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## **Biology of North American Tortoises**

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## Reproduction of Gopher Tortoises in North-central Florida

by

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**Abstract.** We obtained data on the reproduction of the gopher tortoise (*Gopherus polyphemus*) in north-central Florida from 1981 to 1987. The smallest radiographed female tortoise with shelled eggs had a 232-mm carapace length. The overall mean clutch size was 5.80 (range 3–10) and did not vary significantly from those of tortoise populations on a sandhill site (5.73), a planted pine site (5.83), and a pasture site (6.50). Most mature females radiographed during mid-May to mid-June had shelled eggs. The mean egg diameter and clutch size increased with mean carapace length. Nests were in burrow mounds, sandy roads, or roadsides, and one each was found in a clear-cutting and in a scrub-oak thicket. Evidence of egg and hatchling depredation was observed.

**Key words:** Age of reproduction, clutch size, Florida, *Gopherus polyphemus*, nesting, predation, radiography.

Gopher tortoise (*Gopherus polyphemus*) populations in Florida declined despite a 1988 statewide prohibition on taking tortoises. Although the decline may in part be attributed to agriculture, mining, illegal harvest, and certain forestry practices, urbanization poses the greatest threat to this fossorial reptile (Auffenberg and Franz 1982; Diemer 1987a). In recent years, numerous gopher tortoise populations were relocated as mitigation for the

loss of xeric habitats on development sites (Diemer 1987b, 1989). One criterion for evaluating the success of relocating tortoises is a population's postrelocation reproductive status. The usefulness of this criterion depends on an understanding of reproduction in indigenous tortoise populations. We present data about the reproduction of gopher tortoises in north-central Florida and synthesize pertinent findings from other researchers.

## Materials and Methods

### Study Sites

Data were gathered during 1981–87 in conjunction with studies of population dynamics on three sites in north-central Florida. We marked and recaptured tortoises during 1982–86 on the Roberts Ranch in Putnam County, during 1981–87 in the Lochloosa Wildlife Management Area in Alachua County, and during 1985–86 on Wolfe's Pasture, 0.6 km southeast of the Lochloosa Wildlife Management Area study site.

The Roberts Ranch study site was a 10.8-ha portion of a larger (160-ha) sandhill, approximately 15 km west of Palatka. The excessively drained sand supported an overstory of scattered longleaf pines (*Pinus palustris*) and mature turkey oaks (*Quercus laevis*); a midstory of smaller turkey oaks, sand-live oaks (*Q. geminata*), and sand-post oaks (*Q. margaretta*); and a diverse ground cover dominated by wiregrass (*Aristida stricta*), various composites (Asteraceae), and legumes (Fabaceae). The site remained unburned for more than 7 years before a hot burn in 1983.

The Lochloosa Wildlife Management Area study site was a 1.1-km grassy roadside strip with a surrounding mature slash pine (*P. elliotii*) plantation, approximately 20 km southeast of Gainesville. The major soil type was a moderately well-drained sand. The dense canopy of tall slash pines and scattered live oaks (*Q. virginiana*) and water oaks (*Q. nigra*) had reduced the herbaceous ground cover of the plantation. The most recent prescribed burn was in 1982. The roadsides were mowed annually, and cattle grazed in the area. In 1984, the landowner cleared timber and replanted slash-pine seedlings in a small section of the southwestern portion of the study site and in larger sections immediately southwest and approximately 0.5 km northwest of the main study site.

We included Wolfe's Pasture as a study site in 1985 when a radio-instrumented tortoise moved there from the Lochloosa Wildlife Management Area. The soil was a moderately well-drained sand. Vegetation included scattered large live oaks, seedling slash pines, bahia grass (*Paspalum notatum*), and hairy indigo (*Indigofera hirsuta*).

### Data Collection and Analysis

Tortoises were snared, manually captured, removed from their burrows with a pulling hook (Taylor 1982a), or captured in pitfall traps (19-L buckets sunk directly in front of the burrow opening). We measured the carapace length (CL) and drilled small holes in the marginal scutes (Cagle 1939) to permanently mark tortoises. Adult tortoises were sexed by morphology (McRae et al. 1981). We aged tortoises by counting plastral growth rings, assuming a 1:1 correspondence between age and ring count (Germano 1988; Landers et al. 1982). We radiographed all confirmed female tortoises to determine clutch size ( $S$ ; Gibbons and Greene 1979). We recorded egg diameter ( $D$ ) as the average of the maximum and minimum diameters (mm) of the egg radiograph image. The egg diameters were averaged by clutch, then averaged again by all clutches ( $\bar{D}$ ). We also averaged  $S$  and CL over multiple captures of each female ( $\bar{S}, \bar{CL}$ ).

With data available only in years 1982–86, we compared  $S$  among the three study sites in a completely randomized analysis of variance. We weighted  $\bar{S}$  by number of clutches to stabilize variability in  $\bar{S}$ , and we separated means with Tukey's test. The productivity trend of each female was estimated by the regression coefficient of  $S$  on year (1982–86 only). We compared productivity trends between individuals from the Lochloosa Wildlife Management Area and individuals from the Roberts Ranch in a two-sample  $t$ -test, weighted by the corrected sum of squares of year to control trend–variance heterogeneity. We used linear regression to test the relations of  $\bar{S}$  and  $\bar{D}$  with  $\bar{CL}$ . Differences in regression equations (either  $\bar{S}$  vs.  $\bar{CL}$  or  $\bar{D}$  vs.  $\bar{CL}$ ) among the animals of the three study sites were assessed with analysis of covariance. Tukey's test was used to separate estimated regression coefficients by study area.

The estimated minimum production of hatchlings was defined as the ratio of all hatchlings captured in a particular year or of all juveniles from that year class captured in subsequent years to the number of shelled eggs produced that year. We assumed that each female laid her eggs in the study sites, that no eggs were laid by females not caught, and that no juveniles immigrated into the study sites.

## Results

### *Size at Maturity*

The smallest female tortoise with detected shelled eggs had a 232-mm CL (Table 1). Approximately 16 annuli were counted on her worn plastron. Three other small gravid females captured at the Roberts Ranch had 233-mm (approximately 15–16 annuli), 233-mm (annuli illegible), and 238-mm (annuli illegible) CL. All other gravid females had a  $\geq 240$ -mm CL. A female on the Roberts Ranch reached maturity during the study: we did not detect eggs in 1983 (209-mm CL, 12 plastral rings) or 1985 (228-mm CL, 14 rings) but in 1986 (242-mm CL, 15 rings). Three immature females on the Roberts Ranch had 194-mm ( $n = 2$ ) and 215-mm CL (11–14 plastral rings). Radiographs of three small females in the Lochloosa Wildlife Management Area coupled to thermistors (222-, 227-, 233-mm CL) also revealed no eggs, although the largest female and a mature male were trapped in early May, and she may have produced eggs later. The smallest gravid female in the Lochloosa Wildlife

Management Area had a  $\geq 242$ -mm CL. Plastral abrasion made tortoises in the Lochloosa Wildlife Management Area especially difficult to age. One immature female grew 1 mm (221–222-mm CL) and 0 plastral annuli (12 rings, both years) between 1982 and 1984. By legible plastral annuli, female tortoises in north-central Florida seemed to reach sexual maturity at 14–18 years of age (Table 1).

The smallest apparently mature male tortoises had 177-mm CL (Table 1) on the Roberts Ranch and 182-mm CL in the Lochloosa Wildlife Management Area. Maturity was indicated by an elongated gular and a well-defined plastral concavity (McRae et al. 1981) in the smaller male and observation of the larger male visiting females. Two young tortoises on the Roberts Ranch first showed male morphological characteristics at 196-mm and 203-mm CL. Other young males on the Roberts Ranch had 188–196-mm CL and showed 9–12 plastral rings. A male in the Lochloosa Wildlife Management Area (204-mm CL, 13 plastral annuli) was first observed visiting females in 1985. By legible plastral annuli, male tortoises in north-central Florida seemed to reach sexual maturity at 9–13 years of age (Table 1).

**Table 1.** Size, age at maturity, and mean clutch size of the gopher tortoise (*Gopherus polyphemus*) by region.

Region	Size <sup>a</sup> at maturity		Age <sup>b</sup> at maturity		Mean clutch size	Source
	Males	Females	Males	Females		
North Florida	177	232	9–13	14–18	5.8	This study
	230	238				
	187	210				
Central Florida		226–236		10–15	5.2	Iverson (1980)
		238				Linley (personal communication)
		255		13	7.8	Linley (1986)
South Florida	222				7.6	Godley (1989)
	225	282	9–13	12	6.9	Douglass (1990)
					8.9	McLaughlin (1990)
Southwest Georgia	230–240	250–265	16–18	19–21	7.0	Burke (1987)
Southwest Alabama					5.3	Landers et al. (1980, 1982)
South Carolina	153		12		3.8	Marshall (1987)
						Wright (1982)

<sup>a</sup> Carapace length in mm.

<sup>b</sup> Years.

### Clutch Size

The weighted  $\bar{S}$  of 62 radiographed female tortoises on the Roberts Ranch ( $\bar{S} = 5.73$ ,  $n = 30$ ), in the Lochloosa Wildlife Management Area ( $\bar{S} = 5.83$ ,  $n = 26$ ), and in the Wolfe's Pasture study sites ( $\bar{S} = 6.50$ ,  $n = 6$ ) was similar (2, 59 df;  $P = 0.598$ ). Tukey's test could not distinguish any pair of means at the  $P = 0.05$  level. The overall weighted  $\bar{S}$  (Table 1) was 5.80 ( $n = 62$ , range 3–10, SE = 0.156) with a 95% confidence interval of (5.49, 6.11).

The trends in weighted mean productivity of individuals in the Lochloosa Wildlife Management Area ( $-0.0702$  eggs/year) and on the Roberts Ranch ( $-0.1301$  eggs/year) were not different (26 df,  $P = 0.790$ ). The mean of the overall trend in weighted productivity was not different from 0 ( $-0.1195$  eggs/year, df = 27,  $P = 0.562$ ). Eighteen tortoises on the Roberts Ranch had shelled eggs in 2 or more consecutive years, and five of these tortoises produced shelled eggs in all 5 years. Nine tortoises in the Lochloosa Wildlife Management Area had shelled eggs in 2 or more consecutive years, and one tortoise produced shelled eggs for 6 consecutive years. The other 29 gravid tortoises on both sites were captured only once or in alternate years.

The mean annual proportion of gravid females was 0.73 (range = 0.40–0.89). We detected shelled eggs 138 times and failed to detect eggs 46 times. Of the failed detections, 12 were of immature

females, 16 were of mature females before 12 May or after 10 June (Table 2), and 18 (only 10% of all radiographs) of the mature females during 12 May–10 June. One female without eggs on 10 May had four eggs on 3 June, and another without eggs on 12 May had seven eggs by 19 May and nested on 18 June. We saw no indication of more than 1 clutch/year.

The rate of increase of clutch size with CL was consistent among study sites ( $F = 0.90$ ; 2, 55 df;  $P = 0.414$ ). The mean clutch sizes of tortoises of equal CL also did not vary by area ( $F = 1.15$ ; 2, 57 df;  $P = 0.323$ ). Ignoring area, clutch size increased with CL ( $t = 4.10$ , 59 df,  $P < 0.001$ ,  $R^2 = 0.222$ ) in the estimated regression model

$$S = -4.744 + 0.04035 \text{ CL.}$$

Thus, a 25-mm increase in CL produced a one-egg average increase in clutch size.

The rate of increase of mean egg diameter with clutch size did not vary among study sites ( $F = 1.00$ ; 2, 54 df;  $P = 0.375$ ). In any area, an expected 1-mm increase in mean egg diameter occurred with every 13-mm increase in CL. However, at any tortoise size, the mean egg diameter varied by area ( $F = 7.50$ ; 2, 56 df;  $P < 0.001$ ). Tortoises in the Lochloosa Wildlife Management Area produced eggs approximately 1.75 mm smaller than similar-sized tortoises from other areas. Thus, mean egg diameter was positively related to CL ( $t = 5.68$ , 56 df,  $P < 0.001$ ,  $R^2 = 0.413$ ) in a regression model allowing mean egg diameters to depend on area: Wolfe's pasture  $D = 21.96 + 0.07585 \text{ CL}$ ; Roberts Ranch  $D = 21.82 + 0.07585 \text{ CL}$ ; and Lochloosa Wildlife Management Area  $D = 20.14 + 0.07585 \text{ CL}$ .

**Table 2.** Total radiographs ( $n$ ) and proportion with shelled eggs (%) of mature female gopher tortoises (*Gopherus polyphemus*) by time interval in north-central Florida, 1981–1987. Most females were radiographed only once per year. Twenty-eight observations were multiple X-rays taken in a single year.

Date	$n$	%
Before 12 May	4	25
12–21 May	75	89
22–31 May	42	88
1–10 June	33	85
11–20 June	10	50
After 20 June	8	0

### Nesting

Female tortoises nested on 8 June 1982 and 18 June 1986; another female was near an uncovered egg on 15 June 1986. Seven nests were in burrow mounds. The mean depth of five measured nests was 13 cm (range 10–18 cm), and their mean distance from the burrow mouth was 41 cm (range 25–53 cm).

Eggs in each of two nests in the Lochloosa Wildlife Management Area, one in a clear-cutting and one along a road, were uncovered within 1–4 weeks of deposition and subsequently removed by

an unidentified predator. On the Roberts Ranch, fox tracks were at a destroyed nest in a sand road. An intact but uncovered nest was in a thick sand-live oak stand on the Roberts Ranch; the eggs were broken or removed within 3 days. Numerous egg-shell pieces were in or near burrow mounds on both sites.

### Hatchling Production

Hatchlings were in nest cavities on 3 October 1983 (Lochloosa Wildlife Management Area) and on 6 October 1983 (Roberts Ranch). On the earlier date, one hatchling was partially in the shell and another was resting at the burrow entrance. The hatchling in the nest and the remaining eggs were destroyed the following day by an unknown predator.

The estimated minimum production of hatchlings in the Lochloosa Wildlife Management Area, where the number of females and eggs was half of that on the Roberts Ranch, was nearly 3 times as great as on the Roberts Ranch (Table 3). The minimum number of offspring per mature female per year was greater in the Lochloosa Wildlife Management Area ( $\bar{x} = 1.1$  tortoises/female/year) than on the Roberts Ranch ( $\bar{x} = 0.37$  tortoises/female/year).

## Discussion

The sizes and ages at sexual maturity of gopher tortoises were within expected geographic and individual variations of previous findings (Table 1). However, tortoises on a southwestern Florida barrier island apparently reached maturity at comparable ages but at larger sizes than tortoises from northern Florida (McLaughlin 1990). Size may not be the sole determinant of sexual maturity in *G. polyphemus* (McLaughlin 1990).

The overall clutch size (5.80) of gopher tortoises was also comparable to charted size in other recent findings (Table 1). Earlier literature references to clutch size in the gopher tortoise were reviewed by Iverson (1980) and included some unsubstantiated high estimates. However, a large female (356-mm CL) on a central Florida site produced an apparent record clutch of 25 eggs (Godley 1989). In a comparison of clutch sizes within and among the four species of *Gopherus* (Judd and Rose 1989), mean clutch size was highest in *G. polyphemus*.

The high annual percentage of gravid females ( $\bar{x} = 73\%$ ) in our study sites may have been site-specific. Of 47 female tortoises radiographed in May and June 1985 in central Florida, 66% were gravid (Godley 1989). No evidence of egg laying during 1 or more years was reported in some

**Table 3.** Estimated minimum hatchling production in gopher tortoises (*Gopherus polyphemus*) on two north-central Florida study sites.

Site	Year	Radiographed females		Hatchlings	Captures		
		No. gravid	No. eggs		Production estimate (%) <sup>a</sup>	All young of year class <sup>b</sup>	Production estimate (%) <sup>a</sup>
Lochloosa Wildlife Management Area	1982	9	53	4	8	13	25
	1983	9	56	1	2	4	7
	1984	7	37	4	11	11	30
	1985	9	47	7	15	8	17
	$\bar{x}$	8.5	48.3	4.0	9.0	9.0	19.8
Roberts Ranch	1982	18	110	3	3	8	7
	1983	14	76	5	7	7	9
	1984	18	112	0	0	0	0
	1985	13	70	8	11	8	11
	$\bar{x}$	15.8	92.0	4.0	5.3	5.8	6.8

<sup>a</sup>(Number of tortoises captured)/(number of shelled eggs produced).

<sup>b</sup>Year class estimated from plastral annuli.

gopher tortoise colonies where females were not radiographed (Auffenberg and Iverson 1979; Landers et al. 1980). Observations in the field revealed that most (56%) wild female Bolson tortoises (*G. flavomarginatus*) may not lay eggs each year (Adest et al. 1989). Less than half of the female Texas tortoises (*G. berlandieri*) radiographed in 1986 (37.5%) and 1987 (35.7%) did not have eggs (Judd and Rose 1989). In contrast, all but one routinely radiographed female desert tortoise (*G. agassizii*) laid 1 or more clutches in each of 3 consecutive years (Turner et al. 1986).

Our findings and those of previous researchers (Iverson 1980; Landers et al. 1980; Taylor 1982b; Wright 1982) indicate a single annual clutch in *G. polyphemus*. Similarly, no evidence exists to indicate 2 or more annual clutches in *G. berlandieri* (Judd and Rose 1989). However, multiple clutches were reported in *G. agassizii* (Turner et al. 1984, 1986) and *G. flavomarginatus* (Adest et al. 1989).

The clutch size in the gopher tortoise increased with carapace length. In another study in northern Florida, clutch size of the gopher tortoise very nearly significantly ( $r = 0.43$ ,  $n = 16$ ,  $P > 0.05$ ) increased with plastron length—that is, by one egg with each 27-mm increase in length (Iverson 1980). Clutch size also increased with plastron length ( $r = 0.68$ ,  $P < 0.01$ ) in the gopher tortoise in southern Georgia (Landers et al. 1980). At a California site, the sizes of first clutches in 1983 and 1984 but not the sizes of second clutches in 1985 increased with carapace lengths in all desert tortoises (Turner et al. 1986). Clutch size did not increase with carapace length in *G. berlandieri* in southern Texas (Judd and Rose 1989).

We did not specifically address the length of the breeding season but observed burrow cohabitation by a female and 1 or more males from mid-May to mid-November in the Lochloosa Wildlife Management Area. Male courtship behavior was observed in early September and late October (Diemer, unpublished data) and coincided with fall spermatogenesis (Taylor 1982b). Males visited burrows of females from 2 March to 1 November on a southern Florida study site (Douglass 1990). In southwestern Georgia, females were receptive to males only during spring, but males remained sexually active through fall (Landers et al. 1980). If successful copulation does occur in some parts of the species' range in fall, the reasons are unclear. Sperm were

in the endometrial glands of tortoise oviducts throughout the reproductive cycle (Palmer and Guillette 1988). Sperm could possibly be carried over winter until the spring nesting season, but whether these sperm are used for fertilization is not known (Palmer and Guillette 1988).

Mid-May to mid-June is the prime nesting period in gopher tortoises (Iverson 1980; Landers et al. 1980). Nesting occurred from late May through late June in South Carolina (Wright 1982). However, the discovery in northern Florida of several females with oviductal eggs in April and one female with well-calcified oviductal eggs on 26 March suggested an earlier start of the main portion of the nesting season (Taylor 1982b). April through May was the primary nesting season of tortoises on a southwestern Florida barrier island (McLaughlin 1990). Ovarian regression follows nesting in the summer months, and vitellogenesis resumes in fall (Iverson 1980; Landers et al. 1980; Taylor 1982b).

Nests were also located away from gopher tortoise burrows in southwestern Georgia (Landers et al. 1980). However, most (85% of 110 nests) were in or near burrow mounds, and the eggs were 15–25 cm below the soil surface. The mean distance from the burrow entrance was 18 cm ( $n = 93$ ). Two clutches in north-central Florida were in burrow mounds approximately 15 cm below the surface (Arata 1958). Seventy-four percent of the nests in a South Carolina study were in the female's burrow mound close ( $\bar{x} = 16$  cm) to the entrance (Wright 1982). Nine percent were in abandoned burrow mounds, but the other 17% were in sand near ( $\bar{x} = 11$  m) a burrow mound. Eggs were at depths of about 10 cm, estimated from several observations of nesting females. Eggs in a nest in Louisiana were 12-cm deep in a burrow mound and 25 cm from the burrow entrance (Martin 1989).

Nest-depredation rates were 89% ( $n = 38$ ) in southwestern Georgia (Landers et al. 1980) and 74% ( $n = 23$ ) in South Carolina (Wright 1982). Seventy-one percent ( $n = 7$ ) of the nests were depredated on one southwestern Alabama site, but none ( $n = 4$ ) was destroyed on another site (Marshall 1987). Raccoons (*Procyon lotor*) destroyed most nests in southwestern Georgia (Landers et al. 1980), whereas armadillos (*Dasypus novemcinctus*) were the primary predators of eggs

in southwestern Alabama (Marshall 1987) and south-central Florida (Douglass and Winegarner 1977). Nests were depredated by raccoons and opossums (*Didelphis virginianus*) in South Carolina, but dog (*Canis familiaris*) prints were also around one freshly destroyed nest (Wright 1982). Striped skunks (*Mephitis mephitis*) and gray foxes (*Urocyon cinereoargenteus*) are also predators of eggs (Hallinan 1923; Douglass and Winegarner 1977; Landers et al. 1980).

On several occasions, eggs of gopher tortoises were uncovered but not immediately destroyed or carried away. Predators infrequently (8% of depredated nests) destroyed only part of a clutch in southwestern Georgia (Landers et al. 1980). All eggs were usually destroyed when a nest was uncovered on a South Carolina study site (Wright 1982).

The destruction of nests precluded our determination of incubation periods. The incubation period of gopher tortoises is 80–90 days in northern Florida (Iverson 1980), 102 days in southwestern Georgia (Landers et al. 1980), and 110 days in South Carolina (Wright 1982). Clutches from captive tortoises in northern Florida hatched from mid-August through September (Iverson 1980).

Hatching occurred from 29 August to 9 October in southwestern Georgia (Landers et al. 1980). The hatching process was described by Arata (1958).

Partially or entirely unhatched clutches were occasionally found by others (Arata 1958; Iverson 1980; Wright 1982; Marshall 1987). Only 14% of 179 protected and closely monitored eggs in southwestern Georgia failed to hatch (Landers et al. 1980). In Mississippi, most of the five or six eggs in each nest ( $n = 40$ ) hatched (Brode 1959). However, 50% of the hatchlings were unable to escape the characteristic hard-packed overburden of the Mississippi clay hills and subsequently died in the nest.

Hatchling gopher tortoises may immediately excavate burrows, enlarge insect or rodent holes, or temporarily use larger tortoise burrows or shelter under vegetation or litter (Douglass 1978; Wright 1982; Diemer, unpublished data). A hatchling gopher tortoise in Alabama used an egg chamber for a burrow (Marshall 1987).

Hatchling and juvenile gopher tortoises are extremely vulnerable to depredation by a variety of mammalian, avian, and reptilian predators

(Douglass and Winegarner 1977; Fitzpatrick and Woolfenden 1978; Maehr and DeFazio 1985; Diemer 1987a; Layne 1989). Hatchlings have also been injured or killed from fire ant (*Solenopsis saevissima*) bites (Landers et al. 1980).

The estimated minimum production of hatchlings was probably biased by female and juvenile moves on or off the study sites. Undoubtedly, not all juveniles were captured. The estimated lower mean minimum hatchling production on the Roberts Ranch could be attributed either to difficulty in detecting small burrows in the thick ground cover or to higher depredation rates in the area. Factors of underestimated productivity are the emigration of ovipositing females and the cryptic appearance of juveniles. Conversely, overestimation would result from juvenile immigration and eggs laid by females that were not captured.

Depredation rates of eggs and hatchlings vary among sites and years but are generally high and severely depress recruitment. The depredation of gopher tortoise hatchlings was 70% during the first year and 41% during the second year of a study in South Carolina (Wright 1982).

In northern Florida, the recruitment potential, measured by burrow counts, may be reduced by about 94% from the time of egg laying through the first year (Alford 1980). The estimated minimum hatchling production in southwestern Georgia was about 0.58 hatchlings/female/year (Landers et al. 1980). In all four species of North American tortoises, apparent low recruitment is confounded by the cryptic appearances, small sizes, and possibly reduced surface activities of the juveniles (Douglass 1978; Schneider 1980; Shields 1980; Judd and Rose 1983; Turner et al. 1985; Adest et al. 1989; Corn 1994; Diemer, unpublished data). Yet, high hatchling mortality of Bolson tortoises was indicated in a study isolating problems from cryptic appearance (Adest et al. 1989).

We found that most variables of reproduction in gopher tortoises were quite similar among three north-central Florida sites with dissimilar habitats. Our findings were also comparable to those of previous researchers. However, we emphasize the substantial geographic and individual variation in this species. A data base should be constructed by gathering information on reproduction during several years at other Florida sites—for instance, information on tortoise reproduction on Florida's

southern coasts is minimal. Future investigation topics should include annual and geographic variations in nest depredation rates and hatchling survival, viable sperm storage, and multiple clutch frequency. The intervals between copulation, fertilization, and egg shelling remain unclear. Information is also needed on the reproductive status of seemingly isolated females in extremely low-density or fragmented habitats; past intensive human depredation in the Florida panhandle and ongoing rampant urbanization in the peninsula left no shortage of appropriate study sites.

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