manage the area as a quail-hunting reserve until 1979. After that year, salvage operations ceased and biennial, growing-season fires were implemented to mimic the timing of natural fires in this region. Tortoise burrows on the WT were marked in 1988 when numbered metal tags were placed above 168 openings and entrance widths were measured as described for the CNF. Recensuses were made in 1992 and 1995.

During each initial survey, intensive searches were made to discover all burrows. On the CNF, each burrow was classified into one of three categories. Burrows that retained

Figure 2. Representative views of forest structure. **Top:** Conecuh National Forest, Alabama. **Bottom:** Wade Tract, Georgia.

Figure 3. Representative views of different categories of gopher tortoise burrows. **Top:** Active (AC). **Middle:** Abandoned (AB). **Bottom:** Invaded by an armadillo (DIL).

an outline similar to the anterior profile of a tortoise shell (rounded top, flattened bottom; width greater than height) and ruts leading down the entrance in positions consistent with tortoise feet were termed "active" (AC; Fig. 3). Often these burrows had plastral skid marks and footprints indicating recent use. Our definition for this category corresponded to the "active plus inactive" categories of Auffenberg and Franz (1982) and Mushinsky and McCoy (1994). Burrows that had eroded outlines to the entrance and no evidence of tortoise use were classified as "abandoned" (AB; Fig. 3; as in Mushinsky and McCoy, 1994). Burrows with rounded openings were classified as being "invaded by an armadillo" (DIL; Fig. 3). These burrows typically had a single rut created by the more medially located legs of mammals; often the holes either were filled with leaves or had three-toed footprints and drag marks from a tail. Because signs of armadillos were never observed leading down a tortoise-shaped burrow and signs of tortoises were never observed leading down an armadillo-shaped burrow, we assumed that our "active" and "invaded by an armadillo" categories represented mutually exclusive use. Armadillos were present on the WT, but burrows conforming to these animals were rare and none of the burrows that we monitored was invaded by these mammals. Therefore, this category was not used at this site.

At each subsequent census all burrows marked during the initial surveys were reclassified using the same three categories. A fourth category of "filled" (FIL) was added for those burrows whose entrances had become completely occluded by soil. Burrows defined by Auffenberg and Franz (1982) as being "old" corresponded to our "abandoned" plus "filled" categories.

Occasionally, burrows escaped detection during a census. Invariably, these were discovered to be filled when found at later sample periods. For statistical analysis of survival we eliminated such burrows from the data set. For creation of survival curves we included them and assumed that they were filled during the missing census period. At each census, each study site also was surveyed intensively for newly created tortoise burrows. These additions were appended to subsequent censuses. Because vegetation was sparse on the CNF and surveys were conducted immediately after prescribed fires on the WT, we assume differences in our ability to detect burrows on the two sites were negligible.

To characterize burrows at the two sites, we counted the number of burrows in seven size classes created to cover the range of entrance widths (5 cm intervals from ≤ 15 to > 40 cm). To examine patterns of burrow longevity between the two sites we compared burrows that were classified as being active in 1992 with their status in 1995. We counted the number of filled vs. open (active, abandoned, or invaded by an armadillo) burrows and explored these data for effects of size and site. Size was examined in the statistical design by creating three categories based on entrance width: small ($\leq$ 20 cm), medium (> 20 but ≤ 30 cm), and large (> 30 cm). Because the WT had few small burrows, the effect of burrow size on burrow longevity was tested only for medium and large burrows when compared between sites.

To examine patterns of use by tortoises, we counted the number of burrows known to be active in 1992 that were still active in 1995 and compared this with the number that were inactive (abandoned by a tortoise or invaded by an armadillo). Again, the effects of size and location were examined by including these grouping variables in the statistical analysis. We used logistic analyses of contingency tables (PROC CATMOD; SAS, 1990) to test for patterns of burrow survival and occupancy between sites and among size classes. For these tests, the response variable was burrow status (open vs. filled or active vs. inactive).

To estimate rates of burrow filling and abandonment, we used the repeated measures of burrow status to estimate

Table 1. Sample burrow transition matrix. Status categories are "active" (AC), "abandoned" (AB), "invaded by an armadillo" (DIL), and "filled with soil" (FIL). Data are probabilities of burrows from a status category in year x being categorized in each status category in year $x + c$. Four such matrices were calculated for the five census periods on the Conecuh National Forest and two matrices were calculated for the three census periods on the Wade Tract. Values averaged within each site were used to estimate survival curves (see text).

Year x Status	Year $x + c$ Status AC	AB	DIL	FIL
AC	.77	.13	.08	.02
AB	.32	.30	.25	.13
DIL	.13	.04	.78	.05
FIL	.00	.00	.00	1.00

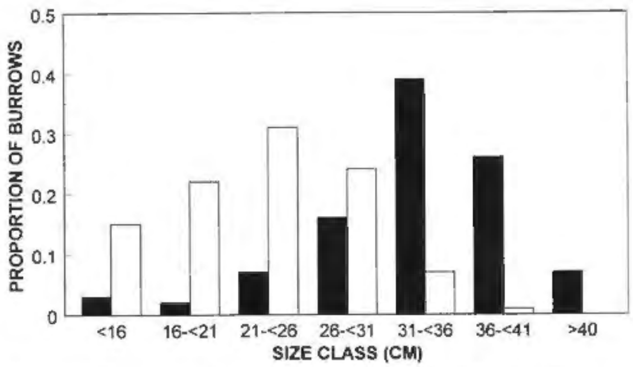

Figure 4. Burrow size distributions for the Wade Tract (solid bars; $n = 168$) and the Conecuh National Forest (open bars; $n = 490$).

inter-census transition probabilities among the four burrow status categories (Table 1). This approach follows stage-based models of demography (Caswell, 1989). We used this approach rather than traditional survivorship analyses because burrows were not constrained to an ordered progression through each category (e.g., an abandoned burrow might revert to being active). For the CNF, four matrices, representing each of the possible inter-year comparisons, were created for each of the three size categories of burrows. For the WT, two such inter-census matrices were constructed for medium and large burrows; this site did not support sufficient small burrows for analysis (see below). The means of these matrix values (calculated separately for each site) were used to create survivorship curves for the rate at which active burrows became filled with soil (longevity) and the rate at which active burrows were abandoned by tortoises (occupancy); from these curves we calculated half lives for the two variables (the predicted time for half of the remaining burrows to become filled or abandoned). These values were used to interpret the meaning of significant effects documented by the logistic contingency table tests. Because the age of most burrows was unknown at the first census, these half lives are minimum estimates of longevity and occupancy.

RESULTS

The two sites differed in size distribution of burrows (Fig. 4; size by site interaction; $p < 0.001$), with a greater proportion of large and fewer small burrows on the WT as compared with the CNF. The proportion of active burrows that were filled by 1995 was not significantly different between sites [Table 2; status (AC + AB + DIL vs. FIL) by site (medium and large categories only) interaction; $p = 0.17$] but was greater for medium than large sizes [Table 2; status (AC + AB + DIL vs. FIL) by size (medium and large categories only) interaction; $p = 0.005$]. The three-way interaction for site, size (medium and large categories only), and status (AC + AB + DIL vs. FIL) was not significant ($p = 0.23$). For burrows on the CNF, the three size categories differed in the proportion of filled burrows [Table 2; status (AC + AB + DIL vs. FIL) by size interaction; $p = 0.00002$]; survival of large and medium burrows did not differ significantly [Table 2; status (AC + AB + DIL vs. FIL) by size (medium and large categories only) interaction; $p = 0.15$], indicating that medium and large burrows had increased survival compared with small burrows.

For large burrows, population projection matrices indicated minimum burrow half lives of 24 yrs for both the CNF and the WT (Fig. 5). For medium burrows, minimum half lives were 6 yrs for the CNF and 13 yrs for the WT (Fig. 5); however, contingency table analyses indicated that these values were not significantly different. Finally, for the CNF, small burrows were estimated to have a minimum half life of 3 yrs (Fig. 5). The shapes of survival curves for small and medium burrows were similar to each other and differed from those for large burrows.

Significantly more burrows remained active on the WT than on the CNF [Table 2; site by status (AC vs. AB + DIL) interaction; $p = 0.03$]. Large burrows remained active as frequently as did medium burrows [Table 2; size (medium and large categories only) by status (AC vs. AB + DIL) interaction; $p = 0.64$]. The three-way interaction between site, size (medium and large categories only), and status (AC vs. AB + DIL) was not significant ($p = 0.41$); however, small numbers of medium burrows on the WT may have decreased the likelihood of detecting such an effect. When the three size categories were compared for the CNF alone, there was a marginally significant difference in the proportion of active burrows among the size classes [Table 2; size by status (AC vs. AB + DIL) interaction; $p = 0.08$], but this difference was not evident when small burrows were com-

Table 2. Distribution of burrows known to be active in 1992 among size, site, and status categories in 1995. Size categories are small (≤ 20 cm), medium (> 20 cm but ≤ 30 cm), and large (> 30 cm); sites are the Conecuh National Forest (CNF) and the Wade Tract (WT); status categories are "active" (AC; recently used by a gopher tortoise), "abandoned" (AB; recently abandoned by a gopher tortoise), "invaded by an armadillo" (DIL), and "filled with soil" (FIL).

Size	Site	Status AC	AB	DIL	FIL
Small	CNF	10	5	8	15
	WT	0	0	0	0
Medium	CNF	33	16	33	13
	WT	4	1	—	3
Large	CNF	35	11	13	4
	WT	61	19	—	6

compared with medium ones [Table 2; status (AC vs. AB + DIL) and size (small and medium categories only) interaction; $p = 0.78$]. On the CNF, many of the abandoned burrows were invaded by armadillos. The proportion of such burrows did not differ among small, medium, or large burrows [Table 2; size by status (AB vs. DIL) interaction; $p = 0.55$]. Based on our population projection matrices, we estimated minimum half lives for tortoise occupancy of a burrow to be 12 yrs for large burrows and 5 yrs for medium ones on the WT (Fig. 6); minimum half lives on the CNF were 3 yrs for large and 2 yrs for medium and small burrows (Fig. 6). The contingency table analyses documented a significant difference in half life estimates for medium and large burrows on the WT vs. those on the CNF. Similarly, large burrows remained active for longer half lives than did medium burrows; the half lives of small and medium burrows did not differ significantly (Fig. 6).

DISCUSSION

Our data describe differences in the dynamics of tortoise burrows on the Wade Tract compared with the Conecuh National Forest. Principal among these is a difference in burrow size between the two sites. Because the width of a tortoise burrow correlates with the size of the tortoise using that burrow (Martin and Layne, 1987), our burrow size distributions estimate the sizes of tortoises on the two sites. Based on this, the WT is dominated by very large animals with progressively fewer smaller ones. This is expected of a long-lived organism that has relatively low reproductive output. Because environmental conditions on the WT are close to those expected of much of the ancestral tortoise habitat, our data for burrow and tortoise sizes provide an assessment of tortoise population structure on clay-based soils prior to habitat modifications associated with human settlement. The CNF has few individuals as large as those on the WT and many more small animals. The predicted size distribution of animals on the CNF is similar to that reported for several other sites with intensive human land use (Alford, 1980; Stout et al., 1989; Godley, 1989; Diemer, 1992b).

The length of time that a tortoise burrow remained an opening in the soil surface differed among burrow size classes but not between sites. Large burrows remained open for longer periods of time than did medium burrows, regardless of site. Additionally, when small, medium, and large burrows were examined within the CNF, small burrows had significantly reduced life spans relative to medium and large

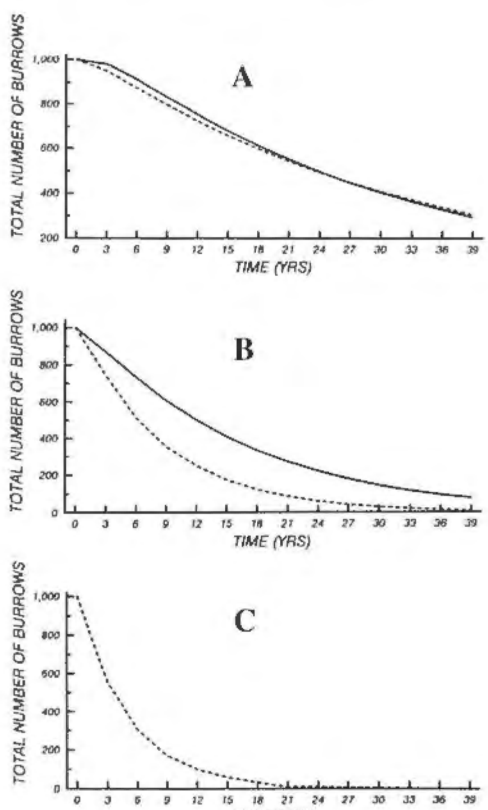

Figure 5. Predicted survival of gopher tortoise burrows on the Wade Tract and the Conecuh National Forest. Curves are hypothetical survival (reflecting losses due to filling) of 1000 initially active burrows followed over time. Solid lines represent the Wade Tract, dashed lines are the Conecuh National Forest. These curves are based on transition probabilities generated from repeated sampling of each site. See text for explanation. **A.** Large burrows. **B.** Medium burrows. **C.** Small burrows.

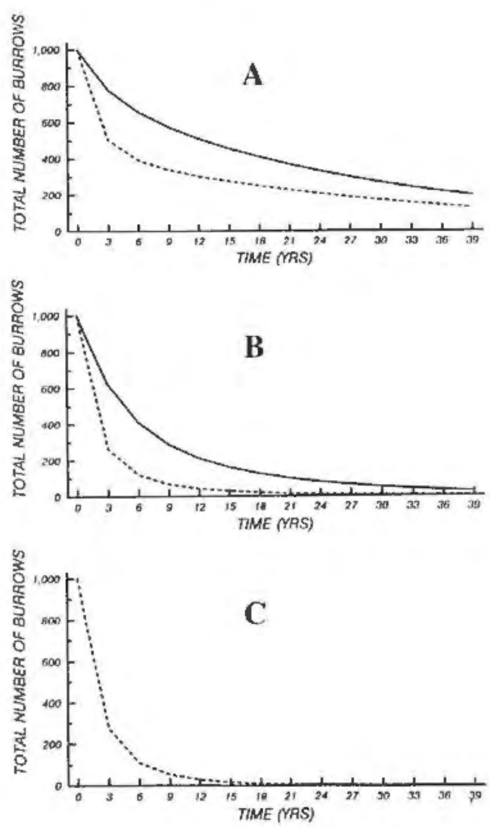

Figure 6. Predicted use of gopher tortoise burrows on the Wade Tract and the Conecuh National Forest. Curves are hypothetical abandonment by tortoises of 1000 initially active burrows followed over time. Solid lines represent the Wade Tract, dashed lines are the Conecuh National Forest. These curves are based on transition probabilities generated from repeated sampling of each site. See text for explanation. **A.** Large burrows. **B.** Medium burrows. **C.** Small burrows.

burrows. Thus, burrow longevity increased with increasing burrow size, but this effect did not appear to be influenced by factors that differ between the WT and the CNF. Contrary to our expectation, the clay-based soils and more abundant roots of the WT did not increase burrow longevity relative to that of the sandy and sparsely vegetated soils of the CNF.

Burrows on the WT were occupied by tortoises for longer periods of time than those on the CNF. Large burrows had slow rates of filling (minimum half life of 24 yrs at both sites) but were occupied by tortoises for 12 yrs on the WT and only 3 yrs on the CNF. Our estimate for occupancy of a large burrow by a tortoise is roughly half the estimated life span of an adult tortoise (Landers et al., 1982; Cox, 1989). For medium burrows, minimum half lives were significantly decreased to 6–13 yrs and tortoises were present for longer time periods on the WT (5 yrs) than on the CNF (2 yrs). Small burrows had very rapid rates of abandonment and filling; minimum half life was 3 yrs with tortoises being present for 2 yrs (see also Wilson et al., 1994). Because turnover rates were so rapid and consecutive samples were taken for 5 years, most of the medium and small burrows on the CNF were of known age by the end of the study period. This was not the case for large burrows. Thus, our survival curves probably underestimate rates associated with use and filling of large burrows, but are relatively unbiased for the smaller size classes.

Our results indicate that reduced occupancy of burrows by tortoises on the CNF is not caused by a reduction in burrow longevity. Additionally, large burrows appear to be constrained by the physics of their size and soil structure to a set life span even if used constantly. The observed patterns of abandonment are consistent with either dispersal of animals from sites where forage quality deteriorates or with increased mortality, including poaching. In areas such as the WT, where vegetation is lush, tortoises are unlikely to abandon burrows in search of food. Instead, animals may abandon burrows to search for mates or because erosion makes maintenance too difficult. From this, we infer that ancestral longleaf pine forests were characterized by large burrows that remained features of the landscape for decades and to which tortoises showed great fidelity. In areas such as the CNF, where forage is sparse and where forest management practices may result in a dense overstory, large tortoises abandon burrows frequently, apparently in search of areas with more appropriate forage or nest sites (Auffenberg and Franz, 1982; Herrington, 1996). Such movements may increase adult mortality due to exposure to vehicular traffic and human predation (Landers and Buckner, 1981; Taylor, 1982). These processes could lead to reduced numbers of large burrows, more rapid burrow turnover rates, and reduced site fidelity by tortoises. The abandoned burrows remain features of the landscape and appear to be invaded readily by animals such as armadillos.

Altered burrow dynamics could affect the diversity of understory plants associated with the apron mounds of tortoise burrows. Kaczor and Hartnett (1990) documented that plant species richness on sandy soils is increased on old abandoned mounds relative to recently abandoned ones. They also noted that percent cover of annual plants is greater on recently abandoned mounds than on old ones. These findings, coupled with our observations, suggest that patterns of mound dynamics on managed forest lands may promote short-lived, weed-like understory species compared with those of old-growth forests.

Additionally, the reduction of burrow size and, therefore, longevity on some managed forest lands could impact the diversity of burrow commensals by changing the probability of successful migration to new burrows. The commensal fauna includes over 360 species, some of which are small and flightless arthropods (Jackson and Milstrey, 1989); the latter characteristics may make these animals less adept at inter-burrow movements. To date, no examination of such impacts has been undertaken.

Alternatively, some commensal forms may be impacted positively by altered dynamics of tortoise burrows on managed forest lands. An example may be the recent reinvasion of armadillos into habitats of the southeast, an event that has raised some concern (Carr, 1982). Armadillos are abundant on the CNF and frequently invade tortoise burrows; they are less abundant on the WT and only alter tortoise burrows infrequently. One possible explanation for the differences that we observed in the lengths of time that tortoises occupied burrows at the two sites is that armadillos on the CNF may drive tortoises from their burrows. We suggest that this explanation alone is unlikely because, in areas of the CNF where pines were thinned, resulting in increased understory vegetation and forage, tortoises displayed increased site fidelity (Herrington, 1996).

These observations lead us to propose an alternative hypothesis regarding armadillos. We argue that widespread alteration of the ancestral longleaf pine ecosystem (Means and Grow, 1985; Simberloff, 1993) has resulted in decreased site fidelity of tortoises on many of the remaining patches of suitable habitat. Our data suggest that increased numbers of abandoned burrows will be found on such sites, a factor that could enhance the rate at which armadillos invade. Careful examination of separate sites, especially those maintaining characteristics of the ancestral ecosystem, are needed to evaluate this scenario.

Our descriptions of burrow longevity should assist in determining how these structures impact forest dynamics (Kaczor and Hartnett, 1990; Hermann, 1993). Conservation efforts at preserved sites, especially National Forest lands of the southeastern Coastal Plain, should recognize that human activities that alter age distributions of tortoise populations will impact the size and turnover rate of soil disturbances created by their burrows. This, in turn, should affect plants and animals associated with these soil disturbances.

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