BURROW ABANDONMENT BY GOPHER TORTOISES IN SLASH PINE PLANTATIONS OF THE CONECUH NATIONAL FOREST

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Abstract: We investigated burrow dynamics and factors associated with abandonment of burrows by gopher tortoises (*Gopherus polyphemus*) in mature slash pine (*Pinus elliottii*) plantations of the Conecuh National Forest (CNF) in southcentral Alabama. Our objectives were to determine how frequently gopher tortoises abandoned burrows in pine plantations, if burrow abandonment was associated with changes in vegetation conditions, and how rapidly these changes occurred. Burrow survey data collected over 5 years indicated gopher tortoises abandoned burrows at an average rate of 22%/year. We believe burrow abandonment occurred frequently in pine plantations, primarily in association with a change in overstory structure that shaded active burrows. Abandoned gopher tortoise burrows had greater total basal area ($P = 0.012$), hardwood basal area ($P = 0.016$), and tree density ($P = 0.003$) than did active burrows. There was a significant positive correlation between age of active gopher tortoise burrows and canopy closure (total basal area: $r^2 = 0.19$, $P = 0.007$; pine basal area: $r^2 = 0.20$, $P = 0.004$; tree density: $r^2 = 0.14$, $P = 0.018$). We estimated that overstory conditions at newly active burrows changed to those observed at abandoned burrows in only 5–7 years. Increases in total basal area to 70 m^2/ha and tree density to 1,400 trees/ha were associated with burrow abandonment. Active burrows had greater total plant cover ($P = 0.009$) and grass cover ($P = 0.016$) than did abandoned burrows. However, we found no correlation between age of active burrows and structure and composition of ground cover vegetation (r^2 values ranged from 0.00 to 0.07; P-values ranged from 0.096 to 0.987). Stand thinning to a basal area of 30 m^2/ha and prescribed growing-season burns should improve habitat quality, thereby increasing burrow fidelity of gopher tortoises.

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Fragmented populations of the gopher tortoise are distributed within the southeastern Coastal Plain, primarily in upland habitats with deep, sandy soils and adequate herbaceous vegetation (Auffenberg and Franz 1982). Habitat loss, modification, and human exploitation have caused a serious rangewide decline of gopher tortoise populations (estimated at 80% in the last 100 yr; Auffenberg and Franz 1982, Diemer 1986). This decline coincides with a reduction in the extent and quality of the longleaf pine–wiregrass ecosystem. Prior to intensive human land use, the plant community in this forest consisted of a widely spaced overstory of uneven-aged longleaf pine (*Pinus palustris*) and a diverse ground cover of herbaceous perennials dominated by wiregrass (*Aristida* spp.) or bluestem grasses (*Andropogon* spp.; Komarek 1974, Stout and Marion 1993). Frequent low-intensity ground fires maintained the openness of these savanna-like forests (Ware et al. 1993). Originally covering 24–36 million ha in the southeastern United States, <1.5 million ha remains today (Kelly and Bechtold 1990, Ware et al. 1993). Scattered, remnant tracts of this ecosystem, including old-growth trees and intact native ground cover vegetation, represent <0.01% of its presettlement distribution (Simberloff 1993, Means 1996).

Repeated logging, clearing for agriculture, open-range livestock grazing, and fire exclusion have transformed most of the original longleaf pine ecosystem into what is now classified as southern mixed-hardwood forest (Ware et al. 1993). Dense, even-aged pine plantations, which did not exist until the 1940s, have replaced much of the former longleaf pine forests (approx 6 million ha; Ware et al. 1993). The conversion of longleaf pine forests to commercial plantations of slash, loblolly (*Pinus taeda*), or sand pine (*P. clausa*) is a significant threat to remaining gopher tortoise populations (Landers and Speake 1980, Diemer 1986).

Gopher tortoise densities are highest in hab-

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itats with an open canopy and lush ground cover vegetation (Auffenberg and Iverson 1979, Garner and Landers 1981). Gopher tortoises are herbivores and feed primarily on legume and nonlegume forbs, wiregrass, and bluestem grasses (Garner and Landers 1981, MacDonald and Mushinsky 1988). Ground cover plant density and composition also influence daily and seasonal movement patterns of gopher tortoises (McRae et al. 1981). For example, Auffenberg and Iverson (1979) reported that gopher tortoise home range size was inversely proportional to the biomass of ground cover vegetation. However, canopy closure in pine plantations may reduce or eliminate forage vegetation and potential nest sites (Landers and Speake 1980, Diemer 1986). Fire exclusion or dormant-season prescribed burns in pine plantations encourage the growth of hardwood trees and a dense shrub midstory that could further change the structure and composition of gopher tortoise habitat (Means and Grow 1985, Mushinsky and Gibson 1991). These habitat changes may result in burrow abandonment and emigration by gopher tortoises (Diemer 1992).

Several studies have described the vegetation conditions associated with various densities of gopher tortoises (Landers and Speake 1980, Lohoefener and Lohmeier 1981, Auffenberg and Franz 1982, Mushinsky and McCoy 1994), but no studies have analyzed vegetation conditions required for gopher tortoises to continue to use burrows in a given habitat type. Evaluation of the specific vegetation factors resulting in burrow abandonment in pine plantations could improve management of the gopher tortoise. In this study, we examined habitat factors associated with gopher tortoise burrow abandonment. Our specific objectives were (1) determine how frequently gopher tortoises abandon burrows in pine plantations, and (2) determine if burrow abandonment is associated with changes in vegetation conditions and how rapidly these changes occur.

STUDY AREA

We conducted this study at 6 sites (16–93 ha) within the CNF in Covington County, south-central Alabama (31°2′–31°9′N, 86°30′–86°41′W). These sites have deep sandy soils predominantly of the Troup and Fuquay series. The CNF is heavily affected by forestry operations. During the late 1960s and early 1970s, these sites had sparse stands of longleaf pine (J. R. Lint, CNF, personal communication). In the early 1970s, scattered, large longleaf pines left standing to promote natural pine regeneration were harvested. Between 1970 and 1979, each site was intensively prepared (raking, plowing, scoring the soil with heavy machinery) and re-planted in closely spaced slash pine (J. R. Lint, CNF, personal communication). The U.S. Forest Service winter-burned these sites every 3–4 years from 1985 to 1996.

METHODS

Tortoise Capture and Burrow Surveys

We collected gopher tortoises during a mark–recapture program from 1991 to 1996. We captured gopher tortoises annually from June to September via wire live traps positioned against burrow entrances, and we marked them by notching marginal scutes with a triangular file (Aresco 1998). Our capture and marking methods were approved by the Auburn University Institutional Animal Care and Use Committee (IACUC PRN 9612-R-0598).

We initially surveyed burrows and marked them with numbered metal tags in 1991. At each subsequent biannual census (1992–96), we reclassified all burrows marked during previous surveys and made intensive searches to discover new burrows. We classified each burrow into 1 of 3 categories: (1) "active" (opening shaped like a tortoise shell and entrance often had plastral skid marks and footprints indicating recent use), (2) "abandoned" (eroded outlines and no evidence of recent tortoise use), and (3) "filled" (completely filled with soil).

Vegetation Sampling

From August through September 1996, we sampled overstory and ground cover vegetation at all available burrows on 4 of the 6 study sites. Our sample included 78 active burrows, 45 burrows abandoned in the last 4 years of the study, and 60 random plots. We rejected random locations if they were within 10 m of a gopher tortoise burrow (in any category). We used regression analysis to determine if vegetation characteristics at burrows abandoned early in the study (e.g., 1992, $n = 8$; 1993, $n = 10$) had changed during the time since abandonment.

Overstory data consisted of species composition, number of trees per hectare, tree basal area (BA; m^2/ha), and number of shrub stems per hectare. We measured diameter at breast height (dbh) and tallied by species all trees and shrubs taller than 2 m within a circular plot (5-m radius; 0.008 ha) around each burrow and random location. We counted woody shrub stems 1–2 m in height within a circular plot (2.5-m radius; 0.002 ha) around each burrow and random location.

For collection of ground cover plant data, we sampled 5 1-m^2 quadrats at each burrow and random location: 0.5 m to the rear, 1 m to the left and right, and 0.5 m and 3 m to the front. Data for each quadrat consisted of the identity and percent cover of those plant species below a height of 1.0 m whose canopies covered some portion of the quadrat. We grouped ground cover plant species at each sampling location into the following 7 growth-form categories: (1) arborescents (i.e., tree seedlings), (2) nonarborescents (i.e., woody shrubs), (3) legume forbs, (4) nonlegume forbs, (5) all forbs (legumes, nonlegumes), (6) grasses, and (7) woody vines. We calculated mean percent cover for each growth-form category from the 5 quadrats at each sampling location. Means are reported in absolute cover rather than relative cover.

Data Analysis

Tortoise Burrow Fidelity.—We estimated the frequency of burrow abandonment via the 5-year status history of all gopher tortoise burrows active in 1991. We calculated the average annual rate of burrow abandonment as the mean percentage of gopher tortoise burrows that changed in status from active to abandoned or filled from 1 year to the next.

Vegetation.—We used a randomized complete block analysis of variance (ANOVA) to examine differences in overstory vegetation (total BA, pine BA, hardwood BA), tree density (no. trees/ha), shrub density (no. stems/ha), and ground cover vegetation (total plant cover, species richness, mean absolute cover for each growth-form category) between active burrows (n = 78), abandoned burrows (n = 45), and random plots (n = 60). We treated each of the 4 sites as blocks and used blocking to remove site effects (e.g., soils, management regime, disturbance history) from the analysis. We arcsine transformed percentages (i.e., % cover) and square-root transformed counts (i.e., tree density, species richness) prior to analysis so they would better meet the normality assumption of ANOVA (Zar 1984). We used the Tukey compromise test for post hoc mean separations

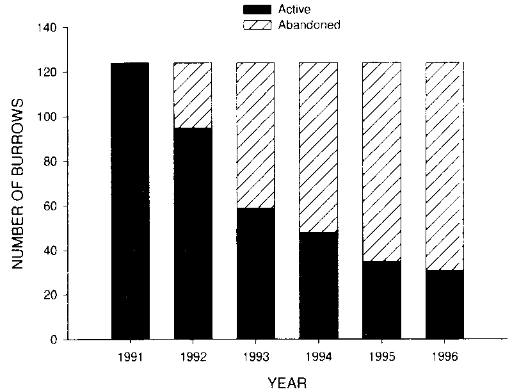

Fig. 1. Five-year change in burrow status of active gopher tortoise burrows surveyed in 1991 on the Conecuh National Forest, Alabama (n = 125). Mean burrow abandonment rate was 22%/year.

(Abacus Concepts 1989). We considered a 0.05 probability level statistically significant.

To further elucidate vegetation factors associated with burrow abandonment, we compared overstory and ground cover vegetation at pairs of abandoned burrows and active burrows. For each of 10 marked gopher tortoises, we compared vegetation at the burrow it presently occupied to the burrow it abandoned. Our sample size was limited to those marked gopher tortoises that permanently abandoned a burrow in the last 4 years and could be relocated at their present burrow. While gopher tortoises sometimes reuse abandoned burrows, the abandoned burrows selected for this analysis were not reoccupied by a gopher tortoise during the study. We used a paired t-test to detect differences in means for each overstory and ground cover vegetation category between pairs of active and abandoned burrows.

Because we had a sample of active burrows of known age (created from 1991 to 1996 and still active in 1996; n = 40), we investigated how vegetation at active burrows changes over time in pine plantations. We used linear regression analysis to determine if a relation existed between the age of an active burrow and the structure and composition of vegetation at that burrow. Furthermore, for each vegetation variable (e.g., total BA) that demonstrated a significant positive correlation with burrow age, we used a linear regression equation to estimate the number of years at which vegetation changed from conditions observed at newly created burrows (burrow age = 0) to those characteristic of newly abandoned burrows (burrows

Table 1. Mean values for structure and composition of overstory vegetation sampled August–September 1996 at active (n = 78) and abandoned (n = 45) gopher tortoise burrows and random plots (n = 60) on the Conecuh National Forest, Alabama.

	Plot type							
	Active burrow		Abandoned burrow		Random plot		ANOVA P-value	
Vegetation variable	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	Plot type	Site
Total BA (m^2/ha)	50.5A[a]	5.34	102B	10.3	115B	13.6	0.012	0.001
Hardwood BA (m^2/ha)	5.34A	1.15	21.8B	4.73	31.4B	5.95	0.016	0.029
Pine BA (m^2/ha)	30.7A	4.10	37.8A	6.04	41.4A	7.00	0.316	<0.001
Tree density (no./ha)	961A	64.9	1,420B	118	1,520B	123	0.003	<0.001
Stem density (no./ha)	2,260A	351	2,910A	455	2,790A	377	0.318	0.003

[a] Means within a row denoted by the same letter are not different ($P > 0.05$; Tukey's compromise test).

abandoned ≤2 yr). First, we defined the condition at abandonment as the mean value of each vegetation variable measured at all newly abandoned burrows (abandoned 1–2 yr, n = 27). We then substituted each of these mean values (Y) into the linear regression equations describing the relation between age of active burrows and vegetation and solved for time (X).

RESULTS

Tortoise Burrow Fidelity

In 1991, we located 124 active gopher tortoise burrows. In 1996, only 31 (25%) of these burrows remained active (Fig. 1). From 1991 through 1996, active burrows were abandoned at an average rate of 22%/year.

Overstory and Ground Cover Vegetation: Block Design

Overstory structure differed among active burrows, abandoned burrows, and random plots. Abandoned burrows and random plots had greater canopy closure than active burrows. Mean total basal area was 2 times greater (P = 0.012), tree density 1.5 times greater (P = 0.003), and hardwood basal area 4 times greater (P = 0.016) at abandoned burrows and random plots than at active burrows (Table 1).

Total plant cover was greater at active burrows than at abandoned burrows (P = 0.009; Table 2). Ground cover vegetation was composed primarily of bluestem grasses (e.g., *Andropogon* spp.), nonarborescents (e.g., *Ilex* spp., *Vaccinium* spp.), and forbs (e.g., *Pityopsis graminifolia*; Table 2). Wiregrass was virtually absent on our study sites. Grass cover was approximately 1.5 times greater at active burrows than at abandoned burrows and random plots (P = 0.016).

Vegetation at Paired Active and Abandoned Burrows

Overstory structure differed between pairs of active and recently abandoned burrows (Table 3). Mean total BA was 2.5 times greater (P = 0.022), tree density 1.7 times greater (P = 0.005), and pine BA 4 times greater (P = 0.034) at abandoned burrows than at active burrows.

Table 2. Mean values for species richness and composition of ground cover vegetation grouped by growth form sampled August–September 1996 at active (n = 78) and abandoned (n = 45) gopher tortoise burrows and random plots (n = 60) on the Conecuh National Forest, Alabama.

	Plot type							
	Active burrow		Abandoned burrow		Random plot		ANOVA P-values	
Vegetation variable	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	Plot type	Site
Species richness (no.)	22A[a]	1.0	20A	1.0	18A	1.0	0.094	0.008
Total plant cover (%)	28A	2.4	21B	3.0	24A,B	2.5	0.009	<0.001
All forbs (%)	7.9A	0.8	5.3A	0.8	6.1A	0.9	0.184	0.003
Nonlegume forbs (%)	5.8A	0.7	4.0A	0.6	4.6A	0.8	0.122	<0.001
Legume forbs (%)	2.1A	0.2	1.4A	0.3	1.5A	0.3	0.102	0.013
Grasses (%)	11.0A	1.4	8.1B	1.6	7.4B	1.4	0.016	<0.001
Nonarborescents (%)	5.0A	0.8	3.1A	0.6	6.5A	1.2	0.183	0.010
Arborescents (%)	2.2A	0.3	2.3A	0.5	2.7A	0.6	0.280	<0.001
Woody vines (%)	2.0A	0.4	2.0A	0.8	1.8A	0.7	0.464	0.027

[a] Means denoted by the same letter are not different ($P > 0.05$, Tukey's compromise test).

Table 3. Mean values for structure and composition of overstory and ground cover vegetation based on 10 pairs of abandoned and active burrows each used by the same gopher tortoise on the Conecuh National Forest, Alabama, 1992–96. Mean values were compared with paired *t*-tests.

Vegetation variable	Abandoned burrow		Active burrow		*P*-value
	$\bar{x}$	SE	$\bar{x}$	SE	
Overstory					
Total BA[a] (m²/ha)	105	22.5	43.8	7.60	0.022
Tree density (no./ha)	1,650	100	963	149	0.005
Hardwood BA (m²/ha)	13.6	3.61	8.56	2.74	0.288
Pine BA (m²/ha)	80.8	26.7	20.2	5.96	0.034
Ground cover					
Species richness (no.)	16	3.0	20	2.0	0.191
Total plant cover (%)	20	5.2	32	7.8	0.133
All forbs (%)	6.9	2.3	7.1	2.0	0.862
Nonlegume forbs (%)	3.9	1.1	5.9	1.6	0.231
Legume forbs (%)	2.9	1.6	1.2	0.40	0.631
Grasses (%)	8.0	1.7	16	5.0	0.154
Nonarborescents (%)	1.1	0.53	4.0	2.2	0.095
Arborescents (%)	2.1	1.2	2.7	1.0	0.368
Woody vines (%)	2.3	1.2	2.2	1.8	0.746

[a] BA = basal area.

Table 4. Summary of regression analyses for burrow age–vegetation relations at active (n = 40) and abandoned (n = 45) gopher tortoise burrows within mature slash pine plantations in southcentral Alabama. Active burrows were created within the last 0.5–5.0 years, and abandoned burrows were abandoned within the last 1–4 years.

Burrow type	Vegetation variables	r^2	*P*-value
Active	Overstory		
	Total basal area (m²/ha)	0.19	0.007
	Pine basal area (m²/ha)	0.20	0.004
	Hardwood basal area (m²/ha)	0.07	0.095
	Tree density (no./ha)	0.14	0.018
	Ground cover		
	Total plant cover (%)	0.00	0.816
	Legume forbs (%)	0.01	0.510
	Nonlegume forbs (%)	0.02	0.458
	All forbs (%)	0.02	0.419
	Grasses (%)	0.00	0.987
	Nonarborescent woody plants (%)	0.07	0.096
	Arborescent woody plants (%)	0.06	0.660
	Species richness (no.)	0.00	0.785
Abandoned	Overstory		
	Total basal area (m²/ha)	0.00	0.802
	Pine basal area (m²/ha)	0.00	0.716
	Hardwood basal area (m²/ha)	0.02	0.379
	Tree density (no./ha)	0.00	0.717
	Ground cover		
	Total plant cover (%)	0.01	0.550
	Legume forbs (%)	0.00	0.992
	Nonlegume forbs (%)	0.00	0.970
	All forbs (%)	0.00	0.972
	Grasses (%)	0.01	0.443
	Nonarborescent woody plants (%)	0.02	0.389
	Arborescent woody plants (%)	0.02	0.620
	Species richness (no.)	0.00	0.910

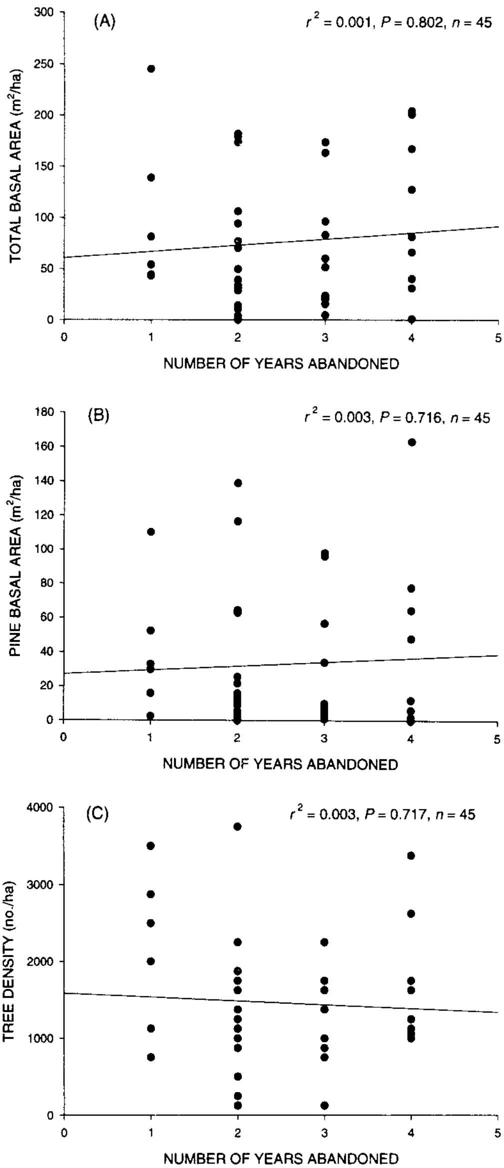

Fig. 2. Relation between overstory structure and age of abandoned gopher tortoise burrows on the Conecuh National Forest, Alabama. (A) total basal area, (B) pine basal area, and (C) tree density.

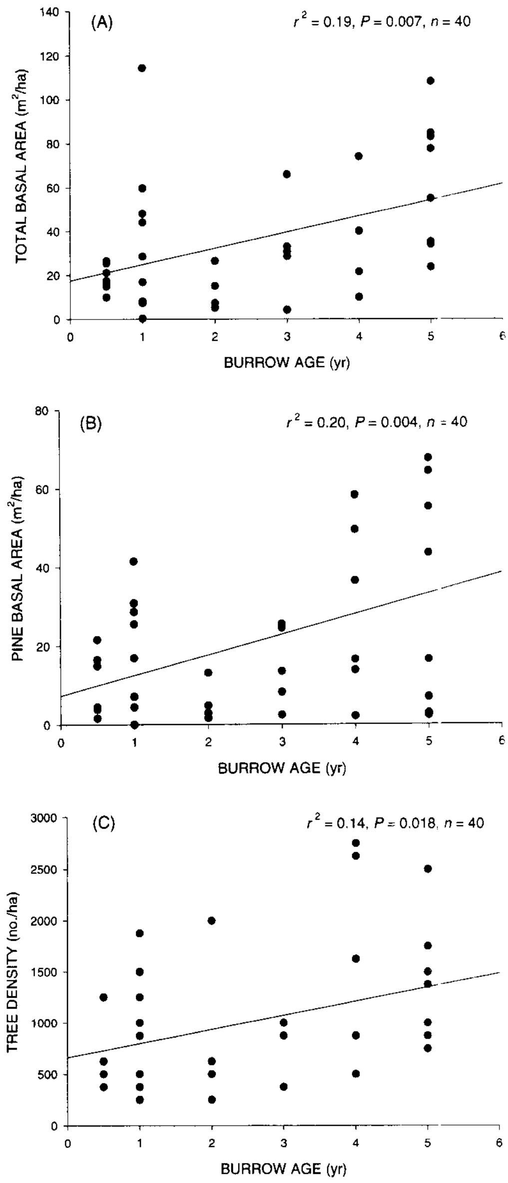

Fig. 3. Relation between overstory structure and age of active gopher tortoise burrows on the Conecuh National Forest, Alabama. (A) total basal area, (B) pine basal area, and (C) tree density.

The structure and composition of ground cover plants did not differ statistically between pairs of active and abandoned burrows (Table 3).

Burrow Age and Vegetation

There was no significant relation between number of years a burrow was abandoned (n = 45) and either overstory vegetation or ground cover vegetation (Table 4, Fig. 2). Vegetation at burrows abandoned early in the study did not change during the time since abandonment. In addition, there was no significant relation between age of active burrows (n = 40) and any component of the ground cover vegetation (Table 4). However, there were significant positive relations between age of active burrows and total BA, pine BA, and tree density (Table 4, Fig. 3).

Table 5. Estimated time (yr) for overstory vegetation to change from conditions observed at newly active gopher tortoise burrows to conditions at newly abandoned burrows on the Conecuh National Forest, Alabama. Mean values at burrows active for ≤1 year (n = 16) are shown under Active, and mean values at burrows abandoned for ≤2 years (n = 27) are shown under Abandoned. Regression equations were derived from data presented in Figure 3. Time until change (X) is derived by substituting values under Abandoned (Y) into the equation.

Vegetation variable	Active	Abandoned	Regression equation	Time until change
Total BA[a] (m^2/ha)	28.8	70.0	$Y = 17.5 + 7.39X$	7.0
Pine BA (m^2/ha)	14.6	30.5	$Y = 7.26 + 5.20X$	5.0
Tree density (no./ha)	797	1460	$Y = 661 + 138X$	6.0

[a] BA = Basal area.

From these regressions, we inferred that overstory density (i.e., canopy closure) increased rapidly with age of active burrows, but overstory density did not increase significantly with time after burrows were abandoned. Newly abandoned burrows had mean total basal area of 70 m^2/ha and mean tree density of 1,460 trees/ha. We estimated that overstory vegetation changed from conditions observed at newly created burrows to those at newly abandoned burrows in 5–7 years (Table 5). Therefore, burrows are only expected to be active for 5–7 years in mature pine plantations before they are abandoned.

DISCUSSION

In slash pine plantations of the CNF, active gopher tortoise burrows were located in areas with the most open canopy. Burrow abandonment was associated with successional changes in the structure and composition of overstory vegetation that resulted in canopy closure. Microhabitat at abandoned burrows was characterized by a dense midstory of young hardwood trees (e.g., *Quercus* spp., *Cornus* spp.) and shrubs (e.g., *Ilex* spp.) within mature stands of closely planted slash pine. Overstory density, as measured by tree basal area and tree density, was significantly greater at abandoned burrows and probably resulted in sufficient shade to contribute to abandonment. Gopher tortoises abandoned burrows about as rapidly as the canopy closed, with only 25% of active burrows still occupied by a gopher tortoise after 5 years.

Studies of demography and burrow dynamics in high-quality habitats suggest high burrow fidelity may have characterized gopher tortoise populations in ancestral longleaf pine forests (Diemer 1992, Guyer and Hermann 1997). Diemer (1992) found 92% of active burrows in a natural longleaf pine habitat in northern Florida were still occupied by a gopher tortoise after 4 years. In southwestern Georgia, gopher tortoises rarely created new burrows or emigrated from study areas in a natural longleaf pine habitat (Diemer 1992). However, in a slash pine plantation and adjacent roadside habitats in northern Florida, Diemer (1992) reported that only 27% of burrows remained active after 4 years. Our study provides further evidence that rates of burrow abandonment are much higher in pine plantations.

Gopher tortoise densities and movement patterns can be influenced by the abundance and quality of forage plants (Auffenberg and Iverson 1979, McRae et al. 1981, Auffenberg and Franz 1982). Therefore, changes in ground cover vegetation around gopher tortoise burrows may result in burrow abandonment in certain habitats. However, we believe ground cover vegetation was not the primary factor influencing burrow abandonment in our study. The results of our paired comparisons indicated a stronger association between overstory vegetation (i.e., canopy closure) and abandonment than for ground cover plants and abandonment. In addition, overall quality and quantity of ground cover vegetation throughout the CNF study sites, as judged by total plant cover and species richness, were uniformly low and were only slightly greater at active gopher tortoise burrows. Canopy closure in pine plantations inhibits sunlight penetration and may reduce herbaceous ground cover, especially grasses and perennial forbs (Clewell 1986). However, even in areas with relatively open canopy on the CNF, total plant cover and species richness remained low. Site preparation techniques used on the CNF in the 1970s likely destroyed or severely damaged rootstocks of native ground cover species such as wiregrass, preventing their regrowth following soil disturbance (Schultz and Wilhite 1974, Moore et al. 1982, Outcalt and Lewis 1988). As a result, herbaceous plant cover and species richness at random plots on the CNF were 2–

4 times lower than those reported from longleaf pine habitats with intact, native ground cover (Walker and Peet 1983, Clewell 1986, Kaczor and Hartnett 1990, Peet and Allard 1993). The paucity of both grasses (7% cover at random plots) and forbs (6% cover at random plots) on the CNF suggests gopher tortoises do not abandon burrows to seek areas with greater ground cover, because ground cover is equally low throughout the habitat.

Surveys on the CNF indicated some burrows became inactive for several weeks, months, or from 1 season to the next, but burrows were later reoccupied by the same or a different gopher tortoise. During our 5-year study, 19 of 93 burrows (20%) abandoned for 1 year or more were later reoccupied by a gopher tortoise. These movements and those among existing active burrows under favorable canopy conditions may have occurred in response to changes in forage, social interactions, or both. However, permanent abandonment seemed to occur in response to canopy closure making that burrow unsuitable for future gopher tortoise use. The burrow dynamics in this study suggested suitable microhabitat was limited and gopher tortoises abandoned burrows frequently in association with rapid successional changes. Diemer (1992) reported the same "continuous cycle of burrow creation and abandonment" in slash pine plantations in northern Florida.

Canopy closure may affect gopher tortoises in several ways. Excessive shading of a gopher tortoise burrow will restrict opportunities for basking or nesting. Smith (1992) reported that gopher tortoises basked 76% of the time while out of their burrows, a behavior necessary for maintaining optimal efficiency of physiological processes like digestion (Hutchison 1979). Douglass and Layne (1978) found that most gopher tortoises basked within 1 m of burrow entrances, and that most activity beyond the burrow mound (e.g., foraging, courtship) was preceded by variable periods of basking. They reported that heating rate of gopher tortoises was 3 times faster in direct sunlight than in shade. Basking at the burrow entrance, rather than some distance away, may help gopher tortoises avoid depredation.

In addition to thermoregulation sites, burrow mounds are also important nest sites and require nearly full sunlight for proper incubation (Hallinan 1923, Mount 1975, Landers et al. 1980). Landers et al. (1980) reported that 85% of nests in their southwestern Georgia study site were <1 m from the burrow entrance. Hence, canopy closure in pine plantations may force female gopher tortoises to move greater distances in search of nest sites with sufficient sunlight. Female gopher tortoises in pine plantations and dense scrub-oak stands in northern Florida moved to open roadsides and firebreaks to find suitable sunlit nest sites (Diemer 1986). Therefore, an increase in canopy cover that directly shades a burrow for most of the day may alter normal gopher tortoise activities sufficiently to cause burrow abandonment.

MANAGEMENT IMPLICATIONS

Low burrow fidelity in pine plantations may have important biological consequences that could affect gopher tortoise population recovery. Gopher tortoises expend valuable energy while searching for appropriate burrow sites and creating new burrows, therefore less energy may be available for growth and reproduction (Aresco 1998). Movements associated with locating a new burrow site may also increase risk of depredation, especially of juveniles whose shell elements are not yet fully ossified (Wilson et al. 1994). Poor habitat quality may force gopher tortoises to use available marginal habitat as long as it has an open canopy and sufficient forage (e.g., roadsides, agricultural fields). Movements associated with low burrow fidelity may scatter individuals, fragment populations, reduce the likelihood of successful reproduction, and increase mortality.

Hence, gopher tortoise populations should respond favorably to habitat management programs that reduce canopy cover and increase abundance and quality of forage plants (Landers and Speake 1980, Diemer 1986, Mushinsky and Gibson 1991). Improvements in forage vegetation and gopher tortoise burrow fidelity should increase recruitment and population recovery by producing faster-growing gopher tortoises that mature earlier (Mushinsky et al. 1994). Stand thinning to a minimum basal area of 30–40 m^2/ha and prescribed growing-season burns (every 1–3 yr) should be successful management techniques for improving gopher tortoise habitat in pine plantations. Growing-season burns suppress the growth of hardwood trees and increase the palatability and nutritional value of gopher tortoise forage plants (Komarek 1974, Waldrop et al. 1992). Frequent low-intensity ground fires also stimulate many native grasses and forbs to flower and produce seeds (Hartnett 1987, Platt et al. 1988). Fire-adapted ground cover vegetation in unaltered longleaf pine forests may help to carry ground fires, whereas the loss of native ground cover in pine plantations, especially wiregrass, may result in patchy, ineffective prescribed burns (Clewell 1989). Reestablishment of native ground cover on mechanically disturbed sites may require replanting or reseeding in addition to prescribed burns.

Clearly, with the extensive loss and fragmentation of the original longleaf pine habitat, pine plantations on national forests and private lands provide some of the largest available areas of remaining contiguous gopher tortoise habitat. The continued survival and future recovery of gopher tortoise populations should be accomplished by protecting and managing remaining longleaf pine habitat and restoring appropriate habitat conditions in pine plantations.

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