

## GROWTH OF THE TORTOISE *GOPHERUS POLYPHEMUS* IN SLASH PINE PLANTATIONS OF SOUTHCENTRAL ALABAMA

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**ABSTRACT:** We examined growth patterns of gopher tortoises in slash pine plantations using recapture data from a five-year period. Growth data were fitted to the von Bertalanffy and logistic asymptotic growth models. The von Bertalanffy model provided the best fit to the recapture data. Gopher tortoises grew more slowly than they did in any other published study and were estimated to require at least 20 years to attain sexual maturity. Intensive soil disturbance associated with site preparation and conversion to pine plantations in the 1970's destroyed much of the native ground cover. Therefore, slow growth, which resulted in delayed maturity, was attributed to poor forage quality of sparse ground cover vegetation, especially legume and nonlegume forbs. Our study provides evidence that anthropogenic activities associated with historic widespread conversion of longleaf pine habitats to pine plantations may continue to impact current gopher tortoise populations.

**Key words:** Testudines; Testudinidae; *Gopherus polyphemus*; Gopher tortoise; Growth; Habitat quality; Pine plantations; von Bertalanffy model

GOPHER tortoise populations have experienced a dramatic range-wide decline (an estimated 80% in the last 100 yr) as a result of habitat loss and degradation and human exploitation (Auffenberg and Franz, 1982; Diemer, 1986). Delayed sexual maturity of the gopher tortoise is a limiting factor to population growth and recovery (Iverson, 1980; Landers et al., 1982; Mushinsky et al., 1994). Time required to reach sexual maturity may be an especially critical variable for populations in decline because slow growth rates in some populations may extend the juvenile stage for several years, thus increasing exposure to depredation and reducing survival and recruitment (Auffenberg and Iverson, 1979; Butler and Sowell, 1996).

The gopher tortoise is an herbivore, and the amount of herbaceous ground cover is correlated with population densities, movement patterns, and growth rates (Auffenberg and Iverson, 1979; Landers et al., 1982; Mushinsky et al., 1994). The closed canopy in pine plantations has a negative effect on gopher tortoise populations by reducing or eliminating forage vegetation and basking/nest sites, and by altering tortoise movements and burrow

use (Aresco and Guyer, 1999; Diemer, 1992; Landers and Speake, 1980). Previous studies of the gopher tortoise in southwestern Georgia (Landers et al., 1982) and central Florida (Godley, 1989; Goin and Goff, 1941; Mushinsky et al., 1994) demonstrated that growth rates can vary due principally to variation in climate and habitat quality. Data from additional sites, especially from northern populations, are needed to clarify the effects of geographic location and land use history on growth of gopher tortoises.

In this study, we examined growth patterns of gopher tortoises located within pine plantations on the Conecuh National Forest in southcentral Alabama. Our specific objectives were to (1) describe gopher tortoise growth rates and estimate age at maturity in habitats heavily impacted by forestry operations and, (2) compare growth patterns of Conecuh tortoises to those published for gopher tortoises from other studies. In addition, we compared data describing forage quality at our study site to that published from a longleaf pine (*Pinus palustris*) sandhill habitat in central Florida that has been actively managed for gopher tortoises (Mushinsky et al., 1994).

### MATERIALS AND METHODS

#### Study Area

We conducted this study at six sites located within the Conecuh National Forest

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(CNF) in Covington County, southcentral Alabama. During the 1960's, these sites had scattered, large longleaf pines that were left standing to promote natural pine regeneration. Between 1970 and 1979, each site was clearcut, intensively prepared (raking, plowing, scoring the soil with heavy machinery), and replanted in closely spaced slash pine (*P. elliottii*) (J. R. Lint, CNF, personal communication). The U.S. Forest Service winter-burned these sites every 3–4 yr from 1985–1996. At the time of this study, these sites were dominated by mature stands of closely spaced slash pine and a dense midstory layer of shrubs (e.g., *Ilex vomitoria*) and scrub oaks (e.g., *Quercus incana*, *Q. margaretta*) (Aresco and Guyer, 1999). Ground cover vegetation was composed primarily of bluestem grasses (e.g., *Andropogon* spp.), low shrubs (e.g., *Ilex* spp., *Vaccinium* spp.), and forbs (e.g., composites) (Aresco and Guyer, 1999). Soils were deep sands predominantly of the Troup and Fuquay series.

#### *Tortoise Capture and Measurements*

A mark-recapture program was initiated at four study sites in 1991 and was expanded to include all six sites in 1992. We attempted to capture all resident gopher tortoises on each site annually. From June to September (1991–1996), adult and juvenile gopher tortoises were captured in live traps positioned against burrow entrances. Traps were shaded with burlap and checked twice daily. Gopher tortoises were marked (by notching the marginal scutes with a triangular file) and measured with vernier calipers [maximum straight-line carapace length (CL), maximum straight-line plastron length (PL), maximum width (MW), maximum height (MH), plastral concavity (PC), anal notch (AN), and anal width (AW)]. Measurements were recorded to the nearest 1.0 mm and followed McRae et al. (1981). Whole body mass of each gopher tortoise was recorded to the nearest 1.0 g with a digital top-loading balance. Our methods were approved by the Auburn University Institutional Animal Care and Use Committee (IACUC PRN 9612-R-0598).

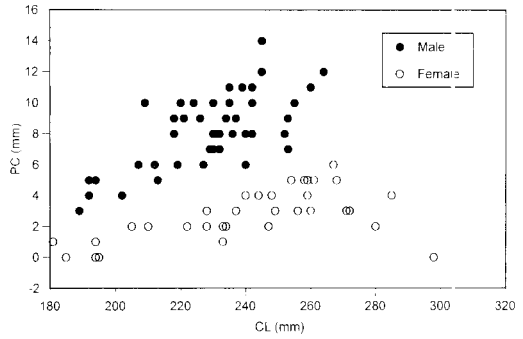


FIG. 1.—Plastral concavity in relation to carapace length of male ( $n = 53$ ) and female ( $n = 35$ ) gopher tortoises from southcentral Alabama.

We used depth, size, and shape of plastral concavity to determine the sex of adult gopher tortoises (McRae et al., 1981). Plastral concavity is the most pronounced sexually dimorphic character in gopher tortoises; males have relatively deeper plastral concavities than females (McRae et al., 1981; Mushinsky et al., 1994). We also observed that the plastral depression was deepest immediately anterior to the anal scutes in males, whereas it sloped more gradually along its length in females (McRae et al., 1981; Mushinsky et al., 1994).

A scatter plot of plastral concavity versus carapace length indicated two morphological groups that we interpreted to be males and females (Fig. 1). Except for one individual, all tortoises  $>230$  mm CL and classified as males had plastral concavities  $>6$  mm; all tortoises  $>230$  mm CL and classified as females had concavities 6 mm or less. Tortoises 180–230 mm CL with plastral concavities 3 mm or greater were classified as males; those with concavities  $<3$  mm were classified as females. In a few cases where plastral concavity did not conclusively classify sex, we used concavity shape and other dimorphic characters such as anal notch to classify sex (McRae et al., 1981). All tortoises  $<180$  mm CL were classified as nonadults. Seven tortoises originally classified as nonadults grew sufficiently during the study to classify their sex at a later capture (four females, three males).

Ages of gopher tortoises were deter-

mined by counting growth rings on the abdominal scute of the plastron (Landers et al., 1982). In our study population, we found that one growth ring was produced annually on gopher tortoises up to 15 yr old (Aresco and Guyer, 1998). Plastral wear and slow growth prevented accurate annuli counts on most gopher tortoises 15 yr or older. We were able to count 20 or more rings on 37 adult gopher tortoises, but these counts could serve only as a lower bound for age and these animals were recorded as >20.

### *Growth Models and Analysis*

We used the growth interval forms of the von Bertalanffy and logistic equations to model gopher tortoise growth because they require only data from recaptures and do not require a knowledge of age (Fabens, 1965; Frazer and Ehrhart, 1985; Frazer et al., 1990). Growth rates (mm/yr) for individual tortoises were calculated as the incremental change in carapace length (mm) divided by the time interval (yr) between captures. Body size was defined as carapace length at the midpoint of the growth interval. Growth models were generated for each sex, including data from nonadults of unknown sex. We included each tortoise only once in the analysis and used growth data from the first recapture interval (>0.7 yr) for each individual (87 growth intervals: 31 males, 23 females, 33 nonadults of unknown sex). The mean recapture interval was 1.3 yr ( $n = 87$ ,  $SD = 0.59$ ). Because each trapping period extended from June to September, there was no need to correct for seasonal variation in growth rates.

The von Bertalanffy growth interval equation that we used was:

$$L_2 = a - (a - L_1)e^{-rd} \quad (1)$$

and the logistic growth interval equation that we used was:

$$L_2 = aL_1/[L_1 + (a - L_1)e^{-rd}], \quad (2)$$

where  $L_1$  is length at first capture,  $L_2$  is length at recapture,  $d$  is time in years between capture and recapture,  $a$  is asymptotic size, and  $r$  is characteristic growth parameter (Fabens, 1965; Frazer and Ehr-

hart, 1985; Schoener and Schoener, 1978). We fitted our recapture data to each equation using nonlinear, least squares regression with the Marquardt algorithm in SAS PROC NLIN (SAS Institute, 1989). For each equation, two parameters were estimated: asymptotic carapace length ( $a$ ), and characteristic growth parameter ( $r$ ). Estimates of 95% "support plane" confidence intervals from the asymptotic standard deviations of each parameter estimate were used to evaluate statistical significance. Parameter estimates were considered significantly different ( $P < 0.05$ ) if the 95% confidence intervals did not overlap. When comparing growth models, the model with the lowest residual error mean square (REMS) (Schoener and Schoener, 1978) and more biologically appropriate asymptotic size estimate (Frazer et al., 1990) was considered the best fit to the recapture data.

### *Vegetation Sampling*

We sampled ground cover vegetation at active ( $n = 78$ ) and abandoned ( $n = 45$ ) tortoise burrows and random plots ( $n = 60$ ) as part of a separate study that described burrow abandonment by gopher tortoises in pine plantations (Aresco and Guyer, 1999). We included these data in this study to compare forage quality between the CNF and that reported from a sandhill habitat in central Florida where tortoise growth has also been studied (Kaczor and Hartnett, 1990; Mushinsky et al., 1994). Our sampling methods were similar to those described in Kaczor and Hartnett (1990) (see Aresco and Guyer, 1999, for a full description of methods). For collection of ground cover plant data, we sampled five 1-m<sup>2</sup> quadrats at each burrow and random location. Data from each quadrat consisted of the identity and percent cover of understory plant species, and we grouped these species into growth-form categories (e.g., forbs). We calculated mean percent cover for each growth-form category and total plant cover from the five quadrats at each sampling location. Means are reported in absolute cover rather than relative cover. Kaczor and Hartnett (1990) reported their data as relative cover, and

TABLE 1.—Comparison of von Bertalanffy and logistic growth interval models for males ( $n = 31$ ) and females ( $n = 23$ ) of *Gopherus polyphemus* from the Conecuh National Forest, southcentral Alabama. Model analyses for each sex also include 33 nonadults of unknown sex. Variable  $a$  is asymptotic carapace length (mm), variable  $r$  is characteristic growth rate, and REMS is residual error mean square. The 95% confidence intervals are shown in brackets and standard errors in parentheses.

Model	Asymptotic size ( $a$ )	Growth parameter ( $r$ )	REMS
von Bertalanffy			
Males	270.6 (11.72) [247.1–294.0]	0.067 (0.007) [0.054–0.081]	10.7
Females	322.6 (24.48) [273.5–371.7]	0.052 (0.007) [0.038–0.068]	13.8
Logistic			
Males	248.5 (4.38) [239.7–257.2]	0.175 (0.010) [0.155–0.196]	11.8
Females	277.9 (7.50) [262.9–293.0]	0.162 (0.011) [0.140–0.184]	16.3

we converted these values to absolute cover for comparative purposes in our discussion.

### RESULTS

Recapture data fit both the von Bertalanffy and logistic models relatively well. The von Bertalanffy model had a slightly lower REMS than the logistic model and, therefore, best described the growth pattern of gopher tortoises on the CNF (Ta-

ble 1). Our recapture data included a sufficient sample of young tortoises and large adult tortoises of both sexes (Table 2, Fig. 2), a prerequisite to generating reliable estimates of asymptotic size and characteristic growth parameter using growth mod-

TABLE 2.—Mean and range of carapace lengths (mm) attained by each age class of *Gopherus polyphemus* ( $n = 180$ ) on the Conecuh National Forest, southcentral Alabama. Standard errors are shown in parentheses. Age was determined using counts of plastral scute annuli.

Age	$n$	$x$	Range
hatchling	17	51 (0.5)	48–55
1	8	62 (2.2)	58–64
2	6	70 (3.2)	66–74
3	11	87 (5.8)	75–101
4	12	98 (10.3)	82–124
5	14	109 (13.7)	93–142
6	8	118 (18.8)	97–163
7	15	128 (11.8)	112–162
8	8	143 (24.5)	116–205
9	6	142 (16.1)	123–166
10	8	153 (10.8)	138–170
11	9	156 (17.5)	135–194
12	4	157 (8.7)	148–169
13	1	166 (—)	—
14	6	205 (20.5)	173–231
15	6	204 (22.0)	172–228
16	3	205 (16.0)	193–228
17	1	205 (—)	—
20+ (Females)	14	241 (19.7)	220–298
20+ (Males)	23	239 (10.8)	222–263

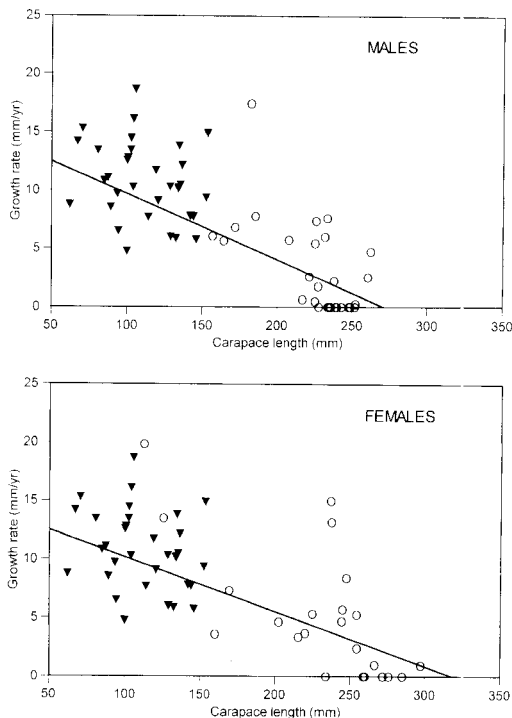


FIG. 2.—Mean annual growth rate plotted against carapace length of males and females of *Gopherus polyphemus* from the Conecuh National Forest, southcentral Alabama. Triangles indicate nonadults of unknown sex.

els (Frazer et al., 1990). The predicted asymptotic size should be slightly larger than the mean size of the largest adults in the population (Frazer et al., 1990). In males, the estimated asymptotic size generated by the von Bertalanffy model ( $a = 270.6$ ) was slightly higher than the mean size of the largest males captured ( $n = 5$ ,  $\bar{x} = 262$  mm CL,  $SE = 8.18$ ). The asymptotic size estimate for females ( $a = 322.6$ ) was greater than the mean size of the largest females captured ( $n = 5$ ,  $\bar{x} = 281$  mm CL,  $SE = 10.2$ ). Mean sizes of the largest gopher tortoises captured of both sexes were within the 95% confidence intervals of asymptotic sizes generated by the von Bertalanffy model. Therefore, we considered the estimates of asymptotic size to be biologically reasonable for our study population (Frazer et al., 1990).

During the 5-yr trapping period, we made 163 recaptures of 87 gopher tortoises. Gopher tortoises displayed a von Bertalanffy growth pattern of rapid juvenile growth, slowing at the onset of maturity, followed by periods of relatively slow growth or no growth by adults (Fig 2). The general pattern of annual growth of tortoises, separated into 4-yr age classes, was: ages 1–4, 12.6 mm/yr; ages 5–8, 11.4 mm/yr; ages 9–12, 7.4 mm/yr; ages 13–16, 8.1 mm/yr; and ages 17–20+, 2.9 mm/yr. Carapace length attained by individuals within each age class varied markedly, and there was a wide range of size overlap among age classes (Table 2).

#### DISCUSSION

Gopher tortoises attain sexual maturity at a minimum size rather than a specific age, and the time required to grow to that size varies among populations (Diemer and Moore, 1994; Mushinsky et al., 1994). Size at which average growth rates are lowest can predict size at sexual maturity in turtles as resources are directed away from growth and towards reproduction (Andrews, 1982; Bernardo, 1993; Kennett, 1996). In this study, we recorded zero growth for most males 230–240 mm CL ( $\bar{x} = 239.5$ ,  $SE = 6.88$ ,  $n = 13$ ) and most females as size approached 260 mm CL ( $\bar{x} = 264.3$ ,  $SE = 17.8$ ,  $n = 6$ ). These growth

patterns are consistent with sexual size dimorphism in gopher tortoises (McRae et al., 1981; Mushinsky et al., 1994). In southwest Georgia, Landers et al. (1982) used necropsy data and behavioral observations to estimate that males reached sexual maturity between 230 and 240 mm CL and females between 250 and 265 mm CL. Their population was less than 175 km directly east of the CNF and our estimated sizes at maturity are concordant with their findings. Based on counts of plastral scute annuli, all tortoises of both sexes on the CNF were at least 20 yr old as they reached their respective sizes at maturity (males:  $n = 17$ ,  $\bar{x} = 233$  mm CL,  $SE = 5.74$ ; females:  $n = 8$ ,  $\bar{x} = 254$ ,  $SE = 7.32$ ). Six males and six females that still had not attained their respective sizes at maturity were 20 yr old or greater. Therefore, we estimate that both male and female gopher tortoises probably require at least 20 yr to reach sexual maturity in the CNF.

On slash pine plantations in southcentral Alabama, gopher tortoise growth fit the von Bertalanffy model slightly better than the logistic model. On managed sites in central Florida, gopher tortoise growth fit the logistic model slightly better than the von Bertalanffy model as judged by REMS values (Mushinsky et al., 1994). In their study, gopher tortoises grew rapidly as juveniles and subadults, and attained a mean carapace length of 208 mm by age 10. In our study population, however, the most rapid growth occurred in the early juvenile stage and decreased sharply as gopher tortoises reached subadulthood (150 mm CL). At age 10, CNF gopher tortoises had attained a mean carapace length of only 153 mm CL. We believe that the quality and quantity of forage plants in pine plantations may not be sufficient to fuel a subadult growth spurt that would be required for gopher tortoises to grow according to a logistic pattern (with maximum growth rate at 63% of asymptotic size) (Andrews, 1982).

Comparative growth data from different habitats throughout the range of the gopher tortoise may elucidate the factors affecting variation in growth patterns. In southwestern Georgia, gopher tortoises up

to 10 yr of age grew 12 mm CL/yr in managed natural longleaf pine habitats and 16 mm CL/yr adjacent to agricultural fields compared to 10 mm CL/yr up to age 10 in our study (Landers et al., 1982). Gopher tortoises on actively-managed sandhill habitats in central Florida grew an average of 19 mm CL/yr up to age 10 (183–264 mm CL) (Mushinsky et al., 1994). In Mushinsky et al. (1994), the characteristic growth parameter ( $r$ ) estimated by the von Bertalanffy model was 0.12 for males and 0.10 for females. In our southcentral Alabama population, the characteristic growth parameters of both sexes (males,  $r = 0.07$ ; females,  $r = 0.05$ ) were significantly lower than those reported in the central Florida population of Mushinsky et al. (1994), as 95% confidence intervals did not overlap. Rapid growth and earlier maturity of gopher tortoises in central Florida may be partially attributed to warmer temperatures during the fall and winter months leading to year-round activity and a longer growing season. In southern Alabama and Georgia, gopher tortoises remain inactive in their burrows during most of the winter months and presumably growth slows or ceases during this period.

Variation in tortoise growth among populations may also reflect differences in habitat condition, specifically thermal characteristics and the abundance and quality of forage vegetation. Canopy closure in pine plantations may affect gopher tortoise growth in several ways. First, a dense overstory inhibits sunlight penetration and reduces forage vegetation (Means and Grow, 1985). On slash pine plantations in our study, tree density was much greater ( $\bar{x} = 1330$  trees/ha) compared to study sites used by Landers et al. (1982) in southwestern Georgia ( $\bar{x} = 570$  trees/ha) (Aresco, 1998; Garner and Landers, 1981). In addition, forestry practices and soil disturbance on the CNF, such as intensive mechanical site preparation in the 1970s, probably permanently destroyed the rootstocks of many native grasses (e.g., wiregrass) and herbaceous plants (Schultz and Wilhite, 1974). Although these anthropogenic activities occurred 20–25 yr ago, destruction of the ground cover vegetation

probably continues to affect the diet of the current tortoise population. Secondly, shading of a gopher tortoise burrow restricts opportunities for basking, a behavioral feature necessary for maintaining optimal physiological processes like digestion (Hutchison, 1979). Douglass and Layne (1978) found that most gopher tortoise activity beyond the burrow mound (e.g., foraging) was preceded by variable periods of basking. Therefore, we attribute slow growth of gopher tortoises on the CNF primarily to a poor thermal environment and sparse plant cover that resulted in poor forage quality.

Active habitat management by prescribed growing season burns (late May to mid-July) maintained open canopy conditions and a thick layer of herbaceous plant cover in central Florida (Kaczor and Hartnett, 1990; Mushinsky, 1992; Mushinsky et al., 1994). In contrast, land-use history on the CNF (e.g., intensive site-prep, closely-planted pines, sporadic winter burning) is reflected in the current condition of ground cover vegetation. Forage, as measured by percentage of ground cover plants at random plots, was much lower on the CNF, with only 24% plant cover compared to 119% in central Florida (Aresco and Guyer, 1999; Kaczor and Hartnett, 1990). Grasses (primarily *Andropogon* spp.) had the greatest percent cover of any plant category on the CNF, but represented only 11% of the ground cover vegetation at active burrows and 7.4% at random plots (Aresco and Guyer, 1999). In addition, legume forbs, primarily *Rhynchosia*, *Galactia*, and *Tephrosia*, represented only 2.1% of the ground cover vegetation at active tortoise burrows and only 1.2% at random plots (Aresco and Guyer, 1999). Mean forb cover (legumes and nonlegumes combined) was 7.9% at active burrows and 6.1% at random plots. In contrast, forage quality was much greater on the central Florida site. Absolute forb cover was 22% at recently abandoned burrows and 40% at random plots (Kaczor and Hartnett, 1990). While a large proportion of the gopher tortoise diet is low nutrient grasses, forbs (especially legumes) are selectively eaten when available and are an

important source of protein, phosphorus, and calcium (Garner and Landers, 1981; Macdonald and Mushinsky, 1988). Therefore, forbs may be especially important for growth of juvenile gopher tortoises, and this dietary component may be severely limited on the CNF.

In old-growth longleaf pine habitats, the size distribution of gopher tortoise populations was dominated by very large, presumably old, individuals, whereas the CNF population is characterized by many more small individuals than large adults (Guyer and Hermann, 1997; W. Michener, personal communication). Following a long history of intensive land use and overharvesting of gopher tortoises in southern Alabama, slow growth to maturity (>20 yr) probably has slowed the CNF tortoise population from recovering to a size distribution and density that was typical of populations in their ancestral habitat (Guyer and Hermann, 1997). Studies of gopher tortoise growth in high quality habitats suggest that rapid growth and earlier ages at maturity were characteristic of gopher tortoises prior to human-caused habitat alteration (Mushinsky et al., 1994). Habitat management techniques such as stand thinning, prescribed early summer burning, and reestablishing native ground cover should increase the chance of gopher tortoise population recovery in pine plantations by improving forage quality and thermal characteristics, thus producing faster-growing tortoises that mature sooner.

Our study provides evidence that anthropogenic activities associated with widespread conversion of longleaf pine habitats to pine plantations on national forests and private lands in the 1960's and 1970's may continue to impact current gopher tortoise populations. Although gopher tortoise populations were not completely extirpated from many of these degraded lands, slow growth and late maturity may contribute to long-term declines. Additional studies throughout the range of the gopher tortoise are needed to help clarify the effects of habitat condition, forage quality, and climate on growth patterns and age at maturity.

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