NESTING ECOLOGY, FEMALE HOME RANGE AND ACTIVITY, AND POPULATION SIZE-CLASS STRUCTURE OF THE GOPHER TORTOISE, *GOPHERUS POLYPHEMUS*, ON THE KATHARINE ORDWAY PRESERVE, PUTNAM COUNTY, FLORIDA

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ABSTRACT

From 1989 to 1991, I conducted field observations on life history characteristics of the gopher tortoise (*Gopherus polyphemus*) on the Katharine Ordway Preserve in north-central Florida. Fourteen adult females were radio-instrumented for up to 505 days to determine home range size, movement, and activity patterns. Home range estimates varied greatly among individual females, ranging between 0.002 and 1.435 ha. Burrow densities ranged between 2.42 and 10.56 ha. The overall population size-class structure was skewed toward adults (> 210 mm carapace length), suggesting a stable or declining population. Over three consecutive nesting seasons, 2008 burrow aprons were checked for eggs. Less than two percent of the aprons contained nests and only two of 18 gravid females deposited their eggs at burrow entrances. The mean clutch size in 1990, at the height of a long term regional drought, was significantly different from 1991, when seasonal rainfall was near average. Clutch size was positively correlated with female carapace length, although carapace length explained only a small amount of the variance. However, a negative correlation between burrow width and clutch size at nests located in burrow aprons suggests that these nests may have been deposited by nonresident females.

RESUMEN

Entre 1989 y 1991, conduje observaciones de campo de las características de historia de vida de la tortuga excavadora (*Gopherus polyphemus*) en la Reserva Katharine Ordway, en el norte-centro de Florida. Con el objeto de determinar el tamaño de ámbito de hogar, sus movimientos y patrones de actividad, se radio-instrumentaron catorce hembras adultas por hasta 505 días. Las estimaciones del ámbito de hogar variaron grandemente entre hembras, con un rango de entre 0,002 y 1,435 ha. La densidad de madrigueras varió entre 2,42 y 10,56 ha. La estructura etaria de toda la población estuvo dominada por adultos (> 210 mm largo del caparazón), lo que sugiere una población estable o en disminución. Por más de tres estaciones

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de anidamiento consecutivas se chequearon 2,008 madrigueras en búsqueda de huevos. Menos de un 2% de las madrigueras contuvieron huevos, y sólo dos de 18 hembras grávidas depositaron sus huevos en la entrada de las madrigueras. El tamaño promedio de la puesta en 1990, en medio de una sequía regional prolongada, fue significativamente diferente que el promedio de 1991 cuando la lluvia caída fue cercana al promedio. El tamaño de puesta estuvo positivamente correlacionado con el largo del caparazón de las hembras, aún cuando el largo del caparazón explicó una pequeña proporción de la varianza. Sin embargo, el hecho de que existió una correlación negativa entre el ancho de las madrigueras y el tamaño de la puesta en nidos localizados en madrigueras, sugiere que estos nidos fueron depositados por hembras no residentes.

INTRODUCTION

Gopher tortoises (*Gopherus polyphemus*) occur in upland habitats in six southeastern states (Auffenberg and Franz 1982). They excavate extensive burrows that provide protection from predators, thermal extremes, and environmental perturbations. Gopher tortoise numbers may have declined by 80% in the past 100 years (Auffenberg and Franz 1982), largely as a result of habitat alteration and human predation (Taylor 1982a; Means 1986; Diemer 1987). The decline in tortoise populations is particularly important because gopher tortoise burrows are used by many other wildlife species (Eisenberg 1983). Sixty vertebrate and 302 invertebrate species have been documented to use tortoise burrows (Speake 1981; Franz 1986; Jackson 1989; Lago 1991).

In north-central Florida, female gopher tortoises attain sexual maturity at a carapace length of 220-230 mm (10-15 years of age) (Iverson 1980; Taylor 1982b; Diemer 1986). Males typically reach maturity at a smaller size than females (200-210 mm carapace length) (Taylor 1982b; Douglass 1986). Longevity estimates range from 40 to 60 years, although growth rate declines with age (Landers et al. 1982).

Gopher tortoises rarely are encountered above ground. However, important population characteristics can be described based on the size and number of burrows. There is a strong positive correlation between carapace length of the resident tortoise and burrow width (Hansen 1963; Alford 1980; Martin and Layne 1987). Carapace length is related to age in gopher tortoises (Auffenberg and Iverson 1979; Landers et al. 1982); therefore, the general size-class structure of a population can be evaluated based on burrow width. Gopher tortoise populations typically are estimated by assessing burrow occupancy using visual cues such as tracks or plastral slide marks. In a long-term study in north-central Florida, Auffenberg and Franz (1982) found that an average of 61.4% of burrows were occupied at any given time. Recent studies have shown that there is considerable variation in burrow occupancy depending upon season, habitat, and geographic location (Burke 1989; Breininger et al. 1991).

Movement from the burrow is related to the diurnal temperature cycle (McRae et al. 1981b). In northern regions, cold temperatures restrict tortoise activity in winter months, whereas in south Florida, tortoises are active year-round

(Douglass and Layne 1978). Most activity is centered around the burrow, although movements associated with social interactions often are long-range (Gourley 1969; McRae et al. 1981b). The home range of the gopher tortoise consists of a feeding or daily activity range centered around the burrow and an annual range that includes longer movements for breeding and nesting forays, search for better food resources, and periodic relocations (McRae et al. 1981b). Home range and movements in the gopher tortoise have been described by Gourley (1969), Douglass (1976), McRae et al. (1981b), Wright (1982), Diemer (1992), and Wilson (1990). Sample sizes in these studies generally were small.

Female gopher tortoises lay a single clutch of eggs per season (Iverson 1980; Landers et. al. 1980). Most nesting occurs from mid-May to mid-June (Iverson 1977; Landers et al. 1980; Diemer 1986). Gopher tortoises show a preference for clear, unshaded areas as nest sites (Hallinan 1923; Landers et al. 1980; Cox et al. 1987). Eggs may be deposited in the mound of excavated sand (burrow apron) at the entrance of an adult's burrow (Hallinan 1923), although females are reported to lay their eggs as far as 134 m from the burrow (Landers et al. 1980).

Clutch size in the gopher tortoise varies geographically. In South Carolina, Wright (1982) reported a mean clutch size of 3.8 (n = 23). In north-central Florida, average clutch sizes range from 5.0 to 6.7 (Hallinan 1923; Iverson 1980; Taylor 1982b; Diemer 1986). The largest clutch size records are from central and south Florida. Burke (1987) reported a mean clutch size of 8.9 on a Palm Beach County site (n = 11). Clutches of 25 and 21 eggs were reported from two central Florida tortoises (Godley 1989; L. Macdonald pers. comm.). Clutch size in the gopher tortoise, as with other turtles, is positively correlated with female carapace length (Iverson 1977; Landers et al. 1980; Jackson 1988; Elgar and Heaphy 1989).

The incubation period also varies geographically, probably reflecting variation in average annual temperature (Landers et al. 1980). For example, the incubation period in north-central Florida is 80 to 90 days (Iverson 1980). In contrast, the reported incubation time is 110 days at the northern extreme of the tortoise's range in South Carolina (Wright 1982).

Predation of gopher tortoise nests is high, particularly in the week after egg deposition (Auffenberg and Weaver 1969). At a southwest Georgia site, 89% of nests left unprotected were destroyed shortly after deposition (Landers et al. 1980). In South Carolina, Wright (1982) reported a 74% nest predation rate. Nest predators include gray foxes (*Urocyon cinereoargenteus*), nine-banded armadillos (*Dasypus novemcinctus*), striped skunks (*Mephitis mephitis*), and opossums (*Didelphis virginiana*) (Douglass and Winegarner 1977; Landers et al. 1980; Diemer 1986; Marshall 1987). However, raccoons (*Procyon lotor*) are undoubtedly the most common mammalian predator (Hallinan 1923; Landers et al. 1980; Diemer 1986). Snakes also may be responsible for nest predation (Landers et al. 1980).

In May 1989, I began field studies on the large gopher tortoise population inhabiting the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam

County, Florida. My project included a telemetry study of adult female gopher tortoises and an assessment of tortoise population size-class structure. The data presented here also include mark-recapture information collected between 1983 and 1990 by R. Franz and C.K. Dodd, Jr., and population census data collected by R. Franz from 1985 to 1991. During 1989 and 1990, north-central Florida underwent a prolonged drought (Motz et al. 1991). In 1991, seasonal rainfall was near average. I was thus able to document the short-term effects of drought on reproduction in gopher tortoises.

The specific objectives of this study were: (1) to determine recapture rates, sex ratio, and growth patterns of gopher tortoises, (2) to estimate home range size and examine activity patterns of adult female tortoises in sandhill and old field habitats, (3) to examine population structure and density of tortoises in different locations and habitats and to assess impacts of human predation on tortoise populations, (4) to determine mean clutch size of gopher tortoises and to evaluate the relationship between female carapace length and clutch size, and (5) to determine whether there were differences in clutch size, hatching success, and hatchling size in 1990, at the height of the long-term drought, compared to 1991, a year of near average rainfall.

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METHODS

A total of 196 gopher tortoises were captured and marked from October 1983 through September 1991. Tortoises caught prior to May 1989 were captured opportunistically by other researchers. I captured tortoises manually, with live-traps (Tomahawk Live-Trap Co., Tomahawk WI), or pitfall traps. A single juvenile was caught in a funnel trap. Tomahawk live-traps were set in front of the burrow entrance, anchored with tent stakes, and shaded (Douglass 1986). Pitfall traps consisted of 19-L plastic buckets sunk flush with the ground directly in front of the burrow entrance (Campbell and Christman 1982). The top of the bucket was covered with brown paper, sand, and litter to camouflage the opening. I checked my traps in the morning, at mid-day, and in the early evening.

The sex of adult tortoises was determined based on shell morphology (McRae et al. 1981a). I measured straight-line carapace length (CL), plastron length (PL), and maximum body width (CW) with 50 cm calipers, and wet body mass using a spring scale. Tortoises were marked for individual recognition by filing a series of notches on the marginal scutes (Cagle 1939). The date, time (Eastern Standard Time), weather (cloudy, partly cloudy, mostly cloudy, clear, rain, or fog), and location were noted for each capture. When a tortoise was caught at a burrow, the width of the burrow was measured 50 cm inside the entrance (Martin and Layne 1987).

From late April through early June 1990, 14 adult female tortoises were fitted with radio transmitter packages (Table 1). Eight of the 14 females were caught in sandhill habitat and six in old field. Refurbished T001RF transmitters (Advanced Telemetry Systems, Inc., Isanti, MN) and batteries with a six-month life expectancy were mounted on the anterior marginal scutes with epoxy gel. The whip antennas were attached laterally to the marginal scutes with spots of epoxy gel. Transmitter packages weighed from 30 to 35 g (less than 2% of the tortoise's weight). Actual battery life ranged from 105 to 353 days. Transmitters were replaced on seven females after the batteries failed.

Tortoises were located using a Telonics 2 receiver and hand-held H-antenna. Each tortoise was tracked at least three times a week. In addition, tortoises were located three times a day (morning [0700-1000], mid-day [1130-1400], and early evening [1600-2000]) for five days during the first week of each month. Numbered wire flags were placed at each new location. Approximate locations were marked on blue-line aerial photographs (scale 1" = 200'). Precise locations were plotted by hand using a compass and meter tape.

Time (EST), weather conditions, air temperature, location number, and the tortoise's position, i.e. above or below ground, were noted each time a tortoise was located. If a tortoise was above ground, its behavior was described as basking, walking, feeding, nesting, or mating. To monitor activity between radio-locations, small sticks were placed at the entrance of burrows occupied by radio-instrumented tortoises (Hallinan 1923). Disturbance to the sticks was noted each time a tortoise was located, and sticks were reset when necessary.

To assess population structure, burrow censuses were conducted at selected sandhill sites on the Preserve (Fig. 1). Nine areas were surveyed over a six-year period either by myself or Richard Franz and students from the University of Florida (Table 2). Of the areas sampled, one (Wall Cemetery Sandhill) was surveyed three times over the six-year period. Surveys were conducted following prescribed burns because burrows were more easily detected after thick ground cover vegetation was removed. To conduct a census, the entire area was canvased by a group of people who formed a line and walked back and forth across the

Table 1. Summary of radio-telemetry data and home range estimates for 14 adult female radio-tagged gopher tortoises on the Ordway Preserve, Putnam County, Florida. Home range was calculated using the minimum convex polygon method (Mohr, 1947).

Tortoise ID No.	Initial CL (mm)	Initial Mass (g)	Habitat	Period Observed	Duration (Days)	Number of Records	Number of Sites	Home (ha) Range
2916	284.0	4050	Old Field	5/17/90-7/10/91	419	519	7	0.024
3816	279.0	3810	Sandhill	4/23/90-9/10/91	505	407	9	1.435
3817	285.0	3500	Sandhill	5/5/90-5/16/91	376	227	4	0.316
3818	256.0	3350	Old Field	5/17/90-7/19/91	428	498	3	0.004
3820	279.0	3780	Old Field	5/11/90-5/23/91	377	407	7	0.076
3821	236.0	2425	Sandhill	5/17/90-6/11/91	390	218	5	0.192
3822	262.0	3850	Sandhill	5/17/90-7/31/91	440	426	11	0.652
3825	272.0	3550	Old Field	5/23/90-8/2/91	467	459	7	0.479
3827	256.0	3180	Sandhill	5/24/90-8/2/91	466	384	5	0.262
3828	249.0	2710	Sandhill	5/30/90-4/28/91	334	286	2	[a]
3830	235.0	2430	Old Field	5/30/90-4/18/91	324	330	3	0.044
3836	257.0	2920	Sandhill	6/8/90-6/13/91	371	400	7	1.414
3838	251.0	2870	Sandhill	6/3/90-4/21/91	323	287	5	0.116
4500	254.0	3650	Old Field	5/17/90-4/9/91	327	345	4	0.002

[a] Linear home range, 2 burrows 39.2 m apart.

burned site. Burrows were measured and categorized by size and activity status Alford 1980; Martin and Layne 1987). Burrows < 140 mm wide were categorized as juvenile; those from 140-230 mm wide as subadult; and those > 230 mm wide as adult. To estimate occupancy, burrows that had obvious tracks or slide marks were considered active. Inactive burrows had a clear entrance but no sign of recent activity. Burrows that were full of debris or had caved in were considered old (Alford 1980; Auffenberg and Franz 1982).

To assess impacts of past human predation on tortoises at the Ordway Preserve, I conducted comparative surveys of populations at the periphery and near the center of the Preserve in 1990. Sample sites < 0.75 km inside the Preserve boundary were classified as perimeter and sites > 0.75 km inside the property line were considered core (Fig. 1). Density estimates were obtained by counting burrows in belt transects measuring 1000 x 25 m (Auffenberg and Franz 1982; Cox et al. 1987). Transects of equal size were sampled in old field and sandhill habitats so that comparisons could be made between the two habitats.

Clutch size was determined by X-raying gravid females (Gibbons and Greene 1979) or by locating nests at burrow aprons. From May 1 to May 15 (1989-1991), tortoises were manually captured or trapped at burrows. Burrow aprons were

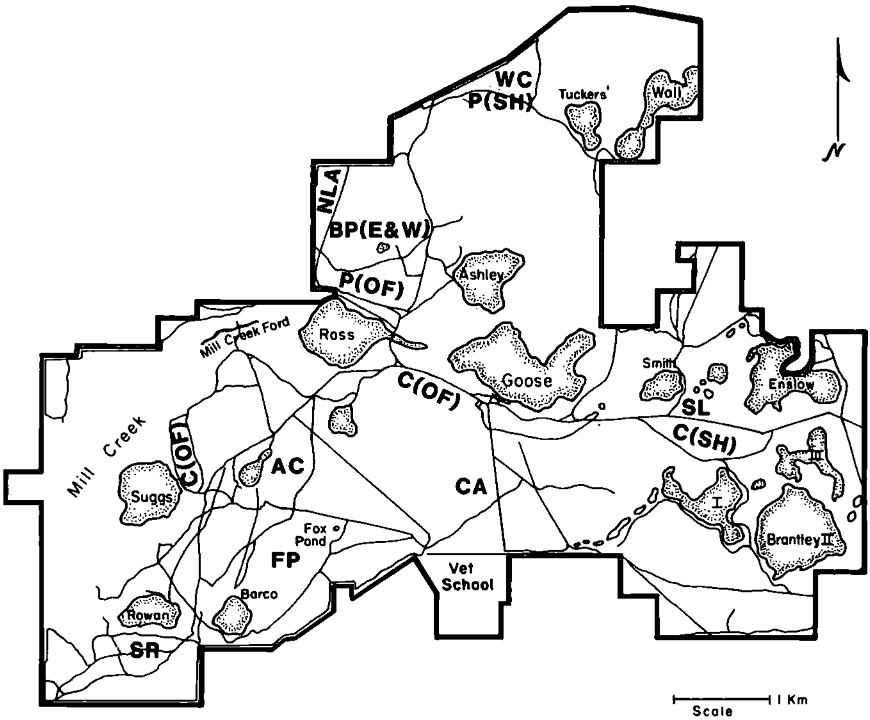

Figure 1. Map of the Katharine Ordway Preserve showing the locations of sandhill (SH) and old field (OF) sites surveyed for gopher tortoise burrows in 1990, and the 1985 to 1991 pre-burn tortoise burrow survey locations. Sites greater than 0.75 km inside the Preserve boundary were considered core (C) whereas those less than 0.75 km inside the boundary were considered perimeter (P). See table 2 for a key to the pre-burn survey locations.

checked for nests beginning in late May. I located nests by probing the sand at the burrow entrance with a 90 cm long, stiff wire. The wire was inserted to a depth of ca 30 cm every 3-5 cm over the entire apron. The area probed included the sand at the entrance up to 1.5 m from the burrow opening. Nests were detected by the sound of the wire striking the porcelain-like egg shells. This technique was non-destructive; no eggs were broken by the wire.

Major habitats occupied by tortoises on the Ordway Preserve include sandhill high pine forests, old fields, and sand live oak hammocks. Burrows in all three habitat types were checked. However, sandhill high pine is the most common upland plant association on the Preserve (Franz and Hall 1991) and most burrows

Table 2. Sandhill sites surveyed for tortoise burrows following prescription burns on the Ordway Preserve, Putnam County, Florida.

Location	Survey Date
New Life Acres Sandhill (NLA)	3/85
Smith Lake Homestead Sandhill (SL)	3/85
Blue Pond Sandhill (west) (BPW)	5/85
Blue Pond Sandhill (east) (BPE)	5/85
Fox Pond Sandhill (FP)	10/86
South Rowan Sandhill (SR)	5/87
Anderson Cue Sandhill (AC)	5/89
Control Area (barn) (CA)	5/91
Wall Cemetery Sandhill (WC)	3/85; 5/88; 5/91

were in this habitat. Burrows of adult tortoises were checked for nests. In 1989 and 1990, active and inactive burrows were checked for eggs, whereas in 1991, active, inactive and old burrows were checked. The same sites were checked each year and an equal number of active and inactive burrows were checked in 1990 and 1991.

Number of eggs, depth from the soil surface to the uppermost egg, distance from the burrow entrance (measured from the point perpendicular to the burrow's upper lip) to the center of the nest, placement of the eggs (layered, tiered, or in one plane), and approximate nest dimensions were recorded at all nest sites. Nests were re-buried and cages were placed over the nests to protect the eggs from predators. Nest cages, following the design of D. R. Jackson (Florida Natural Areas Inventory, Tallahassee), were constructed from 0.64 cm mesh hardware cloth roughly 40 cm square and 12 cm tall. Flaps of hardware cloth were folded out, parallel to the ground and buried to discourage predators from digging under the cage. Cages were anchored with metal stakes at the four corners and along the sides.

In mid-August, nests were checked daily for emerging hatchlings. The incubation period was calculated at nests where the deposition date was known (from daily radio-tracking of gravid females). Straight-line CL, PL and wet body mass of hatchlings were recorded. In 1990, hatchlings were measured after they had emerged from the nest chamber; however, in 1991, some nests were excavated and measurements were taken immediately after hatching.

Data Analysis

The sex ratio of tortoises captured over the six-year period was evaluated using χ^2 analysis (Caughley 1977). A two sample *t*-test was used to compare mean carapace length of male and female tortoises. Recapture rate for each year of the study was calculated as the proportion of marked animals captured in a year to the total number of marked tortoises. Mean annual growth increments were calculated for individuals recaptured one year or more after they had been marked. Linear regression was used to evaluate the relationship between burrow width and carapace length, and to derive a least squares regression line for estimating the carapace length of a tortoise based on burrow width.

Home range of the 14 radio-instrumented tortoises was calculated using the minimum convex polygon method (Mohr 1947). Areas were determined using a digitizer. Analysis of covariance was used to compare mean home range of females in sandhill and old field habitats after adjusting for carapace length and length of time followed. A separate variance *t*-test was used to compare the mean feeding radius of females in the two habitats.

Only active and inactive burrows were included in the analysis of population structure and burrow density. As yet, a site-specific, tortoise-to-burrow correction factor has not been determined for the Ordway Preserve. Therefore, each active and inactive burrow was considered to represent a single tortoise although this will probably overestimate density by a factor of 1.5 to 2. Burrow density, reported in burrows/ha, was calculated for each location. Burrow width was converted to estimated carapace length using the regression equation derived from the carapace length and burrow width measurements. A two-sample *t*-test and separate variance *t*-test were used in the following comparisons of mean estimated carapace length: core vs. perimeter old field; core vs. perimeter sandhill; core sandhill vs. core old field; and perimeter sandhill vs. perimeter old field.

The relationship between female carapace length and clutch size was examined using regression analysis. Mean clutch size between years was compared using a separate variance *t*-test (Ott 1988). Two-sample *t*-tests were used to compare nest depth and distance from the burrow entrance between years. Hatching success for each year was calculated as the number of eggs that hatched successfully divided by the total number of eggs. Hatching success between years was compared using χ^2 analysis (Caughley 1977). Mean carapace length and body mass of hatchlings in 1990 and 1991 were compared using separate variance *t*-tests.

RESULTS AND DISCUSSION

Sex ratio and capture success.– Of 196 tortoises marked over the eight-year period, 89 were male, 69 were female, and 36 were subadult or juvenile. Two individuals were of undetermined sex. The male:female ratio of mature tortoises was 1.3:1 and was not significantly different from 1:1 ($\chi^2 = 2.52$, df = 1, $p > 0.10$). Diemer (1992a) reported male:female ratios of 2:1, 1.5:1, and 0.9:1 for adult tortoises at three north Florida sites. Auffenberg and Iverson (1979) examined 101 museum specimens and found a male:female ratio of 1.06:1.

Table 3. Recapture rates[a] for gopher tortoises on the Ordway Preserve, Putnam County, Florida.

	Year								
Sex	1983	1984	1985	1986	1987	1988	1989	1990	1991
Male	0.0	0.0	0.0	5.6	3.2	11.1	6.3	10.6	7.1
Female	0.0	0.0	11.1	0.0	13.6	4.2	9.4	13.4	25.9
Juvenile	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.6	2.0
All	0.0	0.0	4.3	2.7	6.6	5.6	6.4	11.2	14.1

[a] The number of marked animals captured in a year divided by the total number of marked tortoises.

The total number of captures of known-sex individuals was not significantly different from 1:1 ($\chi^2 = 2.30$, df = 1, $p > 0.10$), indicating that capture-related sex bias did not occur. Eighty-one marked individuals were recaptured over the eight-year period. Although most captures were incidental, recapture rates increased over time as more animals were marked (Table 3). The recapture rate for females was high in 1990, because I selectively trapped for telemetered females. Most opportunistic captures (25%) occurred in frequently traveled locations.

Mean CL of adult male tortoises marked was 244.3 mm (n = 90; range = 207.0-301.5; SD = 17.7). Mature female tortoises averaged 255.2 mm CL (n = 72; range = 221.0-298.0; SD = 16.9). The size difference between sexes was significant ($t = 3.952$, df = 160, $p > 0.001$). Selection may favor females with larger body size for increased reproductive potential (McRae et al. 1981a; Landers et al. 1982). The size difference between sexes may be further accentuated by selection for small body size in male gopher tortoises. During breeding season, males often travel long distances and invest considerable energy in courtship (Douglass 1976; Landers et al. 1982). Small males could more efficiently maintain their body temperature (Swingland 1977) during prolonged courtship events.

Growth.– Mean annual growth increments were calculated for 21 tortoises (5 males, 14 females, and 2 subadults). There was no discernible difference in growth between male and female tortoises. The greatest increases were observed in the smallest individuals (Fig. 2). In southwest Georgia, growth increments were greatest in individuals in the 100-190 mm CL size classes and growth rate declined in large individuals (Landers et al. 1982). A similar trend is evident in growth data collected at a central Florida location (Goin and Goff 1941). Growth rate to sexual maturity is an important population characteristic because juveniles and subadults are especially vulnerable to predators (Auffenberg and Iverson 1979).

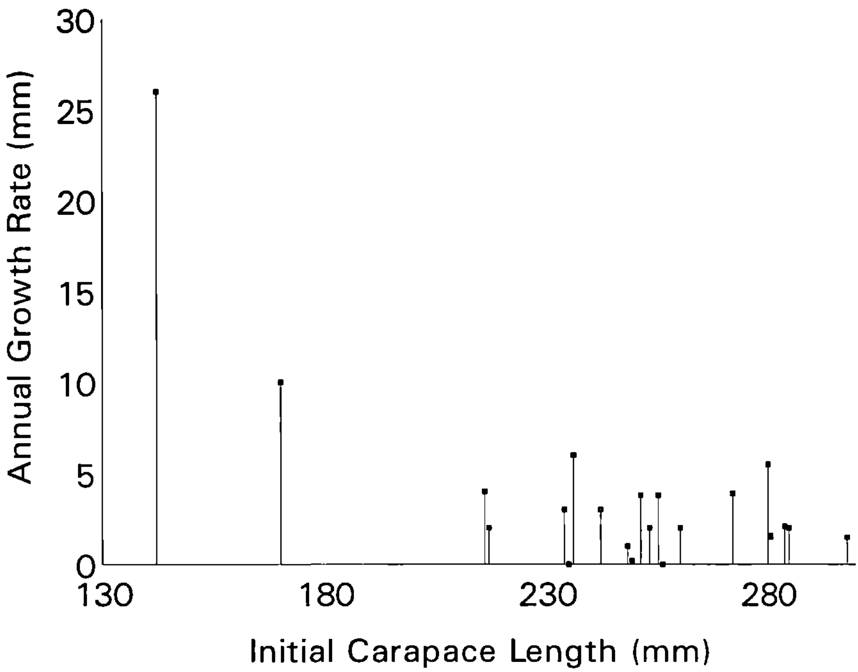

Figure 2. Mean annual growth increments for 21 gopher tortoises on the Katharine Ordway Preserve, Putnam Co., Florida.

Activity patterns.-- Radio-instrumented female tortoises rarely were observed above ground. Of 5199 observations, tortoises were seen at the surface only 97 times (< 2% of all observations). When encountered at the surface, female tortoises most often were basking (76.4%) on or near the burrow apron, followed by walking (16.5%), feeding (4.1%), nesting (1%) and mating (1%). Most observations of basking behavior occurred in March (18.9%) and June (13.5%).

Telemetered tortoises were active in all months of the year. However, the number of active days (indicated by disturbance to sticks set at burrow entrances) were highest from March through November (Fig. 3). Most incidental captures of tortoises occurred from May to October (Fig. 4). Nearly 52% of all females were caught in May and June during peak nesting season. Captures of males were high from May through October and probably reflects long-range breeding forays. Breeding has been reported from February through October (Dietlein and Franz 1979; Iverson 1980; Diemer 1986; L. Smith field notes) and is thought to peak in spring and fall (Taylor 1982b).

Mean number of burrows used per month by telemetered females ranged from 1.1 in January and October to 1.6 in May at the height of the reproductive season. The number of burrows used and inter-burrow movements were greatest from May through September (Fig. 5). Females in sandhill habitat had more than three times as many inter-burrow movements in June as did old field females. Movements of sandhill females in July and August were nearly twice as frequent as old field tortoises. Relocation during summer months probably was related to the availability of food. Herbaceous vegetation is unevenly distributed in sandhills and preferred foods may be depleted during mid-to-late summer causing tortoises to relocate. At a southwest Georgia sandhill site, adult tortoises migrated in late summer as food resources became scarce (McRae et al. 1981b).

Nearly all observations of telemetered tortoises and incidental captures occurred between 1000 and 1800 hrs with peak observations occurring between 1200 and 1400 hrs and 1600 and 1700 hrs (Fig. 6). Similar diel activity patterns have been observed in north and south Florida tortoises (Clements 1956; Douglass and Layne 1978).

Home range and movements.-- Individual burrows were the focal point of tortoise activity. All feeding activity occurred within 17 m of the burrow being used at the time (n = 6, mean = 7.4 m, range = 2.4-16.6. SD = 5.0). The feeding radius of telemetered females in sandhill habitat averaged 11.9 m (n = 4, range = 2.4-16.6 m, SD = 5.6) compared with 5.9 m for old field females (n = 12, range = 2.4-14.5, SD = 3.6). Mean feeding radii of tortoises in the two habitats were not significantly different ($t = 1.75$, $df = 4$, $p > 0.05$), although the sample size was small (n = 16) because tortoises tended to retreat into burrows as I approached. At a Georgia sandhill locality, 95% of all gopher tortoise feeding activity took place within 30 m of the burrow and the mean feeding radius of 45 adult tortoises (including males) was 13.0 m (McRae et al. 1981b). Gopher tortoises depend on burrows for

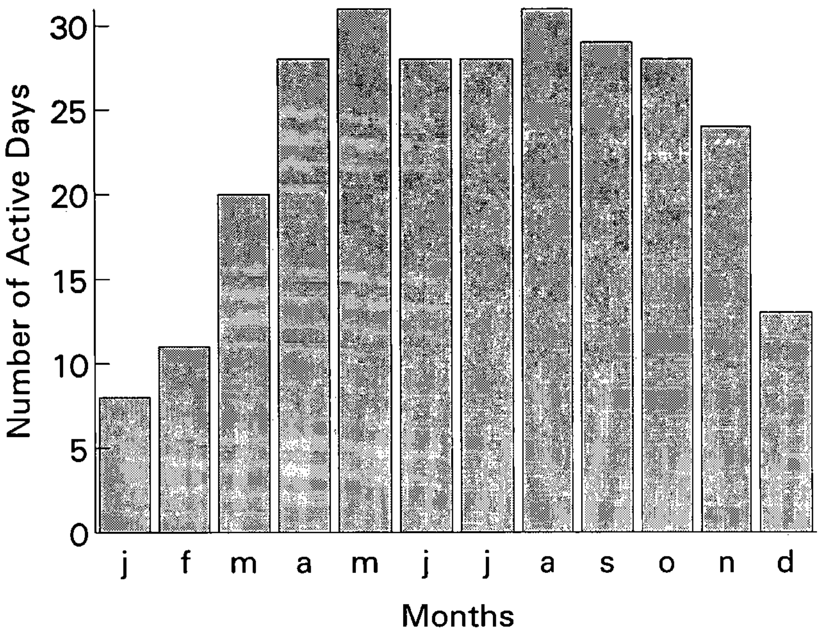

Figure 3. Mean number of active days per month for 14 adult female telemetered gopher tortoises on the Katharine Ordway Preserve, Putnam Co., Florida.

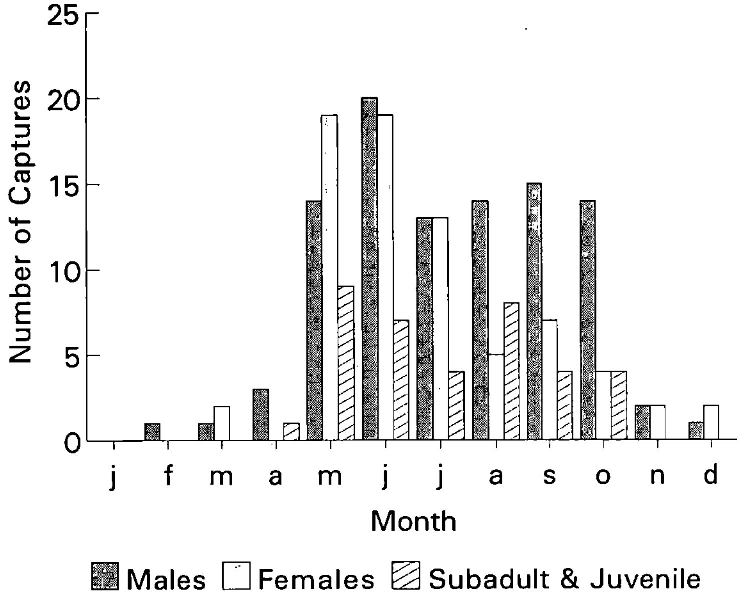

Figure 4. Monthly distribution of gopher tortoise captures on the Katharine Ordway Preserve, Putnam Co., Florida. Data were collected from October 1983 through September 1991.

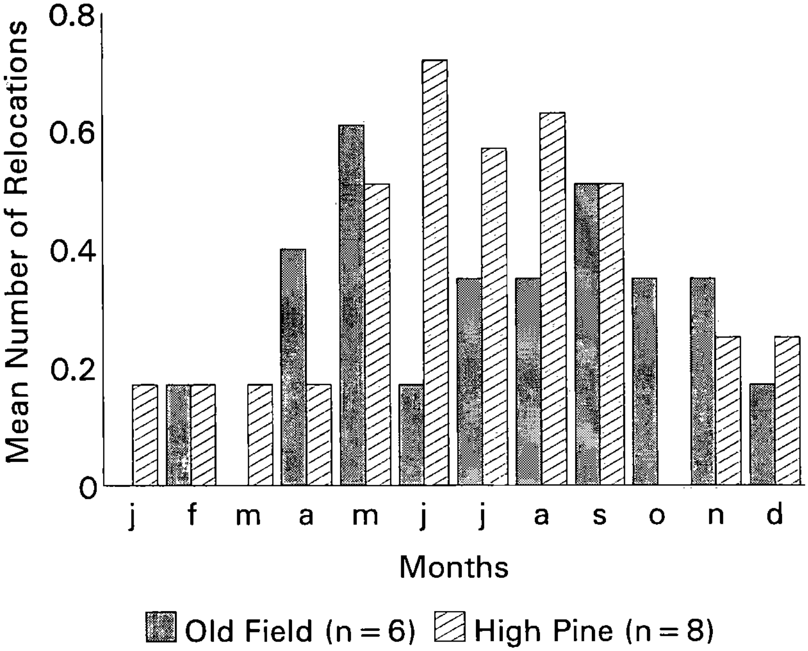

Figure 5. Monthly inter-burrow movements by female gopher tortoises on the Katharine Ordway Preserve, Putnam Co., Florida.

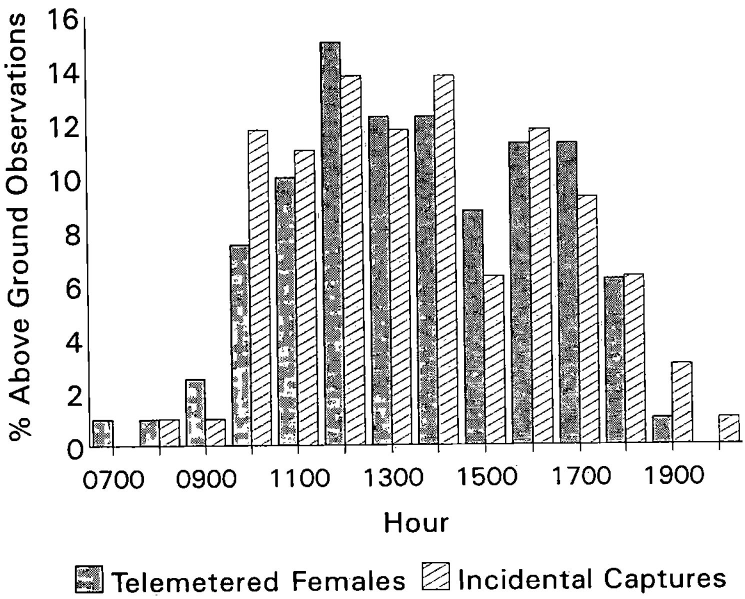

Figure 6. Hourly distribution of observations and captures of gopher tortoises on the Katharine Ordway Preserve, Putnam Co., Florida.

protection against predators and temperature extremes. The foraging range of gopher tortoises probably varies depending upon resource availability. In the Texas tortoise (*G. berlandieri*) daily movements were greatest in populations where food plants were scarce or scattered (Auffenberg and Weaver 1969).

Inter-burrow movements of telemetered females averaged 63.2 m (n = 51, range = 10.2-375.0, SD = 63.4). The longest recorded movement between burrows occurred in June when one female moved 375 m in an afternoon. In late May and June, long distance movements associated with nesting were observed. Mean length of nesting forays was 77.4 m (n = 5, range = 11.0-141.90, SD = 48.86).

Home range size of the 14 radio-instrumented females ranged between 0.002 and 1.435 ha (Table 1). Mean home range size of females, after adjusting for carapace length and length of time followed, were 0.482 ha (S.D. = 0.413) in sandhills and 0.105 ha (S.D. = 0.169) in old fields. The difference between mean home range size in the two habitats was not significant (F = 3.88, df = 13, p = 0.0771). Tortoise size and duration of observation did not explain the variation in home range size between habitats. However, a contributing factor may be that grasses and forbs, which constitute a major portion of the gopher tortoise's diet (Garner and Landers 1981; Macdonald 1986; Macdonald and Mushinsky 1988), are more abundant and evenly distributed in old fields than in sandhills (Auffenberg and Franz 1982). Auffenberg and Iverson (1979) found that gopher tortoise home range size was inversely related to the density of herbaceous ground cover.

Literature records of mean home range size of female tortoises range between 0.08 and 0.70 ha (McRae et al. 1981b; Wright 1982; Doonan 1986; Diemer 1992b). The variation may be related to differences in habitat type, geographic location, and length of study. McRae et al. (1981b) and Diemer (1992b) also found considerable individual variation in home range size.

Population structure and tortoise densities.-- At seven of the nine post-burn surveys, more than 50% of all burrows were in the adult size class (Fig. 7). These results may be biased because subadult and adult tortoises often use more than one burrow in a season (McRae et al. 1981b; Auffenberg and Franz 1982) and the actual tortoise-to-burrow ratio is certainly less than 1:1. Alford (1980) suggested that a lack of small burrows was indicative of high mortality of eggs and young. Although small burrows are difficult to detect, I conducted my surveys following prescribed burns to try to maximize the chance of locating small burrows. Therefore, the truncated size class distributions probably indicate a low recruitment rate and could reflect either a stable or declining population.

Smith Lake and Wall Cemetery sandhills differed from the other areas in that small size classes were well-represented (Figs. 7, 8). In the 1985 census, most burrows at Smith Lake were in the subadult size class (140-230 mm). I surveyed a site adjacent to Smith Lake, using transects, in 1990 and found only subadult and

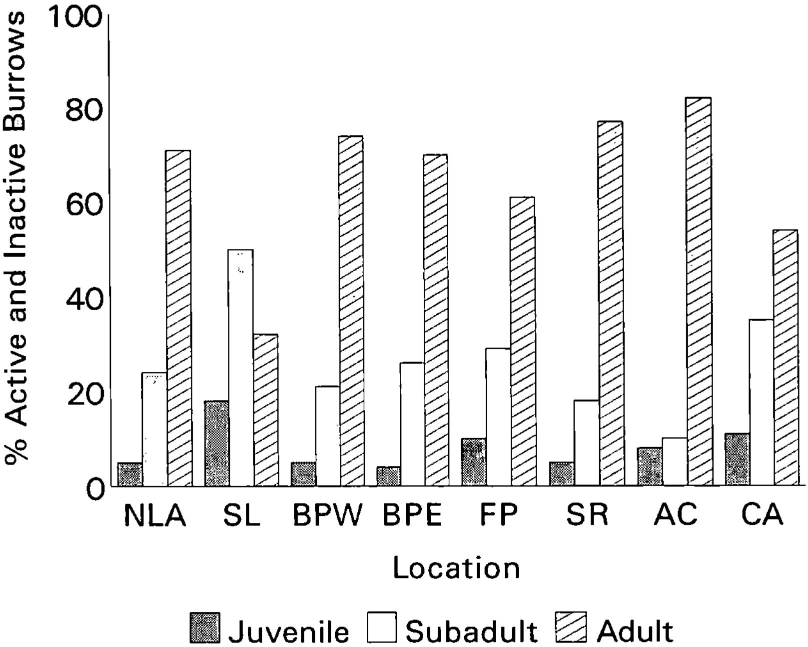

Figure 7. Size-class distribution of gopher tortoise burrows at selected sandhill sites on the Katharine Ordway Preserve, Putnam Co., Florida. The surveys were conducted from 1985 through 1991. Table 2 gives the site names for the abbreviations.

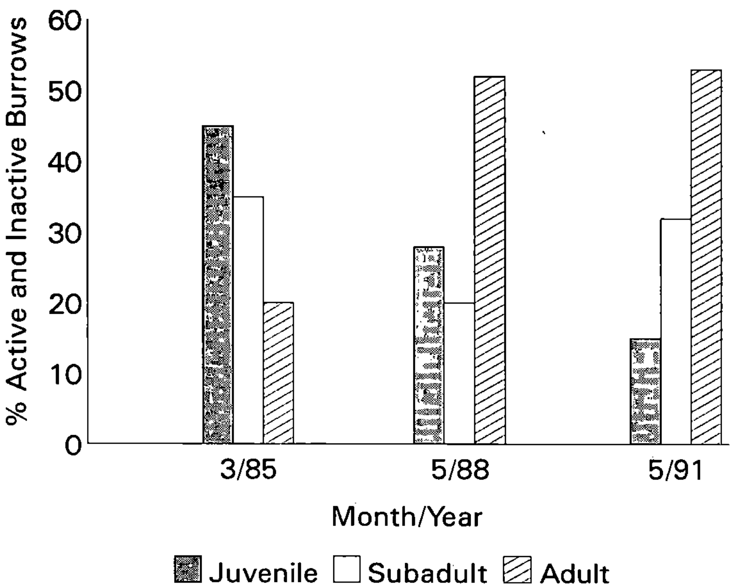

Figure 8. Size-class distribution of gopher tortoise burrows at Wall Cemetery sandhill, Katharine Ordway Preserve, Putnam Co., Florida.

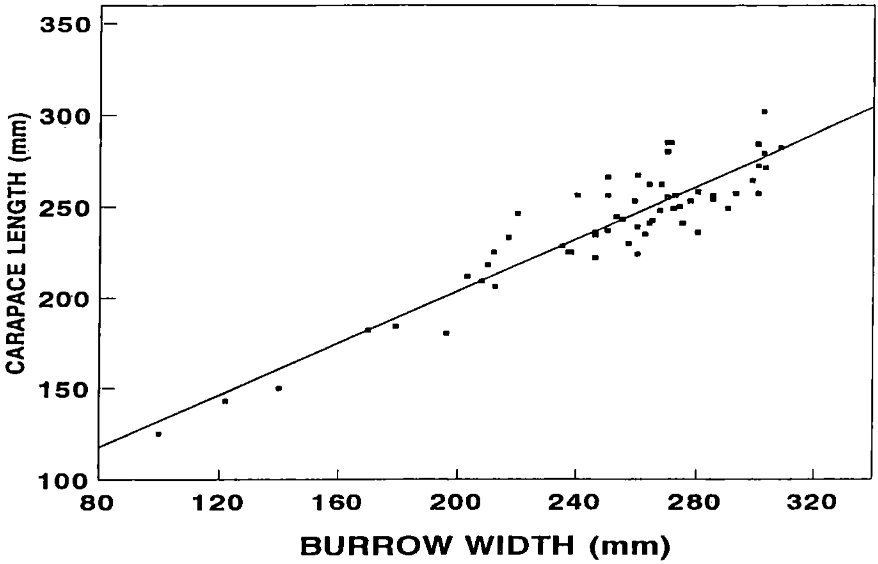

Figure 9. The relationship between burrow width and carapace length for gopher tortoises on the Katharine Ordway Preserve, Putnam Co., Florida. The regression equation is: Carapace length = 62.049 + 0.71 (Burrow width).

small adult-size burrows. Prior to 1979, tortoises in the area had been hunted (T. Perry and R. Franz pers. comm.). Assuming that large tortoises were removed from this population as recently as 1979, hatchling and small juvenile individuals from that period would be expected to be subadults or small adults in 1990. It appears that adult tortoises have not immigrated into this area.

Surveys at three-year intervals at Wall Cemetery (WC) revealed a shift from primarily juveniles in 1985 to adults in 1991 (Fig. 8). This population also was harvested prior to 1979. The observed changes in population structure may reflect growth of individuals from the 1985 population and immigration from surrounding areas.

Estimated carapace length was calculated using the regression line generated from 64 pairs of carapace length and burrow width measurements. Burrow width was a good indicator of tortoise size (Fig. 9); the fit to the data was significant (t = 18.35. df = 62, $p < 0.0001$. r = 0.92). Mean estimated CL at core sandhill and old field sites were significantly different (t = 2.38, df = 20, $p < 0.025$). The core sandhill site, as mentioned above, was harvested prior to 1979. Burrow density at the core sandhill site (2.42 burrows per ha) was comparatively low, reflecting the removal of sexually mature individuals.

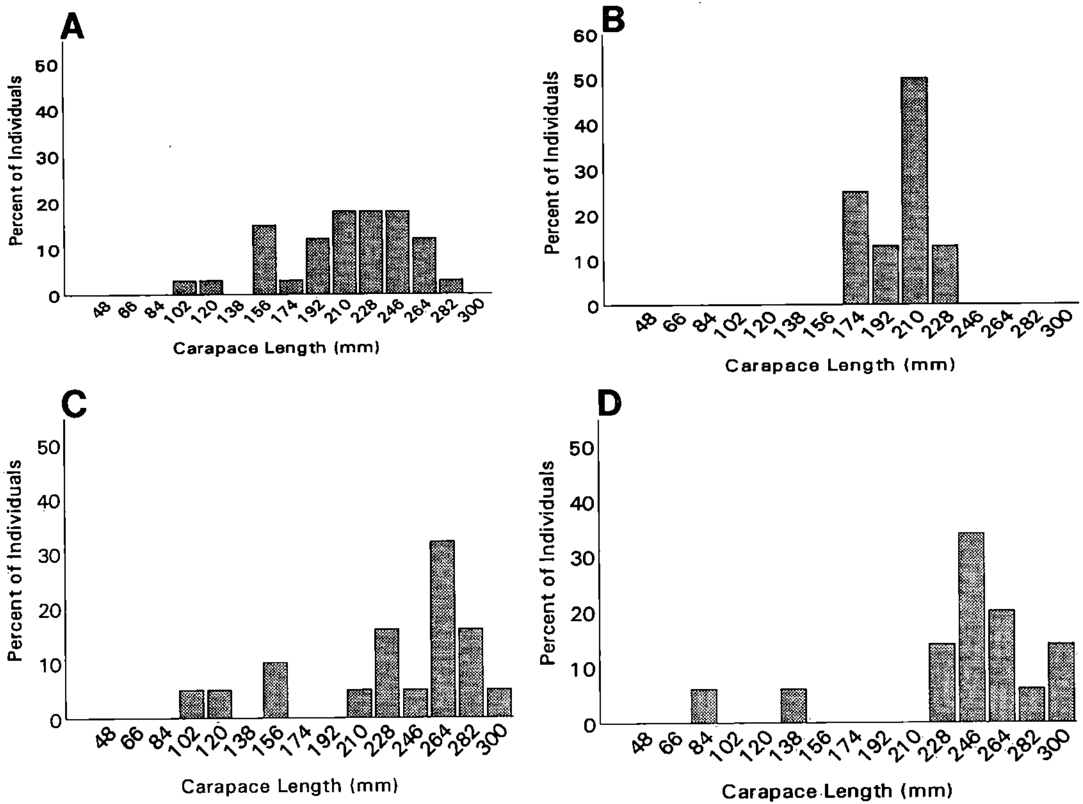

Figure 10. Size-class distribution, using estimated carapace length, of gopher tortoise populations on the Katharine Ordway Preserve, Putnam Co., Florida. A. Perimeter sandhill sites. B. Core sandhill sites. C. Perimeter old field sites. D. Core old field sites.

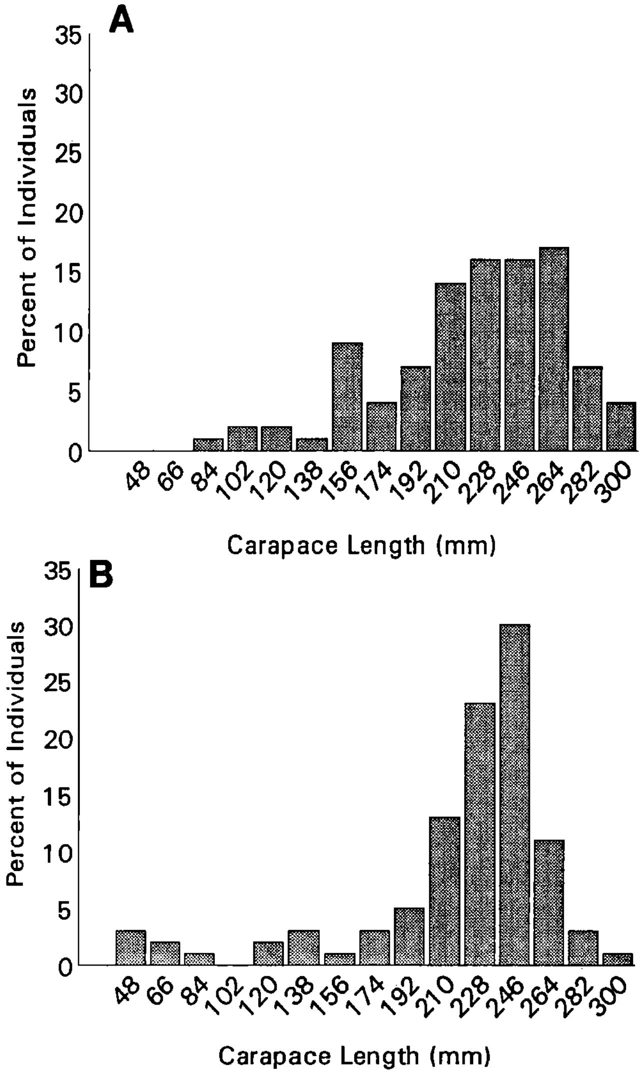

Figure 11. Size-class distribution of gopher tortoise populations on the Katharine Ordway Preserve, Putnam Co., Florida. A. Selected sandhill and old field sites, using estimated carapace length. B. All gopher tortoises captured.

The size-class distributions, based on burrow surveys, for core and perimeter sites were roughly unimodal (Fig. 10). At perimeter sites in both habitats and at the core old field site most burrows were adult size. The core sandhill site was the exception, with all carapace length estimates between 175 and 229 mm. The size-

Table 4. Estimated tortoise size and burrow density in sandhill and old field habitats on the Ordway Preserve, Putnam County, Florida.

Habitat	Location	Number of Burrows[a]	Estimated Carapace Length (mm) Mean	SD	Density (Burrows/ha)
Sandhill	Core	8	208.9	19.4	2.42
Sandhill	Perimeter	35	218.2	42.5	10.56
Old field	Core	15	247.7	54.4	6.00
Old field	Perimeter	19	238.5	57.2	7.60

[a] Total includes active and inactive burrows only.

class distribution for all localities combined and the size-class distributions based on capture data also are unimodal (Fig. 11).

Recent harvest from the populations at the periphery of the Ordway Preserve was not detected. The highest concentrations of burrows were found at perimeter sites in both habitats (Table 4) and mean estimated carapace length of tortoises at the perimeter sandhill and old field sites were not significantly different ($t = 1.32$, $df = 29$, $P > 0.05$). Historically, selected sites were harvested regardless of distance from the boundary fence. Apparently, tortoise hunters removed tortoises well inside the Preserve.

Nest site selection.-- Less than 2% of the 2008 burrow aprons that I examined from 1989 through 1991 contained nests (Table 5), and only 2 of 18 gravid females (as determined by X-ray) deposited their clutches in burrow aprons. It appears that, on the Ordway Preserve, female tortoises select nest sites away from the burrow entrance, verifying the speculation of Carr (1952). These findings differ from general statements in the literature which regard burrow entrances as the primary nesting location (Hallinan 1923; Cox et al. 1987). In southwest Georgia, only 17 of 110 nests (15%) were deposited away from the burrow entrance (Landers et al. 1980); thick herbaceous cover and roots were thought to restrict nesting to burrow entrances and man-made clearings (Landers et al. 1980). Undoubtedly, factors such as vegetative cover and local soil conditions contribute to variation in nest site selection. Availability of alternative nest sites may be particularly important because egg predators may use burrow aprons as visual cues for locating nests.

Table 5. Number of burrow aprons containing nests on the Ordway Preserve, Putnam County, Florida. The first number is the number of nests and the second is the number of burrow aprons searched.

	Number of Nests/Burrow			
Habitat	1989	1990	1991	1989-1991
SLOH[a]	0/0	1/17	1/13	2/30
OF[b]	0/32	1/123	2/149	3/304
SH/HP[c]	2/220	14/738	13/716	29/1674
All Habitats	2/252	16/878	16/878	34/2008

[a] Sand live oak hammock.
[b] Old field.
[c] Sandhill/high pine.

Differences in the nest-to-burrow ratios among the three habitats may be an artifact of sampling. The highest ratio of nests per burrow (6.7%) occurred in sand live oak hammock habitat although only 30 aprons in this habitat were probed (Table 5). The nest-to-burrow ratio was second highest in the sandhill habitat (1.7%) and was nearly equal in 1990 and 1991. The fewest number of nests per burrow (1%) occurred in old field habitat. Vegetative cover in uplands on the Ordway Preserve is variable, depending on frequency of prescribed burns, but open sandy patches are available for nesting.

Most nests found in burrow aprons (78%) were located at active burrows, whereas 19% were located at inactive and 3% were located at old burrows. Active burrows may be preferred as nest sites over inactive and old burrows, because the aprons typically are kept free of vegetation and debris by the resident tortoise. The soil on the aprons of active burrows may be less compacted than at unoccupied burrows, and better suited for constructing nest cavities.

Mean nest depth and distance from the burrow entrance did not differ significantly between years (Table 6). Mean depth of nests (13.8 cm) was comparable to that reported by Diemer and Moore (1994) at another north-central Florida site (mean = 13.0 cm, n = 5). Average nest depth at two south Alabama sites were 14.1 cm (n = 7) and 16.0 cm (n = 4) (Marshall 1987).

Average distance from the burrow entrance to the nest was 18.3 cm. None of the nests were deposited more than 1 m from the burrow opening and one clutch was found 5 cm inside the entrance. Average distance from the opening was comparable to that reported for 93 nests in southwest Georgia (mean = 18.0 cm) (Landers et al. 1980).

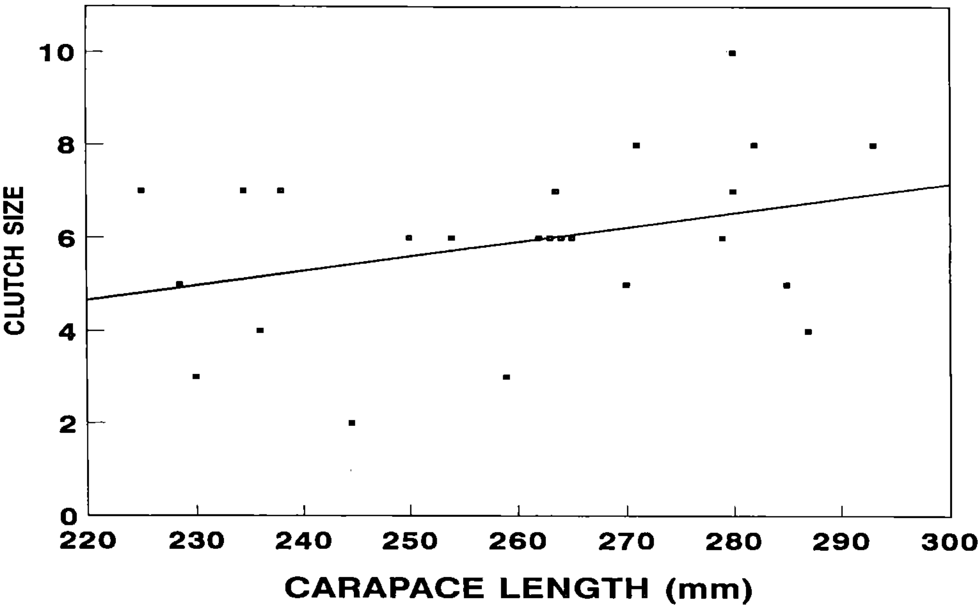

Figure 12. Relationship between clutch size and carapace length of 24 gopher tortoises on the Katharine Ordway Preserve, Putnam Co., Florida. The regression equation is: Clutch size = -2.198 + 0.0312(Carapace length).

Clutch size.– Mean clutch size for the three year period was 5.76 (n = 51, SD = 1.57) (Table 7) which is comparable to literature records of 5.2-5.8 for northern Florida (Hallinan 1923; Iverson 1980; Taylor 1982b; Diemer 1986). Mean clutch size in 1990, at the height of the five-year drought, was less than in 1991 when seasonal rainfall was near average (t = -1.684, df = 39, $0.025 < p < 0.05$). Some of the variation between years might be explained by a difference in female size. Mean carapace length of gravid females for the two years was not significantly different (t = 0.659, df = 21, $p > 0.10$), although the size of females that deposited their eggs at aprons is not known. The relationship between drought and reproduction in the gopher tortoise has not been documented. However, a drought-related decrease in clutch frequency has been reported in the desert tortoise (*G. agassizii*) and in some species of aquatic turtles (Gibbons et al. 1983; Turner et al. 1984). A decrease in the number of individuals that produce eggs during drought also has been documented in four species of aquatic turtles (Gibbons et al. 1983).

I found no evidence that any of the females deposited more than one clutch annually. Three of the 18 females X-rayed were gravid for two consecutive years. In some gopher tortoise colonies, no nesting is thought to occur for many years (Auffenberg and Iverson 1979).

There was a positive correlation between female carapace length and clutch size (Fig. 12). Although the fit to the data was significant (t = 1.73, df = 22, $p <$ 0.05, r = 0.346), CL explained only 12% of the variance in clutch size. A 32 mm increase in carapace length would result in a one egg increase in clutch size.

A negative correlation was found between estimated CL and clutch size for nests found at burrow aprons (Fig. 13). The fit to the data is significant (t = -2.249, df = 25, $p < 0.01$, r = -0.41). The negative correlation coefficient suggests that eggs oviposited at burrow aprons probably were laid by non-resident females.

Incubation and hatching success.– Deposition dates were determined for five nests during the three year period. Nesting dates were 13, 18, and 29 June 1990; and 1 and 3 June 1991. Reported field nesting dates for north Florida tortoises range from 18 May through 18 June (Iverson 1980; Diemer and Moore (1994). The incubation period for the five nests where deposition dates were known

Table 6. Depth and distance from burrow entrance of gopher tortoise nests on the Ordway Preserve, Putnam County, Florida. Measurements are in cm.

		Nest Distance From Burrow			Nest Depth		
Year	N	Mean	Range	SD	Mean	Range	SD
1989	2	25.4	25.4-25.4	0.0	15.7	8.9-22.5	6.8
1990	16	23.7	0.0-100.0	22.5	13.3	0.5-27.5	6.5
1991	16	12.4	-5.0-40.0	13.0	14.2	4.0-25.7	5.5
All Years	34	18.3	-5.0-100.0	19.0	13.8	0.5-27.0	6.1

averaged 87.4 days (range = 67-102), which is comparable to literature records of 80 - 90 days (Iverson 1980). The earliest recorded hatching date was 24 August, whereas the latest was 2 October. Hatching peaked during the last week of August and first week of September. A clutch completed hatching in 1 to 4 days. None of the hatchlings stayed in the nest chamber for more than one week.

Of the eggs at protected nests, 67% hatched successfully in 1990 (n = 75) compared to 97% in 1991 (n = 92). The difference between years was not significant (χ^2 = 2.767, df = 1, $p > 0.05$). In 1990, five of 16 nests failed to produce

Table 7. Clutch size[a] of gopher tortoises on the Ordway Preserve, Putnam County, Florida.

Habitat	N	Mean	Range	SD
1989	3	6.67	(6-7)	0.47
1990	17	5.18	(1-7)	1.34
1991	31	6.00	(2-10)	1.65
1989-1991	51	5.76	(1-10)	1.57

[a] Mean clutch size in 1990 was significantly different from 1991 (t = -1.684, d.f.= 39, $0.025 < p < 0.05$).

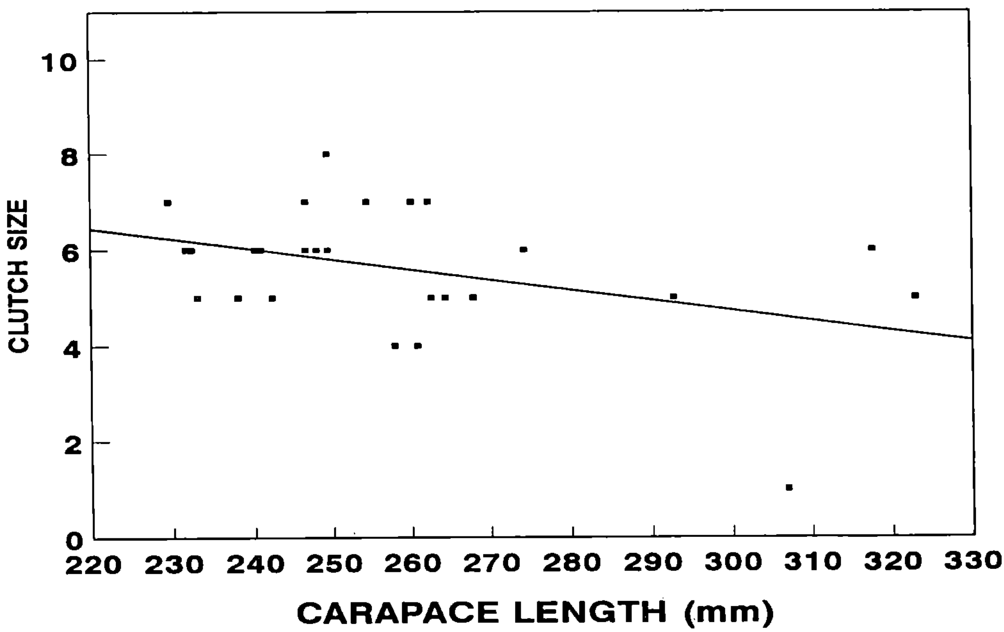

Figure 13. Relationship between clutch size and estimated carapace length at 26 gopher tortoise burrows on the Katharine Ordway Preserve, Putnam Co., Florida. The regression equation is: Clutch size = 11.142 - 0.0214 (Estimated carapace length).

hatchlings. The eggs at these nests were opened in late October and were found to have decayed; they appeared to be infertile. In 1991, all 16 nests had at least partial hatching success. In a southwest Georgia field study, 86% of protected eggs (n = 179) hatched successfully (Landers et al. 1980). Arata (1959) reported a hatching success of 92% for 13 eggs incubated in the laboratory.

Despite protective enclosures in 1990, one nest was raided by a mammalian predator. An unidentified predator dislodged a nest cage and destroyed all six eggs at a shallow nest (< 0.5 cm to the top egg). Raccoon tracks were observed on the burrow apron. In 1990 and 1991, 16 hatchlings at five different nests (12% of all hatchlings) were destroyed by ants. *Solenopsis geminata*, a species of fire ant native to Florida, was collected at four of the nests, and *Conomyrma bossuta* and *Solenopsis pergandei* were collected at one nest. Hatchling gopher tortoises were killed by non-native fire ants (*Solenopsis salvissima*) at two nests in southwest Georgia. Fire ants thrive in disturbed habitats (M. Deyrup, Archbold Biological Station, pers. comm.) and probably are important predators on hatchlings, particularly in ruderal habitats.

Hatchling size.— Straight-line carapace length of hatchlings ranged from 32.0-51.8 mm (Table 8). There was a significant difference between mean carapace length of hatchlings in 1990 and 1991 (t = 10.30, df = 108, $p < 0.001$), probably because some 1991 hatchlings were measured before they had emerged from the nest chamber. Hatchling gopher tortoises do not completely unfold until 3-5 days after they hatch (Arata 1959), and seven day old hatchlings average 48.2 mm carapace length (n = 11, range = 45.0-50.9) (Iverson 1980).

Wet body mass of hatchlings in 1991 was greater than in 1990 (t = 3.88, df = 80, $p < 0.001$). Linley (1987) found significant differences in the wet mass of offspring of different females. Genetic and nutritional constraints of the female are reflected in hatchling body mass (Linley 1987). The five-year drought may have imposed nutritional constraints on female gopher tortoises, thus affecting hatchling body mass. This could be important because in some tortoises, large hatchlings have higher survivorship than small hatchlings (Swingland 1977). Long-term data are needed to detect and interpret yearly variation in life history parameters.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Several findings from this study have important implications for gopher tortoise management. Variation in home range size among individual females should be considered in determining the minimum size of tortoise preserves. Maximum home range values may provide the best estimate of long-term habitat requirements of gopher tortoises because of the considerable variation among individuals (Cox et al. 1987). Sufficient area for nest forays and seasonal

Table 8. Hatchling gopher tortoise measurements for the Ordway Preserve, Putnam County, Florida. Measurements are in mm.

	Carapace Length[a]				Wet Body Mass[b]			
Year	N	Mean	Range	SD	N	Mean	Range	SD
1990	36	48.0	41.0-51.8	2.56	36	30.0	18.2-38.8	3.94
1991	74	42.3	32.0-47.0	2.73	73	33.3	27.0-43.0	4.65

[a] Mean carapace length in 1990 was significantly different from 1991 ($t = 10.30$, d.f. = 108, $P < 0.001$).
[b] Mean wet body mass in 1990 was significantly different from 1991 ($t = -3.88$, d.f. = 80, $P < 0.001$).

movements must be provided to ensure recruitment of new individuals into the population.

Differences in home range size related to habitat also must be considered in determining the optimum size of preserves. Minimum area requirements of tortoises in sandhills, where food plants are scattered, probably are greater than in ruderal sites, where herbaceous cover tends to be thick.

Under favorable conditions, minimum viable population size for the gopher tortoise has been estimated to be 40 to 50 individuals (assuming a 1:1 adult sex ratio) (Cox et al. 1987). Based on home range estimates from this study, 20 female tortoises in sandhills would require 10 to 30 ha of habitat and those in old fields 2 to 10 ha. Home ranges probably overlap, and males and juveniles tend to use a larger area than females (McRae et al. 1981b; Diemer 1992b). Estimates of area requirements may be useful in determining size of recipient sites for tortoise relocation and reintroduction projects. Research is needed to fully evaluate the carrying capacity of different habitats.

Burrow densities and tortoise population structure on the Ordway Preserve varied by location, reflecting the effects of past harvest. Effects of harvest prior to 1979 still were evident in 1990 at a site near the center of the Preserve. Tortoise populations are slow to recover from the impacts of harvest as a result of low reproductive potential and high egg and hatchling mortality. These life history constraints limit the ability of tortoise populations to recover from other human impacts such as habitat alteration.

Clutch size, nesting dates, and incubation period on the Ordway Preserve were comparable to previous studies conducted in north-central Florida. However, in contrast to reports in the literature, it appears that many female tortoises on the Ordway Preserve deposit their eggs away from burrow entrances and that nests at burrow aprons are not necessarily those of resident females. Studies are needed to define specific conditions important in nest site selection and to identify alternative nest sites. Alternative nest sites may be particularly important if egg predators are able to use burrows as visual cues to locate nests. In order to provide suitable nest and burrow sites, a prescribed burning program should be implemented. Summer burns which mimic natural lightning fires remove dead litter and increase production of herbaceous food plants (Platt et al. 1988).

Mean clutch size and hatchling body mass differed in 1990 and 1991. The differences observed may be related to nutritional constraints on females because of the prolonged drought that occurred from 1985 to 1990. Long-term studies are needed to differentiate between normal yearly variation and effects of environmental perturbations such as drought.

Management strategies should include monitoring (and control, if necessary through hunting and trapping) of mammals that prey on tortoise eggs and hatchlings. Human activities have favored small opportunistic predators such as raccoons (Landers 1980). Small mammal predator populations are uncontrolled, because large predators have been extirpated from most of their former range (Marshall 1987; Means 1988). Therefore, hatchling and egg predators probably exert more pressure on tortoise populations now than they have in the past. In areas where tortoise numbers have been depleted, it may be necessary to protect nests from predators and to head-start hatchlings in on-site enclosures.

Under natural conditions, the low reproductive potential of gopher tortoises is compensated by a long life span, low adult mortality and the persistence of extensive, unaltered habitat (Means 1988). Human activities have altered habitat and predator-prey relationships. Remaining tortoise populations and habitat must be actively managed to ensure their survival. Long-term research on gopher tortoise demographics is necessary to develop sound management practices. The protection and management of gopher tortoise populations are particularly important because there are implications beyond a single species. Simply acquiring and protecting upland habitats are not sufficient measures for ensuring survival of gopher tortoise populations. Tortoise habitat must be actively managed, because habitat quality is critical to population survival (Cox et al. 1987; Breininger et al. 1988).

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