

Gopher Tortoise Response to Large-scale Clearcutting in Northern Florida¹

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Abstract: A previously studied (1981–1987) gopher tortoise (*Gopherus polyphemus*) population in northern Florida was surveyed during May–June 1992 to determine tortoise response to large-scale timber removal (1988). Two of 3 burrow concentrations were in or near ecotones between the clearcut and older pine stands. Eighteen of 23 (78%) recaptured tortoises were found in the same general location after clearcutting as before. One female had moved 1.3 km from her previous capture location. Only 13% of all previously-marked tortoises were recaptured in 1992. Size and sex class distributions were not different before and after clearcutting. Mean clutch size of gopher tortoises following clearcutting was larger, growth rate (carapace length) was faster, and size-related gain in mass was greater than for tortoises prior to clearcutting.

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Certain silvicultural practices may adversely affect reproduction, growth, and survival of gopher tortoises (Landers and Garner 1981; Lohoefer and Lohmeier 1981, 1984; Auffenberg and Franz 1982; Lohoefer 1982; Wright 1982; Diemer 1986). Auffenberg and Franz (1982) identified clearcutting and associated piling of debris as sources of mortality for resident tortoises. Conversely, Campbell and Christman (1982) reported that clearcutting and even-age management, at least in mature sand pine (*Pinus clausa*) scrub, may mimic the natural situation of infrequent crown fires and, thereby, provide the variety of successional stages necessary to maintain the native herpetofauna.

Determining how nongame wildlife may respond to clearcutting and other silvicultural practices was identified as a priority by the Florida Game and Fresh Water Fish Commission's wildlife research ranking process. Moreover, requests from state

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and federal agencies for information regarding gopher tortoise management in pine plantations are increasing. We assess changes in demography, fecundity, and body growth in a tortoise population following large-scale clearcutting.

Appreciation is extended to Georgia-Pacific, on whose property this study was conducted. Field assistance was provided by R. Belden, D. Berish, R. Berish, S. Berish, J. Hamblen, E. Knizley, and R. Ramsey, and J. Hamblen assisted in data analysis.

Methods

The approximately 65-ha study site was located in Alachua County, Florida, on Lochloosa Wildlife Management Area (WMA), 20 km southeast of Gainesville. Soil types ranged from moderately well-drained to poorly-drained. The most recent prescribed burn occurred in 1982, and the area was grazed by cattle. The 33-year-old slash pine (*P. elliottii*) plantation was cleared in 1988. Debris was piled into long, parallel rows (windrows), and slash pine seedlings were planted on mechanically-prepared beds between them. Other vegetation in the clearcut included scattered live oaks (*Quercus virginiana*) and cabbage palms (*Sabal palmetto*), winged sumac (*Rhus copalina*), blackberries (*Rubus spp.*), blueberries (*Vaccinium spp.*), milk pea (*Galactia elliottii*), and dog fennel (*Eupatorium capillifolium*). The roadsides and a jeep trail were predominantly vegetated with bahia grass (*Paspalum notatum*), and the windrows were covered with muscadine (*Vitis rotundifolia*). The northwest corner and southwest edge of the study site were clearcut in 1984. In 1992, the northwest corner contained sand live oak (*Q. geminata*), saw palmetto (*Serenoa repens*), taller slash pines, and a more open understory than the area cut in 1988. The southwest edge was predominantly covered by thickly planted pines in 1992.

The demography of a gopher tortoise population on Lochloosa WMA was studied from 1981 to 1987 (Diemer 1992a); movements data were gathered during a 2-year radiotelemetry study (1985–1987; Diemer 1992b). The population was originally distributed along a grassy roadside and in a mature pine plantation. Concurrent forestry operations on parts of the study area influenced tortoise movements, burrow placement, and locations of nesting sites (Diemer 1992a,b).

Approximately 60 ha (ca. 5 ha were wetlands) of the site were surveyed for gopher tortoise burrows from mid-March to early May 1992. Initial transects were conducted on both sides of each windrow, with 1–3 transects between windrows. After concentrations of burrows were identified, serpentine transects were conducted across planting beds and/or along each planting bed to search for burrows of juveniles. Burrows were flagged, numbered, and classified as active (fresh tortoise tracks or plastral scrapes), possibly active (tortoise sign not appearing fresh), or inactive (open but with no discernible tortoise sign). Abandoned burrows (collapsed or filled with debris) were noted and re-checked for activity but not flagged or numbered.

Gopher tortoises were captured in 84 pitfall traps set on 8 May 1992 and 20 additional traps set later in May and June. The traps (19-liter buckets for adults, 8-

and 11-liter buckets for subadults, and 4-liter buckets or coffee cans for juveniles) were sunk directly in front of the burrow openings and covered with brown paper and sand. Holes were drilled in the traps for drainage. Traps were monitored daily for 28–33 days. Tortoises walking or foraging near roads or jeep trails were opportunistically captured. Carapace (CL) and plastron length, tortoise number (if previously marked), mass (M), age (number of plastral rings), sex, and scutal anomalies were recorded. Unmarked tortoises were uniquely marked by drilling small holes in the marginal scutes (Cagle 1939). Maturity and sex were determined from shell morphology (McRae et al. 1981a) or presence of eggs. The distinction between juveniles (tortoises <130 mm CL) and subadults (immature tortoises ≥130 mm CL) was subjectively based on shell compressibility and coloration (Landers et al. 1982). Female tortoises were removed, radiographed to determine clutch size (Gibbons and Greene 1979), and returned to their burrows.

We compared mean clutch size of individuals captured before and during 1992. For tortoises captured >1 time prior to 1992, average clutch size over all captures in the period was obtained. Analysis of covariance was used with (average) CL as the covariate to assure that sample differences in tortoise size would not affect comparisons of average clutch size. Unless indicated otherwise, all reported test statistics were compared to critical values from a *t*-distribution.

We investigated whether CL growth by age and growth by size differed between pre-clearcut and post-clearcut treatment groups. For analysis of growth by age, we performed 2-way analysis of variance of log CL (transformed for symmetry of distribution and for variance stability) with respect to plastral ring count and treatment group. We assumed that age and plastral ring count were linearly related and that treatment group did not affect this relationship. By selecting for analysis only tortoises with 1–7 plastral rings, we hoped to minimize introduction of bias should this assumption fail. We eliminated effects of non-growth periods of the year by selecting spring (April–June) captures. We assured independence of observations by using only the last capture occasion of each tortoise caught >1 time and assigning the tortoise to the treatment group corresponding to its time of last capture (before or during 1992). Because gender of tortoises with <8 plastral rings was not readily determined, we ignored effects of sex in this analysis.

We also studied CL growth by size to circumvent difficulties in satisfying the age-plastral rings assumption above. We fit nonlinear Richards curves (Richards 1959) to growth interval data derived from tortoises recaptured prior to 1992 and during 1992, and we compared model parameters related to growth rate for the 2 groups. We followed the approach of Brisbin et al. (1986) and reparameterized White and Brisbin's (1980) Richards model (model PDD) into the form:

$$(LS_{i+1} - LS_i)/d = 2(m + 1)(S_{\infty}^{1-m} \cdot S_i^{m-1} - 1)/[T(1 - m)] + \epsilon_i,$$

where LS_i is log CL at capture occasion i , d is time (years) between captures, S_i is average CL at times i and $i+1$ (McCallum and Dixon 1990), and ϵ_i is prediction error for growth rate. The model parameters m , S_{∞} , and T describe curve shape, adult size, and time required to reach adult size. Again, non-spring captures were

excluded. Pre-clearcut values of $(LS_{i+1} - LS_i)/d$ and S_i were obtained for captures farthest apart in time for tortoises caught in >1 year during 1981–1987. Post-clearcut values were calculated for the latest capture occurring prior to 1992 and for the 1992 capture for tortoises caught in both periods. A tortoise caught in >1 year prior to 1992 and again in 1992 contributed data to both treatment groups, but we assumed that these data constituted independent replicates as White and Brisbin (1980) implied. We ignored the effect of gender on growth curves for 3 reasons: (1) we believed that gender effects were independent of treatment effects, (2) the relatively smaller tortoises in the pre-clearcut group could be assigned to gender less often than those in the other group, and (3) for tortoises that could be sexed, sex composition was similar in both treatment groups, thus growth rate differences between treatment groups would not be a function of group differences in sex ratios.

Our approach in the comparison of nonlinear growth curves between treatment groups was to determine whether a single growth model fit pooled data about as well as models fit separately to groups of data, and if not, to decide whether the lack of fit was caused entirely or in part by a group difference in the estimate of T . We used model reduction procedures (Maehr and Moore 1992) to test whether the groups of data required models with completely different sets of parameter estimates or whether some pooling of parameters was possible. The best model was that which performed the most pooling of parameters but still provided a reasonable fit to the data, and we selected it by the AIC criterion (Akaike 1973, Maehr and Moore 1992). We used an iterative direct search procedure (option SIMPLEX) in the NONLIN procedure of SYSTAT (Wilkinson 1990) to fit models.

We investigated whether treatment group influenced body mass allometrics of gopher tortoises. We assigned the last spring season capture that yielded CL and M measurements for each tortoise to a treatment group corresponding to the year of capture (prior to 1992, during 1992). Log M was regressed on log CL in treatment \times gender (male, female, undetermined) group combinations. We used AIC to determine whether intercept and slope parameters from the regressions could be pooled over treatment or gender effects, producing a simpler model that fit the data about as well as the separate-groups model.

Results

Gopher tortoise burrows were concentrated in 3 areas of the study site. Two of the 3 clusters were associated with ecotones between the 1984 clearcuts and the 1988 clearcut; minimum distance between burrow concentrations was 250–500 m. Sixty-five gopher tortoises were captured during May–June 1992. Of 58 tortoises captured on the clearcut study site, 81% were located in or near ecotones between the 1988 and 1984 clearcuts. Four tortoises had burrowed into windrows from the 1988 clearcut, and several other tortoises were associated with windrows in older pine stands. Juveniles were frequently captured in burrows located on planting beds.

Twenty-four (37%) tortoises had been previously marked. Twenty-three marked tortoises were from the original study area; 1 female was opportunistically captured in an off-site area in 1984 and 1992. Eighteen (78%) of the 23 marked tortoises from the original study site were captured in the same area before and after clearcutting. Three others (formerly juveniles or subadults, now mature or nearly mature) had moved 150–400 m within the study site. A young male (originally marked as a juvenile) had moved 740 m from a burrow near the northwestern 1984 clearcut to several burrows in the southwestern 1984 clearcut. A previously-marked female was captured off-site in 1992 as she foraged along a grassy roadside near her burrow but approximately 1.3 km from her 1986 capture location; her current and previous locations were connected by a jeep trail.

The overall recapture rate was low; only 13% of 173 marked tortoises (1981–1987) were recaptured. Recapture rates by size and sex were 10% for formerly immature tortoises, 14% for adult males, and 25% for adult females.

Mean size and sex class distribution of gopher tortoises captured during 1982–1986 on the study site was not different from that observed in 1992 ($X^2 = 2.29$, $df = 3$, $P = 0.514$) (Table 1). Female to male sex ratio, which varied annually from 1:1 in 1982 to 1:2 in 1986, was 1:0.9 in 1992. Size class (as defined by Alford 1980) histograms of CL were bimodal for both tortoise groups (Fig. 1). Peaks occurred in the 8.4–10.2 cm and 24.6–26.4 cm size classes in 1992. Corresponding peaks in the composite 1982–1986 histogram were one size class lower than those for 1992.

Means of average clutch size were 7.0 ($N = 14$) for females captured in 1992 and 5.9 ($N = 26$) for the 1982–1986 sample. The CL-adjusted mean clutch size of the post-clearcut sample (6.9) was greater than that of the pre-clearcut sample (6.0; $P = 0.030$, $df = 37$).

Post-clearcut gopher tortoises were 19% larger in CL, on average, than pre-clearcut tortoises with the same plastral ring count ($P < 0.001$, $df = 88$, Table 2). The best-fitting (as determined by AIC) Richards models were distinguished from the worst-fitting models on the basis of whether parameter T was allowed to differ between treatment groups. In the former models, tortoises from the post-clearcut

Table 1. Comparison of size and sex class distributions of gopher tortoises captured in 1992 and in 1982–1986 on Lochloosa WMA, Florida, study site.

	1992	1982–1986	
	No. captured	\bar{x} No. captured/year	Range
Juveniles	18	25	20–36
Subadults	12	9	5–13
Adult males	13	15	9–20
Adult females	15	11	9–15
Total captured	58	60	52–79

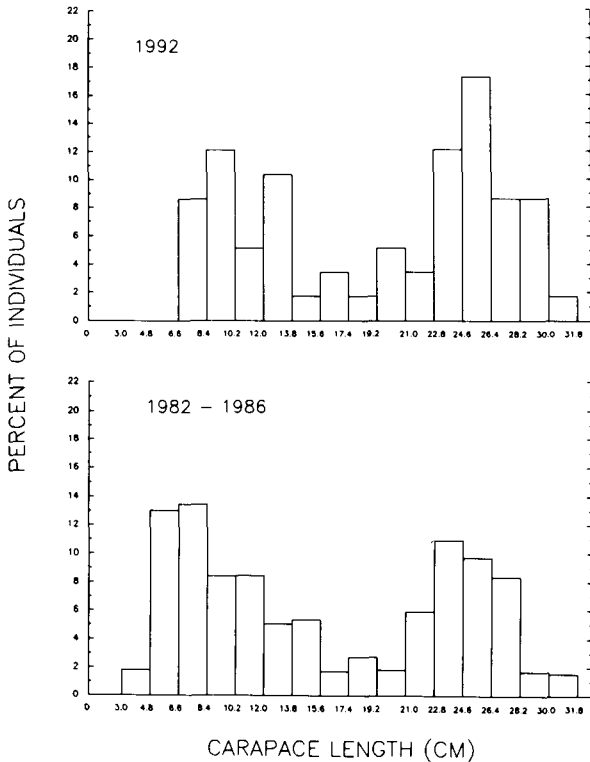


Figure 1. Size class distribution of gopher tortoises captured in 1992 on Lochloosa WMA, Florida, compared with average annual size class distributions, 1982-1986.

sample grew to adult size sooner than did tortoises sampled before the clearcut ($P \leq 0.007$, $df \geq 83$). In the simplest of these models, average adult size ($P = 0.444$, $df = 84$) and growth curve inflection point ($P = 0.109$, $df = 84$) did not differ between treatment groups, and the estimated time difference in attaining adult size was 13.7 years ($P < 0.001$, $df = 85$).

Table 2. Average gopher tortoise carapace length (CL, mm) at ages 1-7 yr (indicated by plastral annuli) before and after clearcutting on Lochloosa WMA, Florida.

No. annuli	Pre-cut			Post-cut		
	\bar{x} CL	SD	<i>N</i>	\bar{x} CL	SD	<i>N</i>
1	65.93	8.71	15	79.50	6.06	6
2	81.45	6.28	11	105.14	16.33	7
3	101.00	14.01	14	120.50	24.25	6
4	124.83	9.91	6	111.00	32.53	2
5	126.14	11.25	7	163.00	29.70	2
6	155.00	22.55	6	180.50	61.52	2
7	157.75	18.87	4	202.67	41.53	3

The best-fitting allometric model as indicated by AIC allowed the proportionate rate of mass growth to differ between treatment groups ($P = 0.050$, $df = 193$). The expected gain in mass with a 10% increase in CL was 30.7% in pre-clearcut tortoises and 31.5% in post-clearcut tortoises, a 2.6% difference.

Discussion

The study site was a mosaic of moderately well-drained and poorly-drained soils. Terrain that sloped toward the scattered wetlands was predominantly covered by hydrophilic vegetation (e.g., *Hypericum spp.*, *Polygala spp.*) and generally did not contain tortoise burrows. The 1992 burrow concentrations were associated with better-drained soils, with ecotones between the 8-year-old and 4-year-old pine stands (2 of 3 areas), and with general tortoise locations before the 1988 clearcut. The majority of gopher tortoises (65%) was captured in the area that had the longest ecotone on the largest block of moderately well-drained soil.

Only 13% of gopher tortoises marked 1981–1987 were recaptured in 1992. Recapture rate during 1981–1987 declined as the interval between recaptures increased, with 37%–56% of marked tortoises recaptured after 1 year, 20%–36% after 2 years, 11%–26% after 3 years, and 9% after 4–5 years (J. E. Diemer, Fla. Game and Fresh Water Fish Comm., unpubl. data). Length of the recapture interval (5–10.5 years) undoubtedly contributed to the low recapture rate in 1992. After the 1988 clearcut, tortoises that had previously concentrated along the narrow roadstrip to find suitable forage and open nesting sites were no longer constrained by the inadequate or marginal habitat of the mature plantation. The more homogeneous, open habitat with abundant forage facilitated dispersal. Although relatively few marked tortoises were recaptured in 1992, annual numbers of captured tortoises and population structures were not different before and after clearcutting; unmarked tortoises replaced uncaptured marked tortoises. Reproduction, immigration, and study site expansion accounted for the prevalence of unmarked tortoises. Subadults, particularly males, may disperse from their natal colony before reaching maturity (Auffenberg and Iverson 1979, McRae et al. 1981*b*, Diemer 1992*b*). Thus, ratios of marked to unmarked tortoises can be influenced by immigration and emigration of immatures, long-distance movements by some adults (McRae et al. 1981*b*, Diemer 1992*a*), and dispersal prompted by habitat modification or plant succession.

Gopher tortoises are able to dig out following certain types of site preparation of sandy soils (Landers and Buckner 1981, Diemer and Moler 1982, Diemer 1992*b*). Thus, it is unlikely that many tortoises were entombed on this site. Exceptions may have occurred if windrow debris was piled directly over burrow openings.

Individual gopher tortoises responded favorably to the 1988 clearcutting operation. Mean clutch size, growth rate, and proportionate rate of mass gain all increased after the clearcut. Although the data do not document a cause for these increases, a logical explanation is the observed (but not quantified) increase in and

diversity of tortoise food items, notably grasses (Poaceae), legumes (Fabaceae), and composites (Asteraceae). Previous studies in southwest Georgia and central Florida indicated that these plant taxa were major gopher tortoise foods (Garner and Landers 1981, Macdonald and Mushinsky 1988). Although additional data regarding tortoise nutrition in various habitats and plant successional stages are needed, Garner and Landers (1981) reported higher mineral content in vegetation on ruderal sites than on natural sand ridges.

Gopher tortoise preference for early successional stages with grassy ground cover and open canopies has been previously documented (Landers and Buckner 1981, Auffenberg and Franz 1982, Campbell and Christman 1982). Campbell and Christman (1982) found that tortoises were rare in mature sand pine stands but were associated with ecotones, clearcuts, and young stands. Landers and Buckner (1981) cited tortoise use of seedling and pole stage slash pine plantations on sandhills but found that tortoises were forced out of thick sapling stages. As the pines mature on Lochloosa WMA, tortoise habitat will deteriorate unless thinning or prescribed burning is implemented. Tortoises might also benefit from smaller clearcuts with increased ecotones between young and older stands.

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