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Population Biology of the Gopher Tortoise (*Gopherus polyphemus*) in Southeast Georgia

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ABSTRACT. – Two populations of gopher tortoises (*Gopherus polyphemus*) were studied in southeast Georgia from 1994 to 1996 to determine population structure and reproductive output. Habitat quality and burrow placement relative to habitat structure and fire management regime were monitored. Habitat quality was correlated with tortoise size and reproductive success. Tortoises from a managed site (Fort Stewart Army Reservation [FSAR]) were larger than tortoises from a non-managed site (George L. Smith State Park [GLS]). Females were significantly larger at FSAR (mean carapace length [CL] = 306 mm) than GLS (mean CL = 290 mm). Mean clutch size was significantly different between sites (FSAR: 6.52 vs. GLS: 4.52 eggs). Eggs and hatchlings varied significantly in mass (FSAR: 42.6 vs. GLS: 40.7 g per egg; FSAR: 32.2 vs. GLS: 29.4 g per hatchling) while hatchling CL did not vary significantly (FSAR: 46.4 vs. GLS: 46.4 mm CL). Habitat characterisitcs at active burrows were similar between sites (FSAR: 25.8 vs. GLS: 26.1% canopy; FSAR: 40.4 vs. GLS: 35.6% groundcover) while overall habitat characteristics were significantly different (FSAR: 40.3 vs. GLS: 76.4% canopy; FSAR: 28.6 vs. GLS: 12.2% groundcover). Tortoises appear to select burrow location based on canopy cover directly above the burrow and percent groundcover around the burrow mouth. Our results indicate that the fire management regime at FSAR results in more available habitat suitable for gopher tortoise than at GLS.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Gopherus polyphemus*; tortoise; reproduction; sex ratio; population structure; habitat; management; Georgia; USA

The gopher tortoise (*Gopherus polyphemus*) is currently listed as a threatened species by the state of Georgia, and is a prominent vertebrate species found in the sandhill community. In the western portion of its range (Alabama, Mississippi, and Louisiana), it is listed as Threatened under the Endangered Species Act (U.S. Fish and Wildlife Service, 1990). Multiple studies have investigated the effect of habitat on distribution of tortoises and/or tortoise burrows (Diemer, 1986; McCoy and Mushinsky, 1992; Aresco and Guyer, 1999; Boglioli et al., 2000). Cox et al. (1987) suggested that it is the management of the habitat that is essential to the long term population viability of this species. The tortoise's presence is readily determined in these communities making it an ideal focal species for those involved in management of this type of habitat.

Most studies have been conducted in Florida, where geographic variation in population structure, size class, and reproductive output is fairly well documented (Iverson, 1980; Wright, 1982; Diemer, 1986; Diemer and Moore, 1994; Mushinsky et al., 1994; Butler and Hull, 1996). The species has also been studied in southwest Georgia (Landers et al., 1982) and the western portion of its range in Mississippi and Louisiana (Smith et al., 1997). Geographic variation in habitat structure and soil types as well as current forestry practices have also been related to variation in population structure and reproductive success (Smith et al., 1997; Aresco and Guyer, 1999). Gopher tortoise populations in southeast Georgia have remained largely unstudied. Regional studies are critical to the proper management of the gopher tortoise in different geographic areas.

From a population standpoint, three considerations are important for long term survival of the gopher tortoise: 1) the condition of gopher tortoise habitat, 2) the minimum size of a tortoise population in order to persist, and 3) the minimal amount of habitat required to support such a population (Cox et al., 1987).

It is apparent that habitat parameters act to influence the amount of energy available for allocation to the three components of growth, maintenance, and reproduction. Exactly how the available energy is utilized with regard to these three components by tortoises in southeast Georgia is uncertain. We report on population structure, reproductive output, hatching success, and hatchling size for two populations of *G. polyphemus* studied from 1994 to 1996. Relationship to habitat quality and management practices are also presented.

METHODS

Research Sites. — Two research sites, George L. Smith State Park (GLS) and Fort Stewart Army Reservation (FSAR), were used in this study. Both are sandhill communities known to support gopher tortoises (Fig. 1). Sites are similar in structure, being sandridges found on the east side of stream systems. Both streams have been impounded to form lakes (Fig. 2). Though similar in size and general appearance, the sites differ greatly in management regimes, resulting in different levels of degradation.

The first site, GLS, is a relatively unmanaged preserve located near Twin Cities, Georgia. The sandhill portion of the park consists of a sand dune deposited along Fifteen Mile

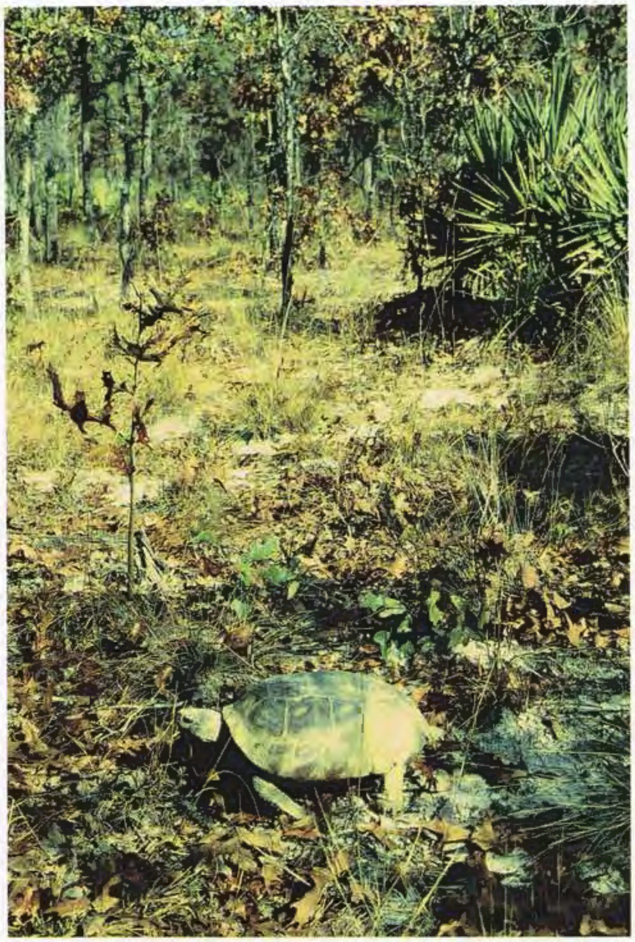

Figure 1. Gopher tortoise (*Gopherus polyphemus*) in sandhill habitat in southeast Georgia. Wiregrass (*Aristada stricta*) and saw palmetto (*Serenoa repens*) are visible in the foreground while turkey oak (*Quercus laevis*) and longleaf pine (*Pinus palustris*) are visible in the background.

Creek. This particular sandhill community is relatively isolated due to development and broad scale agriculture on surrounding property. Although gopher tortoise habitat has been preserved in GLS, tortoise habitat surrounding the park has become fragmented over time, resulting in small colonies existing in patches of sandhill habitat isolated from the park. Furthermore, the sandhill portion of the park has not burned in over twenty years (K. Watson, *pers. comm.*), causing it to become overgrown primarily with turkey oak (*Quercus laevis*).

The second site, FSAR, is a managed preserve on a military installation encompassing areas of seven southeast Georgia counties. Relatively continuous sandhill habitat is present on FSAR, with few barriers to discourage inter-colony migration between sandhill communities. The site is managed for a wide variety of plant and animal species including the gopher tortoise. The particular sandhill utilized for this study consisted of a dune near Turkey Creek in the southeast corner of the installation. Habitat on FSAR is maintained with prescribed burns on a 3–5 yr interval. The primary plant species on both sites are turkey oak (*Quercus laevis*), wiregrass (*Aristada stricta*), and longleaf pine (*Pinus palustris*).

Burrow Surveys. — Both sites were surveyed for all visible tortoise burrows, which were designated as active or inactive (McCoy and Mushinsky, 1992). Burrows displaying signs of recent tortoise activity (footprints, plastron scrape marks, and/or signs of digging) were considered active, and burrows lacking these signs or with leaf litter in the mouth were considered inactive. All active burrows were marked with a 0.5 m section of 1 inch (2.5 cm) PVC pipe with a number tag driven into the ground ca. 1 m from the mouth of the burrow on the apron.

Animal Capture and Care. — Gopher tortoises were trapped in buckets, as described in Breininger et al. (1991). Measurements of straight carapace length (CL), straight plastron length (PL), maximum height (MH), and maximum width (MW) were taken to the nearest millimeter using a set of calipers. Mass was obtained using a 10 kg Pesola spring scale. Each tortoise was assigned a number and tagged with a plastic fish tag (Floy Model FTF-69 Pennant, Floy Tag & Mfg., Seattle, WA) attached to the posterior right costal scute of the carapace with epoxy so that the number could be easily identified. The same number was also notched in the marginal scutes of each tortoise, following the method of Cagle (1939). All tortoises were released within 24 hrs at the site of capture.

Habitat Structure. — Canopy cover was measured with a convex spherical crown densiometer (Lemmon, 1957). Readings were taken by one of us (DNJ) at 50 active burrows and a series of 50 random points throughout each site. Burrows were chosen using a random number table using their identification number. Random point sites were derived by measuring a transect line through the study sites. Dirt access roads through the sites effectievely served as transects (Fig. 2). At randomly chosen intervals along the transects, random points were measured perpendicular to the transect. Points were determined using a random number table to find coordinates within the tortoise habitat as determined by vegetation type.

Groundcover was measured at the same locations as percent canopy. A sampling point was identified one meter from burrow locations and one meter from random points. Four readings were taken at each location (north, south, east, and west) by moving the grid one meter from each location in each of these four directions. These four readings were then averaged to obtain mean percent groundcover. All estimates of percent canopy and percent groundcover at burrows and random points were averaged to obtain a mean percentage for each site.

Radiography and Egg Collection. — All female tortoises were radiographed with a Summit LX 125 V X-ray machine (Summit Industries, Chicago, IL; Gibbons and Greene, 1979). Radiographs were taken with the tortoise in a plastron down position at settings of 63 KV, 100 mA, and 8.0 mAs, using Dupont X-ray film. Five females from FSAR and five females from GLS with known clutch sizes were chosen for oxytocin induced oviposition in order to acquire equal numbers of eggs from each site. Oxytocin saline solution containing 0.5% chlorobutanol (Sigma Diagnos-

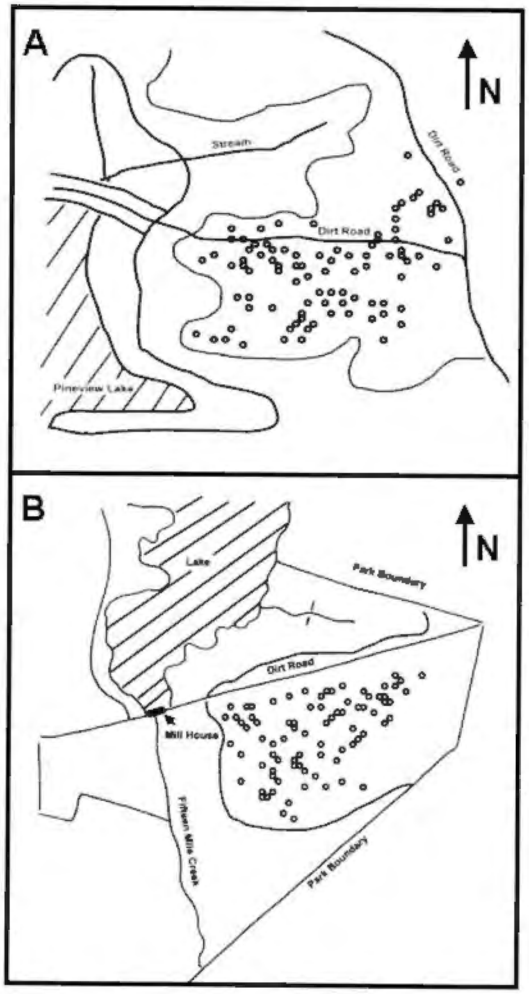

Figure 2. Map of study sites. A) Fort Stewart Army Reservation, Georgia, B) George L. Smith State Park, Georgia. Distribution of active burrows (o) is shown. Sandhill habitat was located east of stream systems which had been impounded to form lakes.

tics, St. Louis, MO) was given intramuscularly in the forelimb at a dose of 20 I.U. per kg body weight (Burke et al., 1996).

Egg Incubation. — Each egg was placed individually in a small plastic container with 250 mg sterilized sand and incubated according to the method described in Spotila et al. (1994). A total of 45 eggs were obtained for incubation (23 from GLS and 22 from FSAR). Eleven eggs from GLS and 11 eggs from FSAR were placed at 31.5°C (female-producing temperature), for a total of 22 eggs. Twelve eggs from GLS and 11 eggs from FSAR were placed at 27.5°C (male-producing temperature), for a total of 23 eggs. Temperature settings were chosen to obtain a balanced sex ratio of hatchlings (as determined from Burke et al., 1996) as well as to determine the effect of incubation temperature on incubation duration for tortoise eggs from southeast Georgia. A balanced sex ratio was needed to control for possible effects of gender on hatchling size. A Physitemp Model BAT-12 (Physitemp Instruments, Clifton, NJ) thermocouple reader was used to monitor internal temperature of each incubator. Temperatures were logged 5 times weekly for the duration of egg incubation. Egg containers were rotated within the incubators weekly to adjust for temperature variation within the chamber, at which time they were weighed and sand moisture replaced as needed by weight to maintain 0.4% sand moisture (Spotila et al., 1994). The mean incubation temperatures were 27.9°C (range = 26.8–28.8°C, n = 69) and 31.4°C (range = 30.7–32.1°C, n = 72).

Hatchling Measurements and Care. — Hatchlings were weighed and measured when the yolk was completely absorbed. Body mass (± 0.01 g) and CL were measured. The hatchlings were released back at GLS or FSAR, depending on where the original clutch was obtained, ca. 1–2 m from the burrow of the parent female.

Statistical Analyses. — We report mean values ± standard errors (SE). A Scheirer-Ray-Hare extension of the Kruskal Wallis Analysis of Variance was performed to compare the effect of sex, site, and their interaction on CL ($p \le 0.05$; Sokal and Rohlf, 1995). Mann Whitney Rank Sum test was used for comparing male CL, female CL, egg mass, hatchling mass, and hatchling CL between sites ($p \le 0.05$). Analysis of Covariance was used to identify differences between study sites for clutch size vs. CL ($p \le 0.05$). Habitat comparison (% canopy and groundcover) was also tested using non-parametric Mann Whitney Rank Sum test ($p \le 0.05$). Contingency tables (χ^2) were used to identify significant differences in sex ratios, hatching success, and burrow surveys.

RESULTS

Population Structure. — We captured 87 tortoises at GLS and 88 tortoises at FSAR. For the purposes of this study, tortoise size/age classes were set at 0–120 mm for juveniles, 121 to 260 mm for subadults, and 261 mm and greater for adults, similar to Landers et al. (1982) with the exception of adult size. Radiographs were used to establish the presence or absence of eggs in individuals, and thereby determine the size of reproductive maturity in females (Gibbons and Greene, 1979; Turner et al., 1986). Minimum female reproductive size was 261 mm CL for this three year study. Of the 87 tortoises captured at GLS, there were 30 adult males, 38 adult females, 3 unsexed adults, 16 subadults, and 0 juveniles. At FSAR, there were 34 adult males, 41 adult females, 3 unsexed adults, 8 subadults, and 2 juveniles.

An effect of both sex and site on adult size (CL) was observed (sex: H = 14.35, df = 1, $p < 0.001$; site: H = 6.34, df = 1, $p = 0.002$; sex x site: H = 8.86, df = 1, $p < 0.01$). Males were significantly smaller than females at both FSAR and GLS. There was no significant difference between males from FSAR (mean CL = 286 ± 2 mm, n = 36) and GLS (mean CL = 287 ± 3 mm, n = 32). However, females from FSAR (mean CL = 306 ± 3 mm, n = 41) were significantly larger than females from GLS (mean CL = 290 ± 2 mm, n = 39). Therefore, there is an effect of both sex and site on female size.

Percentages of adults in various size classes were distributed differently between sites (Fig. 3). Size class distri-

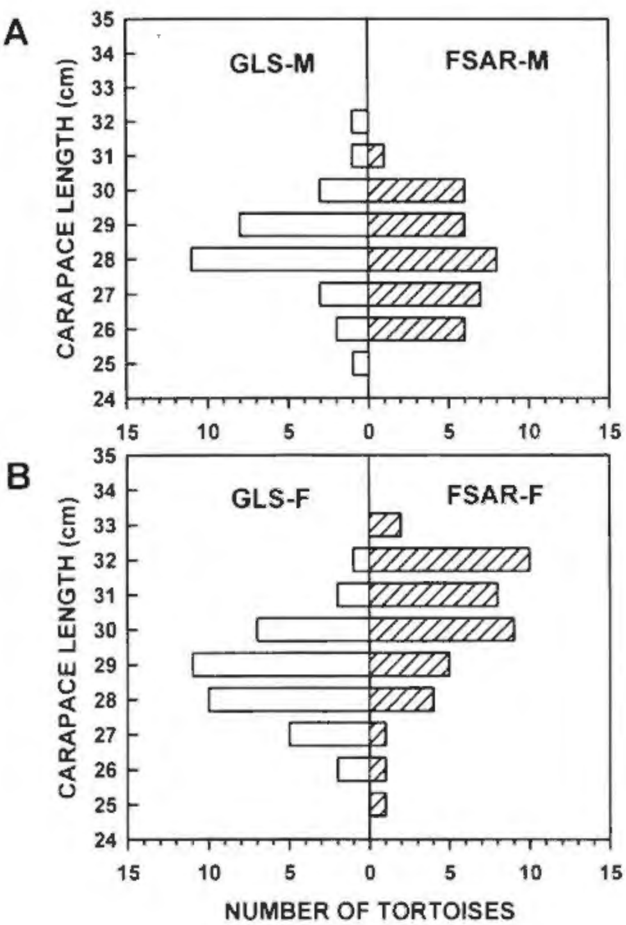

Figure 3. Distribution of straight carapace length (CL) measurements of (A) adult male and (B) adult female gopher tortoises (*Gopherus polyphemus*) for George L. Smith State Park (GLS) and Fort Stewart Army Reservation (FSAR) study sites.

bution indicated a greater percentage of smaller females at GLS than FSAR. Males were more similar between sites with respect to size class distribution. Adult sex ratios varied only slightly between sites. The sex ratio at GLS (1:1.27 males to females) and FSAR (1:1.21 males to females) were not significantly different from 1:1 (GLS: $\chi^2 = 0.350$, df = 1, $p = 0.539$; FSAR: $\chi^2 = 0.210$, df = 1, $p = 0.646$).

Clutch Size. — Differences in clutch size were also observed between the two sites. Females at FSAR produced significantly larger clutches (overall mean = 6.52 ± 0.33 eggs, range = 4–12 eggs, $n = 25$) over three consecutive reproductive seasons than females at GLS (overall mean = 4.52 ± 0.23 eggs, range = 3–7 eggs, $n = 23$; U = 358.0, $p < 0.001$). A higher percentage of females nested at FSAR than GLS during the 1995 and 1996 seasons.

Clutch size was positively correlated with CL (in cm) for all FSAR and GLS tortoises combined (clutch = -13.301 + (0.630 x CL), $r^2 = 0.35$, $n = 42$). Linear regression analyses were also performed independently on FSAR (clutch = -12.123 + (0.609 x CL), $r^2 = 0.314$, $n = 20$) and GLS (clutch = -2.871 + (0.256 x CL), $r^2 = .099$, $n = 22$) and displayed weak positive correlations between clutch size vs. CL with equal slopes (site x CL: F = 1.8678, df = 1,38, $p = 0.1798$). Analysis of Covariance of clutch size vs. site differed significantly between FSAR and GLS (site: F = 6.986, df = 1,39, $p < 0.012$). While CL does influence clutch size(CL: F = 10.451, df = 1,39, $p < 0.0025$), there appears to be effect of site on clutch size independent of female size (Fig. 4).

Hatching Success, Egg Mass, and Hatchling Size. — Hatching success was similar between incubated eggs from FSAR (81.2%) and GLS (87.0%). Hatching success for all eggs incubated in this study was 84.5% ($n = 45$). Hatchlings incubated at 31.4°C pipped an average of 15 days sooner than hatchlings incubated at 27.9°C. The mean number of days before pipping at 31.4°C was 82.2 ± 0.64 ($n = 21$), while the mean number of days before pipping at 27.9°C was 97.2 ± 0.65 ($n = 17$). Egg mass was positively correlated with hatchling mass (F = 148.5, df = 1,36, $p < 0.0001$, $r^2 = 0.799$) and hatchling CL (F = 34.6, df = 1,36, $p < 0.0001$, $r^2 = 0.490$). Egg and hatchling masses were significantly different between sites while hatchling CL was not. Mean egg mass at FSAR was 42.6 ± 0.8 g ($n = 18$) while mean egg mass at GLS was 40.7 ± 1.0 g ($n = 20$) (U = 426.0, $p = 0.029$). Hatchlings from FSAR had a mean CL of 46.4 ± 0.5 mm ($n = 18$), and hatchlings from GLS had a mean CL of 46.4 ± 0.5 mm ($n = 20$) (U = 351.0, $p = 0.988$). Hatchlings from FSAR had a mean mass of 32.2 ± 0.8 g ($n = 18$), and hatchlings from GLS had a mean mass of 29.4 ± 0.8 g ($n = 20$) (U = 435.0, $p = 0.015$).

Burrow Surveys. — The ratio of active to inactive burrows varied significantly between sites when surveyed at the beginning of the study ($\chi^2 = 140.6$, DF = 1, $p \leq 0.0001$). We identified 131 active burrows and 33 inactive burrows for a total of 166 burrows at FSAR within our study area. We identified 89 active burrows and 275 inactive burrows for a total of 364 burrows at GLS within our study area.

Habitat Structure. — Percent canopy varied significantly within and between sites for random point readings. Crown densiometer readings at FSAR averaged 40.3 ± 2.51% ($n = 50$) canopy cover, while the GLS site averaged 76.4 ± 1.79% ($n =$

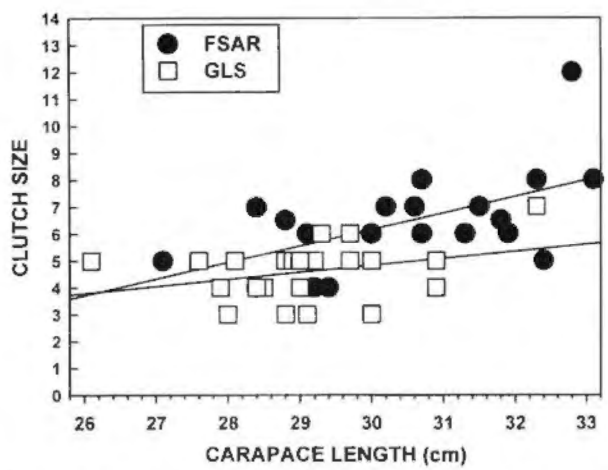

Figure 4. Clutch size vs. straight carapace length for gopher tortoises (*Gopherus polyphemus*) studied at George L. Smith State Park (GLS) and Fort Stewart Army Reservation (FSAR). Positive correlations were observed for both populations (FSAR clutch = -12.123 + (0.609 x CL), $r^2 = 0.314$; and GLS clutch = -2.871 + (0.256 x CL), $r^2 = 0.099$).

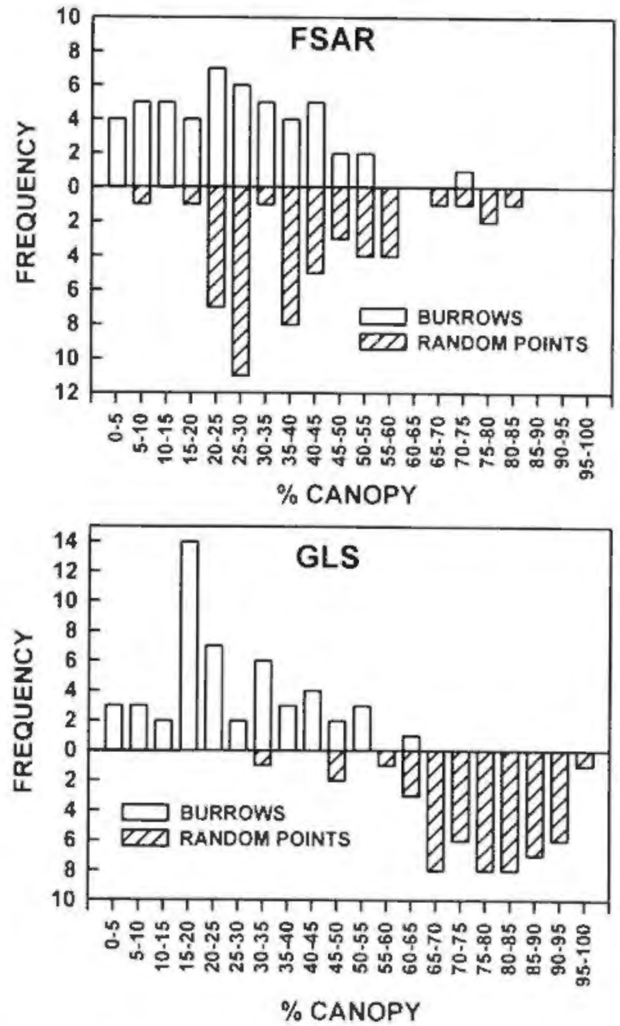

Figure 5. Relationship between percent canopy at active gopher tortoise (*Gopherus polyphemus*) burrows vs. random points within the sandhill habitat for Fort Stewart Army Reservation (FSAR) and George L. Smith State Park (GLS) study sites. Note the similarity in the distribution of percent canopy at active burrows between GLS and FSAR relative to the distribution of percent canopy at random points.

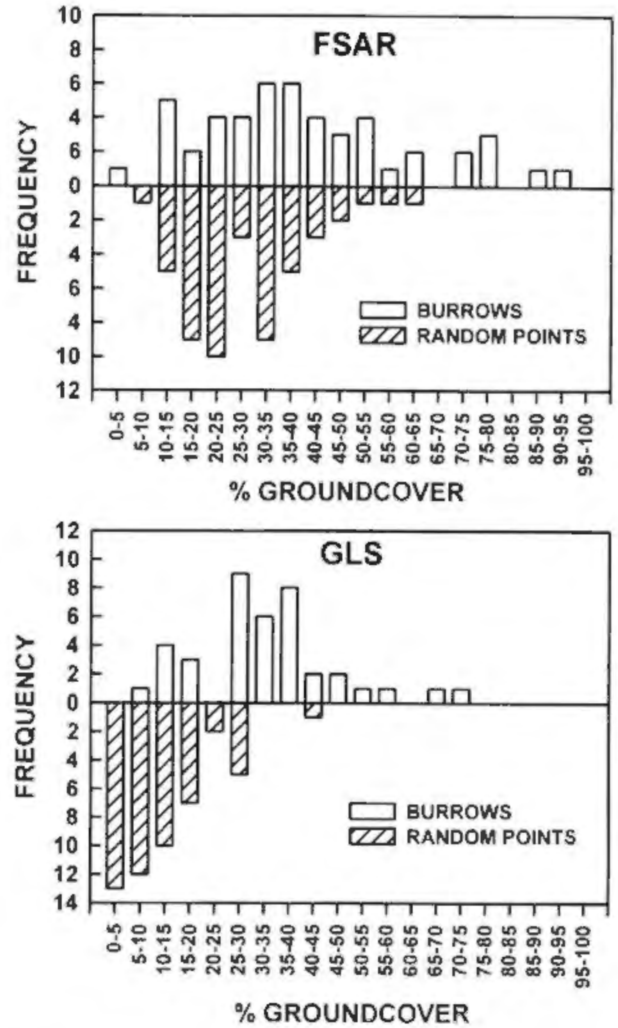

Figure 6. Relationship between percent groundcover at active gopher tortoise (*Gopherus polyphemus*) burrows vs. random points within the sandhill habitat for Fort Stewart Army Reservation (FSAR) and George L. Smith State Park (GLS) study sites. Note the similarity in the distribution of percent groundcover at active burrows between GLS and FSAR relative to the distribution of percent groundcover at random points.

50) canopy cover (U = 3593.0, $p < 0.001$; Fig. 5). However, percent canopy at active tortoise burrows did not vary significantly between sites (FSAR: 25.8 ± 2.19%, $n = 50$; GLS: 26.1 ± 2.06%, $n = 50$; U = 2521, $p = 0.981$; Fig. 5).

Percent groundcover varied significantly within and between sites for random point readings. Groundcover readings at FSAR averaged 28.6 ± 1.75% ($n = 50$), while readings at GLS averaged 12.2 ± 1.31% ($n = 50$) (U = 1605.0, $p < 0.001$; Fig. 6). However, percent groundcover at active tortoise burrows did not vary significantly between sites (FSAR: 40.4 ± 3.03%, $n = 50$; GLS: 35.6 ± 2.13%, $n = 50$; U = 2404.0, $p = 0.406$; Fig. 6).

DISCUSSION

Significant differences were observed in adult size, reproduction, and habitat structure between the two study sites (FSAR and GLS).

Population Structure. — Males are significantly smaller than female in southeast Georgia. Significantly smaller males have also been reported for Florida (Diemer, 1992) and southwest Georgia (Landers et al., 1982). Diemer (1992) reported sex ratios that approach 1:2 in favor of males, while in southeast Georgia sex ratios of 1:1.27 and 1:1.21 in favor of females were observed at GLS and FSAR, respectively. Similarly, a tortoise population relocated from Bulloch County, Georgia to St. Catherines Island, Georgia in May 1994 displayed a 1:1.1 ratio in favor of males (Jones, 1996). Smith et al. (1997) reported sex ratios not significantly different from 1:1 for populations in the western part of the range (Mississippi and Louisiana). Demuth (2001) also reported an adult sex ratio of 1.07:1.0 (males:females) for Merritt Island National Wildlife Refuge on the Atlantic coast of central Florida. The higher sex ratio reported by Deimer (1992) may be the result of sampling method.

Population structure also differed from that reported by Diemer (1992) but was more similar to that reported by Smith et al. (1997). Adults comprised 75% of captured tortoises at GLS and 79% of captured tortoises at FSAR, both well above the 40–54% range of adult percentages reported by Diemer (1992). Smith et al. (1997) observed even higher percentages of adult tortoises (41 females, 46 males and 1 subadult at Ben's Creek WMA; and 72 females, 52 males and 6 juveniles at Marion County WMA). Interestingly, adults comprised 45% of tortoises relocated from a population from Bulloch County, Georgia (20 males, 19 females, 22 subadults, and 26 juveniles; Jones, 1996). Differences in adult percentages in southeast Georgia may be attributed to different sampling methods used to capture tortoises or low numbers of juveniles at GLS and FSAR.

Few juveniles were located at FSAR (2) or GLS (0). This may be due to a variety of factors. It is possible that juveniles may share burrows with adults, place their burrows in highly secretive locations, or block the entrances to their burrows with sand when they are occupied (Auffenberg and Weaver, 1969). Guyer and Hermann (1997) observed that small tortoise burrows have a much shorter half-life compared with larger burrows in the same area. Aresco (1999) observed that juvenile tortoises tend to build burrows under structures such as logs, fallen tree limbs, and stumps. While these factors may further confound locating juvenile tortoise burrows, the low number of juvenile burrows located at GLS and FSAR may also indicate lower recruitment rates in the northern range of this species.

Reproduction. — Reproductive size and fecundity were determined for both populations. Minimum female reproductive size was 261 mm CL for the three year period that clutch size data were obtained, and indicates that in southeast Georgia the critical reproductive size may be larger than that reported for other regions (Iverson, 1980; Landers et al., 1982; Diemer, 1986; Diemer and Moore, 1994; Mushinsky et al., 1994). Landers et al. (1982) noted that females in southwestern Georgia attain sexual maturity at 250–265 mm CL. Females in northern Florida are even smaller at sexual maturity. Iverson (1980) reported sexual maturity at 226–236 mm CL, Diemer (1986) recorded 232 mm CL, and Taylor (1982) noted 210 mm CL. Central Florida females attain sexual maturity at 240 to 250 mm CL (Mushinsky et al., 1994). Smith et al. (1997) reported reproductive female size range from 250 to 310 mm CL. We suspect that critical reproductive size and critical reproductive age are interrelated, and that this potential late onset of reproduction in Georgia could cause lower reproductive potentials of females and slower rates of population growth than populations in more southern regions. The warm climate and longer growing season in Florida makes it possible for tortoises in these areas to be active for a longer period of time than tortoises farther north (Douglass and Layne, 1978, Mushinsky et al., 1994). Mushinsky et al. (1994) noted that this longer period of activity results in these tortoises attaining sexual maturity 6 to 10 years sooner than females in more northerly populations, and hypothesized that the relatively early onset of reproduction in southern populations of tortoises promotes greater reproductive potentials of females and higher potential rates of population growth than in more northerly populations. Diemer (1994) reviewed past studies showing that age at sexual maturity increases from southern populations (Florida populations range from 12 to 18 yrs with increase in latitude) to northern populations (southwest Georgia populations range from 19–21 yrs). Observations from southeast Georgia support a similar age to sexual maturity as southwest Georgia based on annuli counts (Jones, 1996). Age at sexual maturity may be one of the most important influences on population growth in turtles (Congdon et al., 1994).

Clutch size also differs between states and regions, and in the case of our study, between sites in the same region of southeast Georgia. Females from FSAR produced a mean clutch size over a three year period of 6.52 eggs, while females from GLS produced a mean clutch size over a three year period of 4.52 eggs. A tortoise population relocated from Bulloch County, Georgia to St. Catherines Island, Georgia in May 1994 displayed an even higher clutch size for the region (mean clutch size = 8.0 ± 0.31 eggs, range = 6–10 eggs, mean female CL = 314 mm, $n = 13$; Jones, 1996), however, female size was larger as well. Diemer (1986) reported a mean clutch size of 5.8 eggs in northern Florida, and Iverson (1980) observed a mean clutch size of 5.18 eggs per clutch. Butler and Hull (1996) reported a mean clutch of 5.04 eggs per clutch for northeastern Florida. Landers et al. (1982) observed a mean clutch size of 7.0 eggs in southwestern Georgia. Smith et al. (1997) observed a mean clutch sizes of 5.6 and 5.5 eggs in Mississippi and Louisiana, respectively. Demuth (2001) reported a mean clutch of 7.46 eggs, similar to those surveyed from the literature by Butler and Hull (1996) for south and central Florida (7.8 eggs, Linley, 1986; 8.9 eggs, Burke, 1987; 7.6 eggs, Godley, 1989). Interestingly, Wright (1982) reported a mean clutch size of 3.8 eggs in South Carolina which is somewhat similar to the clutch size reported for GLS. South Carolina may represent the northern range limit of *G. polyphemus*. These geographic variations in gopher tortoise populations may be due to differences in habitat quality and nutrition (Landers et al., 1982).

The observed differences in clutch size between FSAR and GLS can only partially be attributed to smaller female size at GLS. A positive linear relationship between clutch size and female CL was observed at both sites. Several studies have shown that clutch size increases with the plastron or carapace length of the female (Iverson, 1980; Landers et al., 1980; Diemer and Moore, 1994, Smith et al., 1997). Values from both sites were plotted in a linear regression analysis to determine the relationship of clutch size vs. carapace length for southeast Georgia. Not only did GLS females produce significantly fewer eggs per clutch, but the females and their respective clutches from both sites formed two fairly distinct groups on the linear regression graph (Fig. 4). If clutch size were influenced only by carapace length, we would expect a fairly even distribution on the graph, with large females producing large clutches and small females producing small clutches. Although a positive correlation exists between clutch size and carapace length in southeast Georgia, as reported from other regions (Iverson, 1980; Landers et al., 1980; Diemer and Moore, 1994), the significant difference in linear regression analyses between FSAR and GLS indicates that other factors are involved in the determination of clutch size, most of which may be site specific.

Incubation studies have focused on two species of *Gopherus*. Our results are similar to the results from both the desert tortoise (*Gopherus agassizii*; Spotila et al., 1994; Rostal et al., 2002) and the gopher tortoise (*G. polyphemus*; Burke et al., 1996; Demuth, 2001). Incubation time varied significantly between eggs incubated at 27.9°C (97.2 days) and eggs incubated at 31.4°C (82.2 days). Demuth (2001) observed 95 days at 28°C and 80 days at 31°C for *G. polyphemus* eggs from central Florida. Similarly, eggs from *G. agassizii* incubated at 28°C averaged 89 days while eggs incubated at 31.3°C averaged 78 days (Spotila et al., 1994; Rostal et al., 2002).

Hatching success from incubator studies has varied. Hatching success was 86.96% for eggs from GLS and 81.22 % for eggs from FSAR. This rate of hatching success was not significantly different from other studies (73.5%, Butler and Hull, 1996; and 77%, Burke et al., 1996; $\chi^2 = 0.640$, df = 2, $p = 0.726$). Demuth (2001) incubated eggs at a series of temperatures ranging from 26 to 34°C with an overall hatching success of 48.9%. Hatching success ranged from 58 to 63% for temperatures between 28 to 32°C. High levels of hatching success are also important in that both populations support sufficient males and females capable of fertilizing and producing viable offspring. Observations from field nests have varied (80.6%, Butler and Bull, 1996; 92% Arata, 1958; 86%, Landers et al., 1980; 28%, Linely and Mushinsky, 1994; 67–97%, Smith, 1995). Studies of nests left *in situ* are important for understanding reproductive success within populations.

Egg and hatchling size were observed to be interrelated. Egg mass and hatchling mass were significantly different between sites while hatchling CL was not. Mean egg mass was 42.9 g and 40.7 g for FSAR and GLS, respectively. These figures are similar to egg masses reported from other studies (41.0 g, Iverson, 1980; 37.7 g, Butler and Hull, 1996; 36.0 g, Burke et al., 1996; 38.11 g, Demuth, 2001). Hatchling CL in southeast Georgia (46.4 mm CL) is similar to that reported by Iverson (1980) of 48.2 mm CL in Florida. Demuth (2001) reported hatchling CL's ranging from 44 to 46 mm depending on incubation temperature for the Atlantic coast of central Florida. These differences may be attributed to differences in the reproductive biology of tortoises from different regions (Iverson, 1980). The variation in egg mass and hatchling mass observed between FSAR and GLS may also be related to available energy. An important observation is that while there is variation in hatchling mass which is strongly correlated to egg mass, hatchling carapace length was not significantly different between populations. There is a potential tradeoff between clutch size and egg/hatchling size in *G. polyphemus*. A major prediction of the optimal egg size theory is that, within a population, the amount of variation in reproductive output among females should result primarily from variation in the number of offspring produced and secondarily from variation in egg size (Congdon, 1989).

Habitat Structure. — Location of active tortoise burrows was strongly correlated with canopy cover and groundcover at both sites. Active burrows at both sites had low canopy cover (FSAR: 25.8%; GLS: 26.1%) and high groundcover (FSAR: 40.4%; GLS: 35.6%) relative to overall canopy (FSAR: 4.3%; GLS: 76.4%) and groundcover (FSAR: 28.6%; GLS: 12.2%). Canopy and groundcover were correlated at both sites. Our data indicate less suitable habitat available for burrow placement throughout the GLS site, and more at the FSAR site (Figs. 5 and 6). The fact that there is no significant difference in percent canopy or percent groundcover at active burrow locations between FSAR and GLS indicates that tortoises are seeking similar areas for burrow placement at both sites. Canopy (14.0%) and groundcover (38.4%) results for active burrows at the Bulloch County population site were similar to those at FSAR and GLS, however further study was not possible due to development of the site. Tortoise burrow placement in areas of less canopy and greater levels of herbaceous groundcover has been suggested in Florida (Diemer, 1986). Mushinsky and McCoy (1994) suggest that tortoises may abandon densely canopied areas for many reasons. Aresco and Guyer (1999) documented burrow abandonment levels in slash pine plantations in southcentral Alabama. They demonstrated a relationship between level of abandonment and increase in overstory. Boglioli et al. (2000) observed a similar relationship in longleaf pine forest in southwest Georgia. They observed that tortoises selected areas with 30% canopy while the site averaged 60% canopy. This is further supported by the higher ratio of active to inactive burrows observed at GLS (85 active to 275 inactive) vs. FSAR (131 active to 33 inactive). Canopy can influence energy availability in several ways. A reduction of direct sunlight to the ground may decrease the amount of time that tortoise operative environmental temperatures are met, in turn decreasing the amount of time for normal daily activity patterns. The increased shade associated with areas of increased canopy may hinder the development of eggs, which females often deposit just outside of burrows. It has also been suggested that an increase in canopy may be associated with a decrease in the herbaceous vegetation essential for normal growth, development, and reproduction of the gopher tortoise (Auffenberg and Franz, 1982; Mushinsky et al., 1994). These factors may act to influence the amount of energy attainable by the gopher tortoise. Whether influenced by one or a combination of these factors, tortoises in southeast Georgia are selecting burrow locations with lower than site average mean percent canopy and higher than site average mean percent herbaceous groundcover.

Fire Management. — The differences in habitat structure, clutch size, and egg/hatchling mass between FSAR and

GLS are most likely attributable to management in the form of controlled burns at FSAR, and the lack of such management at GLS. Historically, natural fires during the summer occurred every 5–10 years in the southeast Coastal Plain (Wharton, 1977). Frequent burns favor the fire-adapted longleaf pine and wiregrass, creating an open, savanna-like habitat (Campbell and Christman, 1982). Fire, whether naturally occurring, accidentally started, or deliberately lit for some purpose has been an important ecological force shaping landscapes and ecosystems around the world (Trabaud, 1986). Platt et al. (1988) monitored the effect of fire on the number of species flowering as well as the effect of fire on season of flowering in longleaf pine / wiregrass communities. They observed effects on the amount of flowering and the timing of flowering which would both influence availability of nutrients to gopher tortoises based on seasonality. Many of these effects can be observed on FSAR habitat. Further research on the relationship of tortoise biology and demography to habitat quality is needed.

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