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Reproductive Biology and Demography of Gopher Tortoises (*Gopherus polyphemus*) from the Western Portion of their Range

KELLEY R. SMITH[1,2], JANIE A. HURLEY[1,3], AND RICHARD A. SEIGEL[1]

[1]*Department of Biological Sciences, Southeastern Louisiana University, Hammond, Louisiana 70402-0736 USA;* [2]*Present Address: Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83201 USA [E-mail: smitkell@isu.edu];* [3]*Present Address: 6323 Deloache Avenue, Dallas, Texas 75225 USA*

The gopher tortoise (*Gopherus polyphemus*) was once widespread and abundant in the southeastern USA. However, recent data indicate that the species is being extirpated rapidly, mainly due to habitat destruction, human predation, and lack of recruitment (Auffenberg and Franz, 1982; Diemer, 1986; Diemer et al., 1989; Ernst et al., 1994; Diemer and Moore, 1994). Populations in the western portion of the range (Alabama, Mississippi, and Louisiana) have declined to the point where they have been listed as Threatened under the Endangered Species Act (U.S. Fish and Wildlife Service, 1990). However, most ecological data on *G. polyphemus* are based on populations from Florida and Georgia (e.g., McRae et al., 1981a,b; Auffenberg and Franz, 1982; Landers et al, 1982; Diemer et al., 1989; Smith, 1995). Field data from the western populations are almost completely absent, with the exception of two unpublished reports from Mississippi (Tuma, 1996) and Alabama (Marshall, 1987).

The need for more complete data from the western portion of the range is heightened by the apparent differences in habitat utilization between eastern and western populations. In Georgia and Florida, tortoise habitat largely consists of coastal dunes or xeric uplands, i.e., mainly sandy, well-drained soils dominated by wiregrass (*Aristida stricta*) and longleaf pine-turkey oak (*Quercus laevis*) or scrub communities (Landers et al., 1980; Diemer, 1986). Conversely, most tortoise habitat in Mississippi and Louisiana consists of soils with a low sand content and a more substantial clay component, and plant communities also differ from eastern populations (Wahlenberg, 1946). In Mississippi and Louisiana, there is virtually no upland wiregrass, and the predominant trees are typically loblolly pine (*Pinus taeda*) and slash pine (*P. elliotii*) planted for commercial pine production in place of the original longleaf pine (*P. palustris*) (Wahlenberg, 1946; Ware et al., 1993).

Increasing destruction and loss of habitat in response to human population growth is resulting in rapid declines of tortoise populations in Florida (Diemer, 1986). In addition, increased mortality of tortoises throughout the range due to the recently identified Upper Respiratory Tract Disease

Brown et al., 1994), have led to increased urgency to conserve this species in other parts of its range. Published studies addressing the reproductive biology of *G. polyphemus* have been performed in northern Florida (Iverson, 1980; Butler and Hull, 1996), southwestern Georgia (Landers et al., 1980), and north-central Florida (Diemer and Moore, 1994; Smith, 1995). Despite the threatened status of the gopher tortoise in the western portion of its range, there have been no comparative published studies of the reproductive biology of those populations, and the effects of different timber management and harvesting techniques on tortoise populations are largely unknown. A better understanding of reproductive variation in *G. polyphemus* populations, due to geographic and habitat quality differences, is necessary for successful conservation of this species (Germano and Bury, 1994).

The objectives of our study were to: 1) determine fecundity patterns; 2) delineate seasonal periods of nesting activity; 3) compare components of reproduction from a population located on a site managed for longleaf pine restoration with data from a population located on a site managed for commercial timber production; and 4) compare components of reproduction in the western portion of the range (Mississippi and Louisiana) with available data from the eastern portion of the range (Georgia and Florida).

Materials and Methods. — We collected data at two sites during our study: the Ben's Creek Wildlife Management Area in Washington Parish, Louisiana (30°49'N, 89°55'W) and the Marion County Wildlife Management Area in Marion County, Mississippi (31°11'N, 89°44'W) located about 80 km north of Ben's Creek WMA. Data were collected at the Ben's Creek WMA from April to August during 1991-93. The site is a 5607 ha slash pine (*P. ellioti*) and loblolly pine (*P. taeda*) forest that was privately owned at the time this study was conducted and is currently leased to the Louisiana Department of Wildlife and Fisheries. The area is managed for commercial pine tree production and hunting. Timber is harvested by clearcutting same-aged stands at 10–20 yr intervals. Ben's Creek WMA is burned occasionally, resulting in little understory growth in older same-aged stands of closely spaced trees. A majority of tortoise burrows on this site occur along power line rights-of-way (which are mowed several times each year), and along roadsides.

We collected data from April to August during 1994–95 on Marion County WMA. The site is a 2914 ha forest managed for pine tree production and recreational usage as well as longleaf pine (*P. palustris*) restoration. Prescribed burns are conducted at two to four year intervals. Small (< 1 acre) foodplots (areas cleared, planted, and maintained with vegetation for game species foraging), are maintained throughout the area. Timber is harvested by selective cutting. Tortoise burrows occur throughout the site in forested areas with open canopy cover.

Tortoises were captured manually or in 30.5 x 30.5 x 122 cm Havahart one-door live animal traps placed directly in front of burrow openings. Although both capture methods were used at each site, a majority of tortoises at Ben's Creek WMA were captured by trapping, whereas most tortoises at Marion County WMA were captured manually while road cruising.

Captured tortoises were given a unique mark by drilling holes in the marginal scutes (Ernst et al., 1974). We measured the carapace and plastron length of all tortoises to the nearest 0.1 cm with a tree caliper and recorded body mass to the nearest 10 g with a Pesola scale (Ben' s Creek WMA) or to the nearest 0.1 g with a Fisher Scientific XT Top Loading Balance (Marion County WMA). Sex was determined in adult tortoises by the degree of plastron concavity (McRae et al., 1981b), a sexually dimorphic trait that was well developed in these populations (i.e., no tortoise with a deep plastron concavity was ever determined to have eggs and all tortoises with eggs lacked a concavity). Tortoises were X-rayed at a local veterinarian's office to determine reproductive condition and clutch size, using the technique described by Gibbons and Greene (1979). All tortoises were released at the point of capture within 48 hrs.

Statistical analysis was conducted with StatView 512+ (Abacus, Inc.), and SYSTAT (Systat, 1992). All means are followed by one standard deviation. The alpha level was set at 0.05.

Results. — We X-rayed 44 females from Ben's Creek WMA in 1991–93, of which 22 had eggs (50%). The percentage of females with eggs varied seasonally, reaching 65% in late May to early June and declining to 20% by late June (Fig. 1).

At Marion County WMA, we X-rayed 102 females in 1994–95, of which 36 had eggs (35%). The percent of females with eggs also varied seasonally, reaching a maximum of 80% in early to mid-May for both years of the study, and declining to about 0% by mid-June (Fig. 1). The percent of females with eggs during the peak reproductive season (7 May – 5 June) did not differ significantly between years (1994 = 68.6%, 1995 = 48%; $\chi^2 = 2.57$, df = 1, $p = 0.109$).

Gravid females were first seen at Ben's Creek on 4 May and at Marion County on 21 April. The last gravid females were recorded at Ben's Creek on 30 June and at Marion County on 27 June.

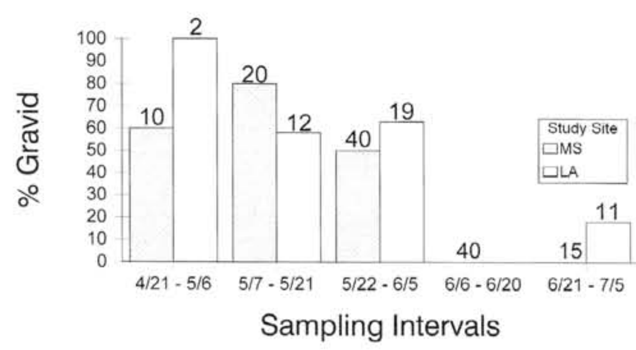

Figure 1. Comparison of seasonal variation in percent females with eggs (gravid) for Ben's Creek WMA (LA, open bars) and Marion County WMA (MS, hatched bars). Data for Ben's Creek WMA are combined for 1992 and 1993 and data for Marion County WMA are combined for 1994 and 1995. Numbers above bars refer to sample sizes.

We had a limited number of recaptured females to estimate reproductive frequency for each population. At Ben's Creek WMA, 11 gravid tortoises were examined in 1992, 5 of which were also examined in 1993; 4 of these (80%) were gravid in both years. Of the 11 non-gravid tortoises examined in 1992, 5 were recaptured in 1993, and 4 of those were gravid. At Marion County WMA, 10 females were examined during the peak reproductive season in both 1994 and 1995. Of these individuals, 3 were gravid in both years, 3 were gravid in 1994 only, 2 were gravid in 1995 only, and 2 were not gravid in either year (Table 1). Although we X-rayed 17 individual females two or more times within a single year at Marion County (at intervals of 10 to 30 days), no female was found to be gravid more than once annually.

The mean clutch size from Ben's Creek WMA population was 5.5 ± 1.17 (range = 4–8, $n = 19$) and there was no significant difference between years (ANCOVA, $F = 0.534$, $df = 1, 16$, $p = 0.475$). The mean carapace length of the gravid females was 27.5 ± 1.31 cm (range = 25.7–31.0 cm, $n = 19$) and there was no significant difference between years (ANOVA, $F = 0.007$, $df = 1, 17$, $p = 0.94$). There was a significant relationship between carapace length and clutch size, but the explanatory power of the regression was relatively low ($F = 11.7$, $df = 1, 17$, $p = 0.003$, $r^2 = 0.408$). The regression equation for clutch size (x) vs. carapace length (y) ($x = 10.197 + 0.569y$) predicted an increase of about 1.1 eggs for each 2 cm increase in female carapace length.

The mean clutch size from the Marion County WMA population was 5.6 ± 1.42 (range = 3–9, $n = 36$) and there was no significant difference between years (ANCOVA, $F = 0.01$, $df = 1, 33$, $p = 0.932$). The mean carapace length of the gravid females was 27.8 ± 1.21 cm (range = 25.0–30.4 cm, $n = 36$), and there was no significant difference between years (ANOVA, $F = 1.24$, $df = 1, 34$, $p = 0.27$). There was a significant relationship between carapace length and clutch size, but the explanatory power of the regression was lower than at Ben's Creek WMA ($F = 10.6$, $df = 1, 34$, $p = 0.003$, $r^2 = 0.237$). The regression equation for clutch size (x) vs. carapace length (y) ($x = 10.234 + 0.569y$) also predicted an increase of about 1.1 eggs for each 2 cm increase in female carapace length.

Because clutch size did not differ between years for either study site, we pooled data between years to test for spatial differences in clutch size. We found no significant difference in mean clutch size between the two study populations (ANCOVA, $F = 0.01$, $df = 1, 52$, $p = 0.919$), nor was there a significant difference in mean female carapace length between the sites (ANOVA, $F = 0.716$, $df = 1, 53$, $p = 0.401$).

Of 88 tortoises captured at the Ben's Creek WMA study site from 1991–93, 41 were classified as adult females, 46 adult males, and 1 subadult. This population did not differ significantly from a 1:1 sex ratio ($\chi^2 = 0.28$, $df = 1$, $p > 0.05$). At Marion County WMA, we captured 130 tortoises from 1994–95, of which 72 were adult females, 52 adult males, and 6 juveniles. This population also did not differ significantly from a 1:1 sex ratio ($\chi^2 = 3.23$, $df = 1$, $p > 0.05$).

Both populations were dominated by larger individuals (Fig. 2). However, in the Marion County WMA population, there were more individuals in the 12–20 cm size classes than at Ben's Creek WMA.

Discussion. — The reproductive patterns of the Marion County WMA population were very similar to those seen at Ben's Creek WMA, despite habitat differences between the two sites. Specifically, we found no differences in mean clutch size, mean female size, or adult sex ratios between the study populations.

Our data appear to support the conclusions of Landers et al. (1980), Iverson (1992), and Diemer and Moore (1994) that *G. polyphemus* lays no more than one clutch per year. Our data also appear to support the suggestion of Landers et al. (1980) and Diemer and Moore (1994) that some females do not nest each year. Based on data from females captured in both years, we estimated the reproductive frequency from the percent of females found gravid in either year of study. For instance, out of 10 females captured in both years of study at Marion County WMA, 2 were not gravid in either year; therefore, the reproductive frequency is estimated as 0.8 (i.e., 80% of females reproduce in a given year). Using the same method, we estimate that the reproductive frequency for the Ben's Creek WMA population as 0.85. It is, however, possible that some of the females recorded without eggs visible by X-ray were actually gravid but had unshelled follicles, or had already nested for the season.

Despite the finding that a majority of females produced eggs each year in both study populations, we found little evidence of recent recruitment, especially in the Ben's Creek WMA population. Although smaller individuals may have been overlooked in our capture efforts at Ben's Creek WMA due to their small body size and small burrows, results from a separate survey of the Ben's Creek WMA study site conducted in 1993 agreed with our conclusion that there was a lack of small-sized individuals in this population (E. Wester, *pers. comm.*).

We hypothesize that habitat quality differences between the two sites may possibly explain the apparent lack of young individuals at Ben's Creek WMA. Ben's Creek WMA is subjected to frequent disturbance by forestry equipment used for intensive management for commercial timber production and clearcutting operations. Powerline rights-of-way, where tortoise colonies are concentrated at Ben's

Table 1. Comparison of reproductive patterns for females X-rayed in both 1994 and 1995 at Marion County WMA.

I.D. No.	Clutch Size 1994	1995
2	7	5
7	6	0
11	5	5
16	0	0
25	9	5
26	0	4
29	5	0
35	5	0
36	0	0
54	0	6

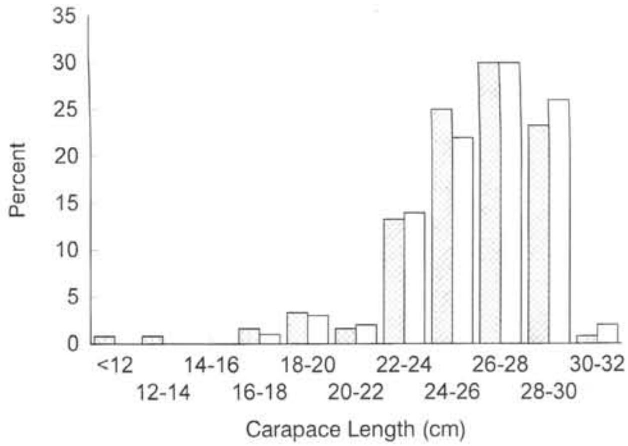

Figure 2. Size distribution of the Ben's Creek WMA (Louisiana, open bars) population compared to the Marion County WMA (Mississippi, hatched bars) population.

Creek, are maintained by annual mowing. Soil can become compacted by the continued use of heavy equipment in forestry management (Powers et al., 1990). Compaction of the clay-rich soils by intensive management may result in destruction of nests or entombment of hatchlings that may not be able to emerge from the hard-packed soil. Hurley (1993) found 9 *G. polyphemus* nests at Ben's Creek that failed to hatch, possibly due to developmental mortality. Developmental mortality can be caused by lack of permeability of the clay-rich, compacted soils. The eggs may suffocate from lack of oxygen or drown because water does not percolate through the soil quickly enough. Postnatal mortality may also occur if hatchlings become entombed in the nest chamber when the soil is so hard that they cannot dig out. In addition, mortality of small, inconspicuous individuals due to injuries caused by forestry equipment may also influence the lower number of young individuals seen at the Ben's Creek WMA study site. Because gopher tortoises may not reach reproductive maturity until 15–20 years of age, and because young tortoises are very inconspicuous, a reduction in recruitment and survival of young individuals caused by land management techniques and timber harvesting methods may not be detected until the number of older individuals has declined significantly (Iverson, 1980; Landers et al., 1980).

In general, clutch sizes of *G. polyphemus* from Louisiana and Mississippi were similar to clutch sizes from northern and north-central Florida, but lower than from southwestern Georgia and central and southern Florida (see Diemer and Moore [1994] and Butler and Hull [1996] for summaries). Clutch size is positively related to carapace length in both western and eastern tortoise populations (Diemer and Moore, 1994; Smith, 1995). Our data suggest that tortoises in the western range lay eggs at approximately the same time of year as do tortoises in the eastern range, where peak nesting activity ranges from mid-April to mid-June (Iverson, 1980; Landers et al, 1980; Diemer and Moore, 1994).

Differences in the ecology of a species throughout its range must be investigated and understood before successful conservation strategies can be formulated and implemented. For example, population viability analysis modeling programs used in the development of conservation strategies require input of life history characteristics such as reproductive rate and age of reproductive maturity, which may vary across a species' geographic range. Although a majority of our knowledge of gopher tortoise biology has resulted from extensive studies conducted primarily in Florida and Georgia, these data may not necessarily apply to the conservation of western tortoise populations. Future work should include comparative studies of gopher tortoise biology from other portions of its range in recognition of potential geographic variation in life history traits.

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Decline of the Loggerhead Turtle, *Caretta caretta*, Nesting on Senri Beach in Minabe, Wakayama, Japan

KATSUFUMI SATO[1], TAKEHARU BANDO[2,6], YOSHIMASA MATSUZAWA[2], HIDEJI TANAKA[3], WATARU SAKAMOTO[2], SHINGO MINAMIKAWA[4], AND KIYOSHI GOTO[5]

[1]National Institute of Polar Research, 1-9-10 Kaga, Itabashi, Tokyo 173 Japan [Fax: 81-3-3962-5743; E-mail: ksato@nipr.ac.jp]; [2]Graduate School of Agriculture, Kyoto University, Oiwake, Sakyo, Kyoto 606-01 Japan; [3]Department of Polar Science, School of Mathematical and Physical Science, The Graduate University for Advanced Studies, 1-9-10 Kaga, Itabashi, Tokyo 173 Japan; [4]Department of Zoology, Faculty of Science, Kyoto University, Oiwake, Sakyo, Kyoto 606-01 Japan; [5]278 Higashiyoshida, Minabe, Wakayama 645 Japan; [6]Present Address: Whale Biology Section, The Institute of Cetacean Research, Tokyo Suisan Bldg. 4-18, Toyomi-cho, Chuo-ku, Tokyo 104 Japan

Three species of sea turtles, *Caretta caretta*, *Chelonia mydas*, and *Eretmochelys imbricata* are known to nest in Japan (Nishimura, 1967; Uchida and Nishiwaki, 1982; Kamezaki, 1986). There are numerous nesting beaches for loggerhead turtles (*C. caretta*) around the main islands of Japan (Uchida and Nishiwaki, 1982) and the Japanese archipelago is an important nesting ground for the loggerhead turtle in the North Pacific Ocean (Nishimura, 1967; Dodd, 1988; Bowen et al., 1995; Kikukawa et al., 1996). The loggerhead turtle is listed as endangered worldwide by the IUCN, and it appears on Appendix I of CITES. In some areas, loggerhead populations appear to be declining (Dodd, 1988). However, there is very little information regarding the current status of loggerheads in Japan.

It is generally difficult to estimate the population size or trends of wild animals, especially marine species. Several indices may be used to estimate sea turtle nesting populations. The number of emergences can be estimated by counting tracks on nesting beaches, however, not all emergences result in successful nesting. The ratio of actual nesting success to number of emergences differs among nesting beaches (Dodd, 1988) and varies from year to year on a beach (Talbert et al., 1980). The number of nests does not represent the number of females nesting because nesting usually occurs repeatedly by a single female in a season. Direct count of nesting females with individual discrimination by tagging is the most reliable method. Even so, estimation of the total population size based on nesting females is impossible at the present time because the natural sex ratio and age structure of the population is not well understood (Meylan, 1982; Dodd, 1988).