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Movements and Home Range of Hatchling and Yearling Gopher Tortoises, *Gopherus polyphemus*

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ABSTRACT. – Fourteen hatchling gopher tortoises were released at their nests within one day of emergence and located daily with radiotelemetry for up to 22 months. Active and dormant periods were evident from burrow activity observations and were found to be closely related to environmental temperature. Most hatchlings dug burrows within one day of release; the mean distance of the first burrow from the nest was 14.6 ± 6.3 m. The mean daily location was 7.7 ± 6.5 m from the burrow. The tortoises dug a total of 83 burrows at a mean rate of 4.8 burrows/tortoise-year and at a mean distance of 17.1 ± 28.7 m apart. The mean home range during the active period was 363 ± 265 m^2, significantly larger than dormant period home ranges. The mean annual range of nine tortoises surviving a year was 2032 ± 1307 m^2, and their mean total range at the end of the study was 2554 ± 1382 m^2. We suggest annual or total ranges should be employed by wildlife managers in estimating the area requirements of this species.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Gopherus polyphemus*; tortoise; hatchlings; ecology; movements; home range; activity patterns; telemetry; Florida; USA

The gopher tortoise, *Gopherus polyphemus*, has sustained population declines primarily because of habitat destruction resulting from urbanization and other human activities (Auffenberg and Franz, 1982). Attempts to slow the declines have escalated recently (Diemer, 1986), and in Florida, relocation of imperiled populations is sometimes chosen as a partial solution (Diemer, 1989). The practice of relocation led Cox et al. (1987) to estimate the minimum area required by an adult animal based on home range measurements by McRae et al. (1981). Those estimates were similar to gopher tortoise ranges estimated by Auffenberg and Iverson (1979), Wright (1982), and Douglass (1986) based on recapture. Diemer (1992) found home ranges of adult tortoises to be larger than those reported by McRae et al. (1981).

Gopher tortoises dig burrows in which they sleep, hibernate, and avoid high temperatures, desiccation, and predators (Pritchard, 1979). Adult burrows average 4.6 m long and 1.8 m deep, and sand excavated from the tunnel is piled in a mound or "apron" just outside the burrow mouth (Hansen, 1963). The apron is a site for basking, courtship, and copulation (Douglass, 1986); and in some cases females deposit eggs in a nest about 10–20 cm deep in the apron (Iverson, 1980).

Adult tortoises and their burrows are relatively easy to locate, but in an intensive nine-year study on the Archbold Biological Station in southern Florida, only 59 tortoises under 100 mm in plastron length were observed (Douglass, 1978). Only three studies to date report on movements and ranges of juvenile or hatchling gopher tortoises. McRae et al. (1981) reported movements of juveniles and hatchlings based on capture and field observations. Radio telemetry was used by Diemer (1992) in northern Florida and Wilson et al. (1994) in southern Florida to track juveniles (1–4 yr). This paper presents the first study of activities and home ranges of gopher tortoises beginning with emergence from the nest using radio telemetry. We observed the tortoises to identify periods of dormancy and activity, to determine how many burrows they dug, how far burrows were from one another and from the nest, the length of daily movements from the burrow, and to estimate seasonal, annual, and total home ranges.

MATERIALS AND METHODS

Study Area. — Our 13 ha study site is located in the southwestern quadrant of the campus of the University of North Florida, Jacksonville, Duval County, Florida. It is bordered to the north and south by thick saw palmetto (*Serenoa repens*), west by a four-lane highway, and east by a slough. Soils in the area include Kershaw and Ortega fine sands (Soil Conservation Service, 1978).

The ecosystem is a sandhill, but with turkey oak (*Quercus laevis*) as the dominant woody species rather than longleaf pine (*Pinus palustris*). Myers (1990) calls these "turkey oak sandhills" and attributes their existence to changes in natural fire regimes that controlled encroachment of hardwoods onto the sandhill. This land was acquired in 1969 to build the university, and the fire management practices before that are unknown. The first recorded controlled burn of the area was initiated in early 1982 and completed in the winter of 1984 (no burning occurred in 1983). The site was burned again in the winters of 1985 and 1986, then not again until the fall of 1991.

Figure 1. Hatchling gopher tortoise, *Gopherus polyphemus*, in Florida. Photo by Ray D. Bowman.

Other woody species present on the site include slash pine (*P. elliottii*), laurel oak (*Q. laurifolia*), and water oak (*Q. nigra*). The understory includes such shrubs as saw palmetto, gallberry (*Ilex glabra*), and pawpaw (*Asimina incarna*), while the ground cover consists of wiregrass (*Astrida stricta*), bluestem (*Andropogon* spp.), dog fennel (*Eupatorium capillifolium*), and bracken fern (*Pteridium aquilinum*).

Data Collection. — We recorded the locations of 14 hatchling gopher tortoises (Fig. 1) once daily between 0800 and 1700 hrs (EST) for up to 22 months. We captured 13 newly hatched tortoises in hardware cloth nest protectors (Landers et al., 1980) as they emerged from five apron nests in September 1991. The fourteenth hatchling's nest was unknown, but because of its size, and because it had an egg tooth and an umbilical scar, we classified it as a hatchling. Each animal was marked for identification with a pattern of marginal scute punctures (Cagle, 1939). The term hatchling refers to tortoises up to one year old, and yearlings are those between one and two years old. On emergence, hatchlings had a mean carapace length (CL) of 51.4 mm and a mean mass of 33.2 g, and by the second spring, the eight surviving yearlings had a mean CL of 67.8 mm and a mean mass of 63.2 g.

We traced tortoise movements by radiotelemetry. Each hatchling was fitted with an SM1 transmitter powered by an HG 312 battery (AVM Instrument Company, Livermore, CA), and tracked with a TR2 receiver (Telonics, Mesa, AZ) and a directional H–shaped antenna. We soldered batteries to transmitter leads to ensure a durable connection and coated the combined assembly twice with liquid rubber (Jansen, 1982) followed with two coats of dental acrylic. Two millimeter lengths of 1 mm ID plastic tubing served as antenna guides, and from three to five of these were glued to the costal scutes with cyanoacrylate glue. The transmitter assembly was glued to the fourth vertebral scute with epoxy gel which was soft enough to make battery changes easy (Fig. 2). We assumed that placement on the down slope of the carapace would least affect digging and burrow use.

Because of the size of the transmitter assembly, epoxy gel sometimes encroached on growth areas, and after about nine months, localized constraint on shell growth was visible in some hatchlings. Thereafter, we placed the assembly on the larger third vertebral scute, and normal growth resumed, the constrained areas becoming progressively less obvious. The total package weight including transmitter, battery, antenna guides, and glue, averaged 2.4 g, and ranged from 5 to 9% (mean 7%) of the weight of day-old tortoises. After a year, the additional weight of the transmitter package ranged from 3 to 5% of tortoise body weight.

Battery life ranged from seven to ten weeks, but to avoid the risk of losing contact with tortoises, we replaced batteries every six weeks. When out of their burrows, tortoises were captured by hand. When in their burrows, tortoises were trapped with a live trap (Havahart, 25 x 7.5 x 7.5 cm) placed at the burrow mouth during active seasons, or dug out during inactive periods. Because burrows were seldom more than 30 cm long and 20 cm deep (Butler, in prep.), tortoises could be dug out without disturbing the burrow mouth. The depth and extent of a burrow and the probable location of an inactive tortoise were determined before digging by simultaneously probing down the burrow mouth and through the sandy soil covering the burrow with slender wires. Tortoises were removed to the laboratory overnight for battery replacement and gluing of transmitter assemblies.

We released tortoises at the point of capture. The first release was at the nest from which they had emerged, and their movements were followed continuously until they dug burrows or became inactive. We interpreted burrows as excavations with dirt roofs as opposed to pallets (Auffenberg and Weaver, 1969) or roofless tunnels covered by vegetation or leaves. We located all tortoises once daily thereafter until their demise. The last of the fourteen hatchlings died in June 1993.

We measured daily temperatures with a Taylor maximum-minimum thermometer (Forestry Supplies Inc., Jackson, MS). We averaged daily maximum temperatures over weekly periods and report mean weekly maximum temperatures, T_W. To determine if tortoises were active, we placed small sticks upright in the sand at each burrow entrance and interpreted downed sticks as active burrows (Hallinan, 1923). Distances of new burrows from old ones and from the nest were measured with a 100 m tape. Tortoise locations were measured as distance and direction from the burrow. Directions were recorded with a compass, and distance was recorded with a meter tape.

We used tortoise locations to determine home ranges with the minimum convex polygon method (Jennrich and Turner, 1969) with the help of the computer program McPAAL (Stüwe and Blohowiak, 1985). When tortoises abandoned burrows and new movements did not overlap former ones, we considered the animal to have moved to a new home range. By including all locations from the first day of capture we were able to calculate not only seasonal but also annual and total ranges by the same method.

Figure 2. Hatchling gopher tortoise with transmitter assembly (without rubber coating). Photo by Joseph A. Butler.

We used the Kruskal–Wallis test to discern significant differences in mean distances from the burrow and mean home ranges. We used the t-test for two means with unequal variances to test for significant differences in burrow activity. We applied a significance level of $P = 0.05$. Means are followed by one standard deviation of the sample.

RESULTS

Of 4996 burrow observations, 2477 (49.6%) indicated active burrows. Activity was observed in every week of the 92-week study period (Fig. 3). During the first week after release, burrows were active 33% of the time, but by October, activity dropped below 20% and did not exceed 20% during any two consecutive weeks until late March. We termed this period of consistently low activity the first "dormant period;" it extended from 29 September 1991 to 28 March 1992 and had a mean daily maximum temperature of 21.7°C. From mid-April through early November, there were no two consecutive weeks of less than 80% burrow activity. We termed this period of consistently high activity the "active period;" it extended from 19 April to 7 November 1992 and had a mean daily maximum temperature of 32.1°C. A second "dormant period" occurred from 29 November 1992 to 20 March 1993 for which the mean daily maximum temperature was 22.4°C (Fig. 3).

A transition period of increasing activity occurred between the first dormant period and the active period (29 March–18 April 1992), and a transition of decreasing activity occurred between the active period and the second dormant period (8 November–28 November 1992). Although the dates given for these transitions are partly due to our procedure of grouping data into weekly summaries, it is apparent from Fig. 3 that hatchling activity changed dramatically over a period of about three weeks during each transition. Several spikes of relatively high activity during the second dormant period correspond to brief temperature increases (Fig. 3). By 24 March 1993 activity was rising again, but there was no clearly identifiable active period following the rise, in part because increased mortality sharply reduced our sample size.

Thirteen hatchlings dug a total of 83 burrows during the 92-week study. One hatchling lived only in pallets until his death in December 1991, approximately three months after hatching. Ten of thirteen hatchlings dug burrows within one week of their initial release; another lived in a pallet for five weeks, then moved and dug a burrow. One already had a burrow when first captured and another's burrowing behavior was not recorded until age seven months. Our tortoises dug an average of 4.8 burrows/tortoise-year.

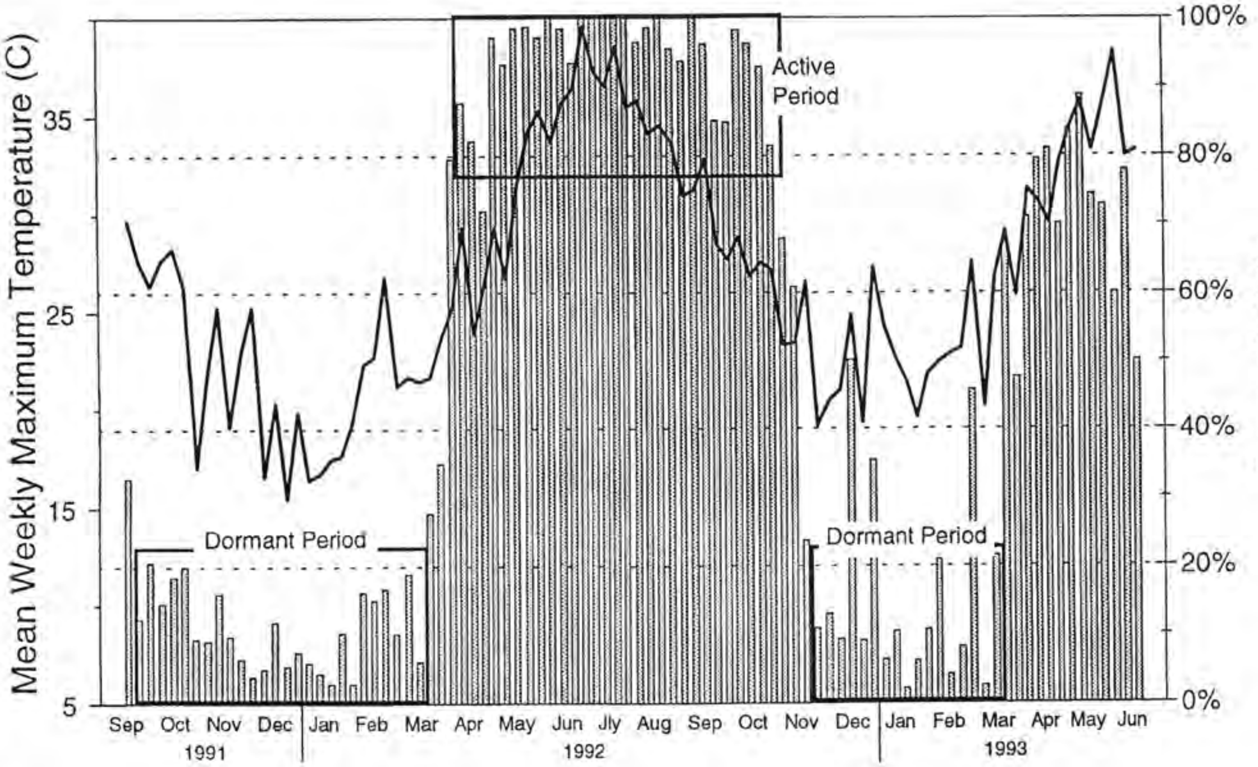

Figure 3. Weekly burrow activity of fourteen hatchling and yearling gopher tortoises (bars) and mean weekly maximum environmental temperatures (line) during the 22-month study.

Tortoises abandoned burrows 72 times to dig new ones (Fig. 4). Fifty percent of the time the new burrows were dug and occupied within one day of leaving the abandoned one. The mean time between abandonment and excavating a fresh burrow was 2 days; the maximum time was 11 days. Tortoises spent the time between burrows in a series of pallets or under litter as reported by Diemer (1992). Thirty-five changes (49%) occurred from April through July, more than in any other period of equal time, and only two tortoises changed burrows during the second dormant period. The mean distance between consecutively dug burrows was 17.1 ± 28.7 m (range = 0.12–139.4 m). Thirty burrow changes (42%) occurred within one week of a battery change.

The mean distance of 10 initial burrows from the nest was 14.6 ± 6.3 m. Most burrow changes extended the distance from the nest. The mean distance from the nest for eight yearlings alive at the end of the activity period was 81.3 ± 48.3 m which did not change appreciably by the end of the study 33 weeks later.

Daily movements include movements away from the burrow not resulting in burrow abandonment. Tortoises were located a total of 288 times (5.8% of total observations) at a mean distance of 7.7 ± 6.5 m from their burrows (Table 1). During the active period, the mean distance from the burrow rose to 9.2 ± 6.9 m, significantly farther (Kruskal–Wallis test, $P = 0.0028$) than in the first dormant period (mean 3.7 ± 3.4 m) but not in the second dormant period (mean 7.0 ± 6.5 m; Kruskal–Wallis test, $P = 0.16$). The longest daily movement of 33.0 m was recorded during the active period.

Fewer home ranges were calculated in dormant periods because tortoises were away from their burrows less often, and because we accepted no fewer than three locations to define a home range (Table 2). We found substantial variation in home range size particularly in the active period. The mean active period home range, 363 ± 265 m^2, is significantly different from either of the dormant period home ranges (Kruskal–Wallis test, $P = 0.0031$ for both comparisons). Nine tortoises survived to become yearlings; the mean of their annual ranges (September 1991 – September 1992) was 2032 ± 1307 m^2. By the end of our study period (25 June 1993) the total range for these yearlings was 2554 ± 1382 m^2 which is not significantly different (Kruskal–Wallis test, $P = 0.20$) from the mean annual range.

DISCUSSION

Douglass and Layne (1978) and McRae et al. (1981) suggested bimodal activity peaks for immature and juvenile gopher tortoises, and Wilson et al. (1994) reported significantly higher tortoise activity in spring than in all other seasons. Our data show consistently high activity from mid-April through early November (Fig. 3). McRae et al. (1981) reported tortoises were most active when the environmental temperature was between 28 and 31°C. Activity diminished above and below that range. In our study, T_W ranged from 23.9 to 39.6°C during the activity period. Because we recorded activity only once in every 24-hour period, we could not observe the length of daily activity periods.

Our observation that most T_W's during our dormant periods were less than 22°C agrees with observations by Douglass and Layne (1978) and by McRae et al. (1981) that tortoises are rarely active below this temperature. Diemer (1992) found juveniles were more active in cold periods than were adults. All the tortoises we studied were active to some extent in both dormant periods.

The first dormant period is longer than the second and includes several weeks with T_W's above 25°C when hatchlings might be expected to be active. All the hatchlings were less active during the first six weeks of the study (22 September–2 November 1991) than the survivors were about a year later during a similar period of identical environmental temperatures (11 October–14 November 1992). We believe the significant difference in activity (t-test, $P = 0.00004$) occurred because the younger hatchlings had the benefit of a food supply from yolk sacs and because the instinct for reclusion inhibits predation. Arata (1958) reported newly hatched gopher tortoises were indifferent to food and attributed this behavior to the presence of large yolk sacs. We believe feeding is not important during the first dormant period. All of our freshly released hatchlings sought cover immediately; only a few took occasional bites of vegetation. None defecated during handling until they were at least eight months old.

The transitions between dormant periods and the active period were brief and occurred during seasons of changing environmental temperature. During the transition from dormancy to activity, T_W increased from 21.7 to 25.2°C, and burrow activity increased from 28 to 79%. An initial drop in T_W from 27.1 to 23.3°C coincided with the transition from activity to dormancy during which burrow activity declined from 68 to 24%.

All our hatchlings dug burrows except the one that died within three months of emergence. Douglass (1978) suggested that hatchlings live in adult burrows, under sand, or under litter during their first winter and dig their first burrows the following spring. Smith (1992) reported that five of her six hatchlings dug burrows within one day of release. Ten out of twelve of ours dug burrows within a week. Four of our hatchlings re-entered their nest burrows briefly upon first release but left within 45 minutes. We observed one of our study animals entering an adult tortoise burrow only once. It spent four days (21–24 June 1993) just inside the burrow mouth after which it was killed by a predator. One hatchling occasionally used what appeared to be the abandoned burrow of a small mammal. A hatchling cohabited with a larger juvenile in the latter's burrow for 12 days in September 1991. A yearling did the same for 12 days in March–April 1993. Two yearlings co-occupied a single burrow briefly in May 1993 before both were taken by a predator. This suggests that hatchlings and juveniles do not

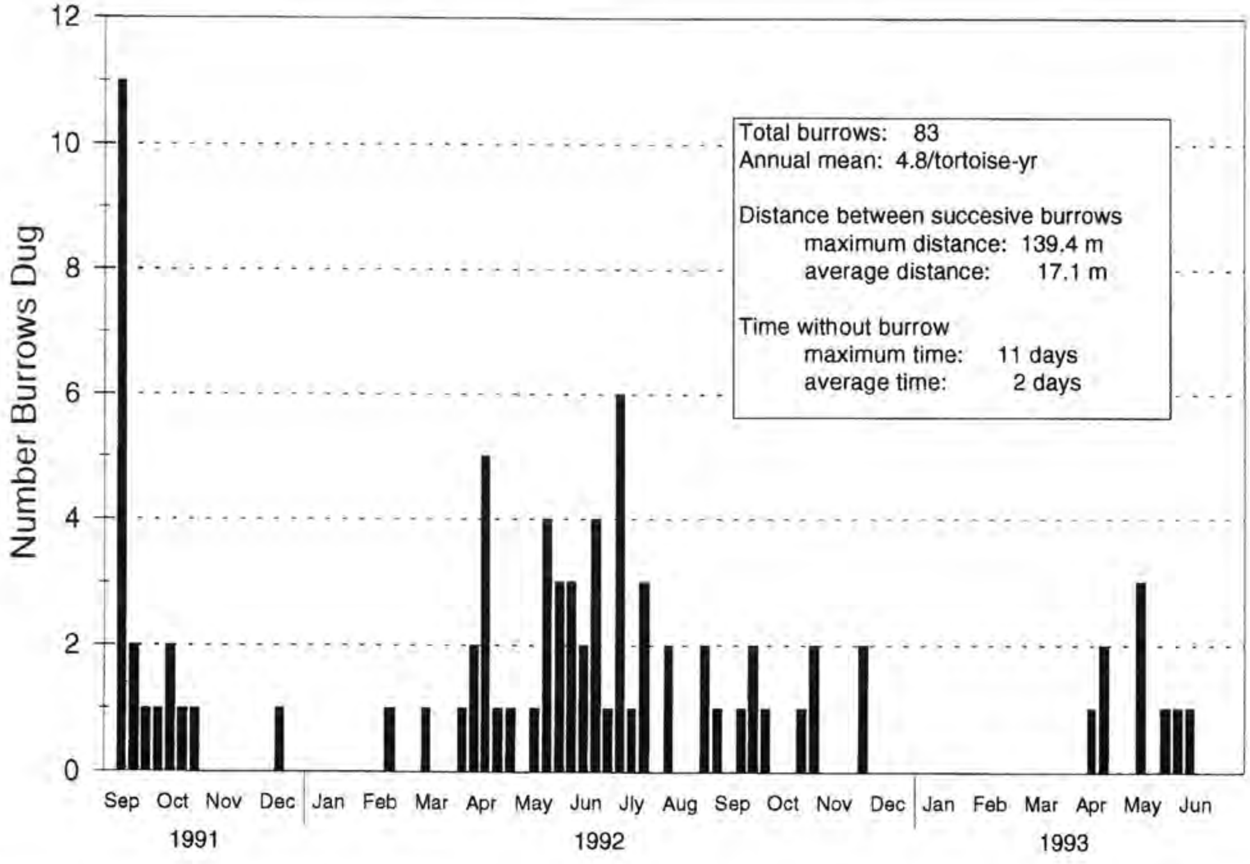

Figure 4. Number of burrows dug by hatchling and yearling gopher tortoises during the 22-month study.

Table 1. Distances moved (meters) by fourteen hatchling and yearling gopher tortoises away from their burrows. SD = standard deviation, *n* = number of observations. The last column includes all data in the 22-month study.

	First Dormant Period	Active Period	Second Dormant Period	Study Period
Mean Distance	3.7	9.2	7.0	7.7
Range	0.3 – 12.0	0.3 – 33.0	0.5 – 21.0	0.3 – 33.0
SD	3.4	6.9	6.5	6.5
n	11	188	15	288

usually defend their burrows against conspecifics. However, in an incident similar to descriptions of adult tortoise behavior (Weaver, 1970), we witnessed a hatchling ramming another who had encroached on the defender's burrow apron.

Most of our tortoises consistently returned to the same burrow. Four hatchlings occupied two burrows alternately (three in one instance). The time of multiple burrow use ranged from 6 to 72 days. One hatchling alternated between two burrows for four days in early September 1991 (shortly after hatching); in all other cases multiple burrow use occurred during the summer activity period. Multiple burrows may allow a tortoise to evade predators more easily or to gain relief from high temperatures more quickly (Wilson et al., 1994).

Our mean of 4.8 burrows/tortoise-year is similar to the 4.4 reported by Wilson et al. (1994) for juveniles, but larger than the 2.6 reported by Diemer (1992) for juveniles and 1.1 reported by McRae et al. (1981) for hatchlings. Our figure may be inflated if tortoises moved in response to handling for battery exchange. Tortoises were collected 134 times for battery changes or other transmitter adjustments. Upon release, they abandoned their burrows 30 times or 22% of the times they were handled. This represents 42% of all burrow abandonments. If these data are eliminated, then the digging rate is 2.8 burrows/tortoise-year, still more than double the figure reported by McRae et al. (1981).

Hatchlings usually dig their first burrow near the nest or initial release point. McRae et al. (1981) found that hatchlings burrowed a mean of 8.3 m from the release point, and Smith (1992), who released hatchlings from nest aprons as we did, reported a mean distance of 10.7 m. Our hatchlings dug their first burrows a mean of 14.9 m from the nest. Consecutively dug burrows by juvenile tortoises ranged between 10–15 m apart in southern Georgia (McRae et al., 1981) and a mean of 14.3 m apart in southern Florida (Wilson et al., 1994). These results are comparable to our mean of 17.1 m between consecutive burrows.

Mean daily movements of juveniles reported by McRae et al. (1981) and Wilson et al. (1994) were respectively 7.8 ± 4.4 m and 7.87 ± 8.56 m. Our mean of 7.7 ± 6.5 m is similar. Mean daily movements plus two sample standard deviations are often used as a "probability density function" to calculate the radius of a circle within which 95% of feeding occurs for an individual (Tinkle, 1967). McRae et al. (1981) reported this function to be 30 m for adult gopher tortoises and, from the data reported above, 17 m for juveniles (2–5 yrs). The same probability density function for our tortoises was 21 m. (The mean daily movement plus a one-tailed 95% confidence interval would seem to be a somewhat better choice for the radius of a 95% feeding circle. For our data this would be a slightly smaller value, 18.5 m.) McRae et al. (1981) found longer mean daily movements for adults after 15 June than before this date, and suggested that food depletion near the burrow caused tortoises to forage farther away. We compared the means of activity period daily movements for our hatchlings before 15 June and after and did not find a significant difference (t-test, $P = 0.3$). Perhaps hatchlings do not consume enough to deplete food supplies near their burrows.

Feeding patterns may also explain why mean daily movements were smaller during the first dormant period than during the second. As suggested above, the presence of yolk sacs probably influenced first dormant period behav-

Table 2. Home ranges (area in square meters) during dormant and active periods and total ranges of fourteen hatchling and yearling gopher tortoises. SD = standard deviation, *n* = number of observations. The last column includes all data for the nine tortoises that survived at least one year.

	First Dormant Period	Active Period	Second Dormant Period	Study Period
Mean Area	4.5	363	6.9	2554
Range	2.7 – 7.2	75 – 1000	3.6 – 12.0	611 – 4232
SD	1.9	265	3.7	1382
n	4	13	4	9

ior. Also, by the second dormant period the tortoises were more familiar with their feeding areas. Mean daily movements during the second dormant period are not significantly different than those of the active period.

We witnessed four long distance moves by four different hatchlings. All the moves resulted in burrow changes. The impetus for long distance movements is not always clear. Sixty-six percent of the long distance moves observed by Wilson et al. (1994) were in response to some disturbance of the resident burrow. Two of the moves we saw immediately followed transmitter battery changes. Two moves occurred in a single day, 48 and 55 m; the other two, 125 and 139 m respectively, occurred over two-day periods.

Several definitions of home range are presented in the literature. Burt (1943) defined home range as "...the area, usually around a home site, over which the animal normally travels in search of food." Rose (1982) took home range to be "...the entire area within which an animal moves." This includes both short distance feeding excursions and long distance movements. Some authors omit the distance between long distance moves (e.g., movements that involve change of burrows) from home range calculations (McRae et al., 1981; Diemer, 1992; Wilson et al., 1994) and in so doing, reduce the estimate of the area used by the animal. Authors often smooth seasonal variations by reporting annual average home ranges.

Our data describe tortoise movements beginning with emergence from the nest and ending with the death of each animal. The results in Table 2 together with those reported by Wilson et al. (1994) confirm the expectation that gopher tortoise home ranges vary seasonally. Further, our active period mean home range of 363 m^2 is virtually identical to the 358 m^2 reported by Wilson et al. (1994) for summer. Juvenile gopher tortoise annual ranges of 490 m^2 reported by Diemer (1992) and 720 m^2 reported by Wilson et al. (1994) are outside the 95% confidence interval for the annual range of our yearlings, 2032 ± 1307 m^2. By the end of our study, the total range for the tortoises had grown to 2554 m^2. It is possible that the handling of our study animals caused them to move farther. Alternatively, the difference between our measurements and those of the cited authors might be attributable to differences in terrain or food supply density. Studies similar to ours could further test our conclusion that hatchlings and yearlings tend to move greater distances and have larger annual ranges than do juvenile tortoises. McRae et al. (1981) noted that "...immatures almost invariably progressed toward the periphery of the colony over the years." Perhaps this inclination is even more pronounced in hatchlings who may disperse from the nest and/or colony over a broad area and eventually settle into smaller individual ranges in subsequent years. Compared to juvenile tortoises, our hatchling and yearling tortoises had larger annual ranges and dug burrows that were farther apart.

Finally, we suggest home range estimates based on seasonal measurements are helpful to field researchers in predicting and interpreting tortoise movements. However, for management and conservation purposes, it would seem that annual or total ranges are more reflective of the area required by the animal.

Acknowledgments

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