Chelonian Conservation and Biology, 2002, 4(2):464–471

Reserve Area Requirements for Gopher Tortoises (*Gopherus polyphemus*)

Jeannine Ott Eubanks[1], Jeff W. Hollister[1], Craig Guyer[2,4], and William K. Michener[1,3]

[1]*J.W. Jones Ecological Research Center, RR 2 Box 2324, Newton, Georgia 31770 USA [E-mail: joeubanks@yahoo.com];*
[2]*Department of Biological Sciences, Auburn University, Auburn, Alabama 36849-5414 USA*
[E-mail: cguyer@acesag.auburn.edu; Fax: 334-844-9234];
[3]*Long Term Ecological Research Network Office, Department of Biology, University of New Mexico Albuquerque, New Mexico 87131-1091 USA;*
[4]*Corresponding Author*

Abstract. – Gopher tortoise (*Gopherus polyphemus*) populations have declined because of habitat loss and fragmentation. Management guidelines established previously to determine tortoise space requirements for development of reserve areas have suggested that 10–20 ha, or sufficient area to encompass 80 active and inactive burrows, were sufficient to maintain 50 animals in a landscape. However, the data used to develop these guidelines underestimate general patterns and, thus, reserve areas calculated from these data also may underestimate space requirements for viable populations. We used data from a population of 123 tortoises in Georgia that were followed for one year via radiotelemetry to create three sets of simulated reserves. First, we delineated reserve boundaries around the perimeters of 80 nearest-neighbor burrows and then counted the number of tortoises that occupied at least one burrow within the reserve. Second, we determined the minimum number of animals known to occupy the reserve by including only those tortoises whose entire annual home range occurred within the reserve. Finally, we expanded reserve boundaries so that the entire annual home range of all reserve occupants was included within the reserve and calculated the number of burrows required to completely enclose the original population. We then assessed the accuracy of existing guidelines for estimating reserve size. Our results indicate that current guidelines underestimate reserve area requirements of gopher tortoise populations. Based on home range analysis, we found that reserve area requirements ranged from 25 to 81 ha. From burrow counts, we determined that 157 burrows were required to maintain 50 animals in a landscape. Based on burrow density, we found that 19 to 41 ha would be necessary to maintain 50 animals. We discuss ways to improve current guidelines and provide an alternative method for estimating reserve area.

Key Words. – Reptilia; Testudines; Testudinidae; *Gopherus polyphemus*; tortoise; burrow; density; home range; longleaf pine; movement; overlap; regression; reserve size; conservation; management; USA

The historic range of gopher tortoises (*Gopherus polyphemus*) overlaps much of the range of longleaf pine (*Pinus palustris*), with tortoises occurring from South Carolina south along the Atlantic Coastal Plain through Florida and west along the Gulf Coastal Plain to Louisiana (Auffenberg and Franz, 1982). Estimates of longleaf pine habitat prior to European settlement range from 24 to 35 million ha (Noss, 1989). However, the present extent of the longleaf pine ecosystem is only about two million ha (a reduction of over 85%), and remaining forests are small and highly fragmented with much habitat in poor condition (Noss, 1989). Increased development pressure has also forced the relocation of gopher tortoise populations from prime ancestral habitats to lower quality non-native areas (Burke, 1989; Burke, 1991; Diemer et al., 1987; Dodd and Seigel, 1991; McCoy and Mushinsky, 1995). Consequently, population densities of gopher tortoises have declined by 80% range-wide (Auffenberg and Franz, 1982; Hermann et al., 2002), resulting in the protection of gopher tortoise populations by the federal government and/or each state government throughout the geographic range of the species (Ernst et al., 1994; TESII, 1995).

In response to increased development in Florida, Cox et al. (1987) devised a set of guidelines for estimating space requirements for gopher tortoises. These authors suggested that, to maintain 50 adult animals in a landscape, a reserve area of 10–20 ha (or sufficient area to encompass 80 burrows) was required. These guidelines, despite being based on limited data, represent the only attempt to determine the amount of habitat necessary to sustain viable populations of gopher tortoises. Thus, recommendations suggested within Cox et al. (1987) have been used to establish guidelines for the development of gopher tortoise preserves in Florida, and are a principal source of information employed by consultants and managers in development of plans throughout the species' geographic range. However, it is critical that accurate reserve estimates be developed to assure that existing and future reserves are large enough to maintain viable populations in the face of increasing habitat loss to development. Therefore, although Cox et al. (1987) provided reserve estimates based on the best information available at the time, continual refinement of their estimates and exploration of alternative methods are needed as new data accumulate describing variation in key variables of gopher tortoise natural history.

In this study, we use data from a gopher tortoise population located in a large, contiguous tract of longleaf pine habitat to test two predictions made by Cox et al. (1987).

Based on home range areas and burrow use patterns calculated from our population, we determine whether 10–20 ha is a sufficient range of areas to maintain a population of 50 adult gopher tortoises. Second, we determine whether reserves established around 80 burrows will contain 50 tortoises. Using current guidelines as a foundation, we suggest improvements to reserve size recommendations made by Cox et al. (1987).

EXISTING GUIDELINES

Reserve Size Based on Critical Area Requirements. — Cox et al. (1987) assumed a minimum viable population to be 50 adults and estimated area requirements for this number of gopher tortoises based on home range sizes from McRae et al. (1981; 0.2 ± 0.2 ha for females and 0.5 ± 0.5 ha for males). These mean home range areas were then used to determine critical area requirements for gopher tortoises:

$$CA = ((HR_F + 1\ SD_F) + (HR_M + 1\ SD_M))/2 \quad [1]$$

where CA = critical area, HR = the mean home range size of F = females and M = males, and SD = one standard deviation of each mean. Thus, the critical area per tortoise was estimated to be 0.7 ha. Because gopher tortoises do not occupy exclusive home ranges (McRae et al., 1981), Cox et al. (1987) recognized that 50 individuals would not require 35 ha (0.7 ha * 50 tortoises) of habitat. Instead, the proposed reserve area could be reduced by an estimate of the amount of habitat shared by two or more tortoises. Cox et al. (1987) estimated that a minimum reserve size would be

$$RA = (n * CA * (1 - O)) \quad [2]$$

where RA = reserve area, n = target population size, CA = critical area (see Equation 1), and O = the proportion of overlap among home ranges. For their analysis, they assumed that mean overlap per tortoise within a population would be approximately 50%. Thus, a population of 50 tortoises would require 18 ha of habitat (Cox et al., 1987).

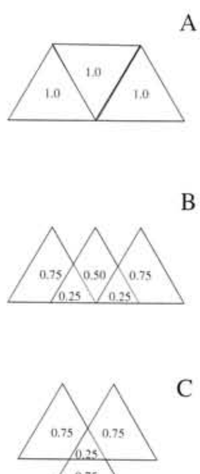

Figure 1. Schematic drawing showing the relationship between spacing patterns of individuals and total area occupied by a population (of 3 tortoises). The amount of space required by populations of equal size changes depending on the patterns of overlap between individuals within a population. When animals use habitat exclusively (A), more area is required to maintain a population than when animals overlap a portion of their home range with at least one other individual (B, C). However, a decrease in the mean proportion of habitat shared with neighboring tortoises may not change predicted reserve areas required to maintain those animals (B, C). Thus, patterns of overlap, rather than a mean overlap value, should be incorporated into any model used to predict reserve size.

Although Cox et al. (1987) were correct in suggesting that overlap among home ranges is important, the formula used to determine reserve size incorrectly estimates space requirements for populations because it does not account for the way overlap is distributed among neighboring tortoises. Depending on the number of overlapping tortoises, reserve size is not always a decreasing function of home range overlap (Fig. 1). An alternate formula is:

$$RA = \sum ((CA * n * O_i)/i) \quad [3]$$

where i = the number of animals that occur in an area (from 1 to n), n = the maximum number of animals that inhabit an area, and O_i = the proportion of the area of the mean home range that is utilized by i tortoises. Thus, this formula divides the total area occupied by an entire population into the areas occupied exclusively by one animal and the areas shared by two, three, …, and n animals.

Use of this formula requires knowledge of overlap patterns by tortoises within a site, yet previously published studies of gopher tortoise movements do not address these patterns. For this paper, we calculated patterns of overlap for tortoises at a relatively pristine site and assumed such patterns were similar to those at other tortoise sites. These overlap patterns then were used to calculate reserve size based on published studies describing movement patterns of gopher tortoises.

Reserve Size Based on Burrow Surveys. — Gopher tortoises excavate and use deep burrows as refuges, obtaining protection both from predation and climatic extremes (Auffenberg and Franz, 1982). Further, tortoises spend the majority of their time in or near a burrow, and many aboveground activities (e.g., foraging, mating, basking) occur within close proximity to burrows (Douglass, 1990). Thus, Cox et al. (1987) suggested that tortoise reserves could be identified most efficiently if tortoise abundance could be inferred from burrow surveys.

Within any site, there typically are more burrows than there are gopher tortoises. Auffenberg and Franz (1982) used a correction factor to reduce the total estimate of usable (e.g., active and inactive) burrows to those actually occupied by gopher tortoises (see Auffenberg and Franz, 1982 for a description of active and inactive burrows). The correction factor varies among sites, with estimates ranging from 0.04–0.75 (see Burke and Cox, 1989; Breininger et al., 1991). However, once this value is known for a site, the number of burrows necessary to encompass n tortoises can be calculated with the following formula:

$$B = n/CF \quad [4]$$

where B = the number of occupied (active) burrows and CF = the burrow-to-tortoise correction factor. For this analysis, Cox et al. (1987) used the correction factor of 0.614 derived by Auffenberg and Franz (1982). Thus, Cox et al. (1987) estimated that an area containing 80 burrows should encompass 50 gopher tortoises.

Establishment of reserves based on burrow surveys is attractive because such surveys are much easier to perform than are examinations of movement patterns of tortoises. However, because tortoises can use several burrows during a year, reserve estimates based on burrow surveys predict only that the target number of individuals will be present within a reserve at a particular point in time and not that these tortoises will have sufficient space within the reserve to carry out their annual activities. Thus, the number of animals in a large contiguous population that might occur within an area containing 80 burrows is likely to be greater than the number of animals that can be retained by an isolated reserve of those same burrows. One way to estimate the expected population of an isolated reserve is to include only those individuals whose home ranges are likely to be entirely circumscribed by the reserve. Alternatively, the target number of burrows required for an isolated reserve might be expanded to include all burrows used during an annual cycle of activity by a contiguous group of 50 animals. We used our data on movement patterns of tortoises to examine these possibilities.

METHODS

Study Site. — The primary source of data for this study was Green Grove, a 100 ha site located in the northeastern portion of an 11,700 ha ecological reserve in Baker County, Georgia (Ott, 1999). Green Grove comprises primarily longleaf pine – wiregrass (*Aristida beyrichiana*) habitat, interspersed with patches of live oak (*Quercus virginiana*) and small abandoned agricultural food plots. Frequent prescribed fires (annual to biannual winter or summer burns) help maintain a diverse assemblage of groundcover species (Drew et al., 1998).

Home Range Size and Overlap. — From April 1997 to June 1998, we investigated the movement and burrow use patterns of the entire adult gopher tortoise population (n = 123) at Green Grove (Ott, 1999). Tortoises were tracked via radiotelemetry 3–4 times per week to either a burrow or a non-burrow location. Estimates of home range size (95% minimum convex polygons) were calculated for each individual using the program CALHOME (Kie et al., 1996). Mean home range area ± 1 SD of females was 0.4 ± 0.6 ha (n = 53; range = 0–3.4 ha), and for males was 1.1 ± 1.2 ha (n = 70; range = 0–4.8 ha). For the current study, we used these mean home range sizes.

To calculate the amount of overlap between tortoise home ranges, we converted home range polygons to grids (0.5 m x 0.5 m pixels). For each tortoise, we assigned a value of 1 to all pixels located within the home range and a value of 0 to all pixels located outside the home range. Grids then were added sequentially so that pixels representing space shared by only 2 individuals received a value of 2, pixels representing space shared by 3 individuals received a value of 3, and so on. Thus, values of 0 indicated that no tortoise occupied that pixel, values of 1 denoted pixels with exclusive use by a single tortoise, and values >1 designated areas of overlap. We determined total overlap area by adding all pixels with values greater >1.

Burrow Status. – At Green Grove, an active burrow was defined as any burrow known from telemetry data to be occupied by a tortoise during the 1997–98 study (Ott, 1999). Burrows that appeared usable (entrance clear of debris and retaining the shape of a tortoise shell) but that were never observed to contain a tortoise were classified as inactive. An abandoned burrow was any burrow whose entrance was occluded, collapsed, modified by an armadillo, or otherwise unusable by an adult gopher tortoise. We classified 254 burrows as active, 61 burrows as inactive, and 93 burrows as abandoned. Our definitions take advantage of the precise information available to us from the telemetry data but differ from those of previous authors (e.g., Auffenberg and Franz, 1982; Cox et al., 1987). For the purposes of this paper, we make the simplifying assumption that the numbers of burrows in these three categories will not differ significantly between the two methods of categorization. We do this because we currently lack the data to test this assumption.

Estimating Reserve Area Based on Home Range Size. — Using mean home range areas and percent home range overlap calculated for tortoises at Green Grove (see above), we applied the formulas for estimating critical area developed by Cox et al. (1987; our Equations 1 and 2) and the corrected reserve size formula (our Equation 3) to determine the amount of habitat required by 50 gopher tortoises at Green Grove and in other published studies.

Estimating Reserve Area Based on Burrow Counts. — We tested the prediction by Cox et al. (1987) that a reserve with 80 burrows is large enough to contain a viable population of 50 gopher tortoises by creating simulated reserves at Green Grove. First, for each of the 315 active and inactive burrows, we identified the 79 nearest-neighbor burrows. Using the movement extension in ArcView (Environmental Systems Research Institute, Redlands, CA; Hooge and Eichenlaub, 1997), we established a minimum convex polygon around each set of 80 burrows, thereby creating 315 simulated reserves (we will refer to these as ORIGINAL reserves). Within each 80-burrow reserve, we identified individual tortoises that occupied at least one burrow over a one-year period. We then calculated population size within each 80-burrow reserve in one of three ways.

First, to determine the maximum number of tortoises known to use an 80-burrow reserve, we counted all individuals that occupied a reserve, whether a home range occurred entirely or partly within the boundaries of an ORIGINAL reserve (we refer to these as MAXIMUM reserves because the estimate of population size is maximized). Second, we determined the minimum number of animals known to occupy a reserve by removing individuals whose home ranges extended outside the boundaries of an ORIGINAL reserve, thereby ensuring that all inhabitants would occur within a reserve at its establishment (we refer to these as MINIMUM reserves because population size is minimized).

Table 1. Published data on burrow density (burrows/ha) and tortoise density (tortoises/ha) from established gopher tortoise reserves or study sites within the southeastern United States.

Reserve Location	Study Site	Area (ha)	Burrows/ ha	Tortoises/ ha	Source
Ichauway, Macon County, GA	Site GG	100.0	4.1	1.3	Present study
	Site RD	14.7	4.6	0.9	J. Ott, unpublished data
	Site SP	24.3	8.0	5.0	"
	Site SD	29.3	5.0	3.4	"
	Site TW	53.6	11.3	2.5	"
Conecuh National Forest, Covington Co., AL	Site A	5.3	22.9	7.1	C. Guyer, unpublished data
	Site B	10.8	9.0	2.2	"
	Site C	9.2	11.6	5.0	"
	Site D	38.0	4.8	1.3	"
	Site E	7.0	9.5	2.7	"
	Site F	6.8	14.1	7.4	"
Hillsborough County, FL	Site E	32.4	49.1	14.0	McCoy and Mushinsky, 1995
	Site L2	1.5	43.7	18.5	"
	Site MB	0.6	25.0	9.4	"
	Site SK	0.9	41.9	10.5	"
	Site U1	5.9	13.9	4.6	"
	Site V	1.9	25.8	9.3	"
Sarasota County, FL	Site LO	2.4	16.9	5.1	"
Fort Benning, Muscogee County, GA	Site D6	4.9	4.1	0.8	C. Guyer, unpublished data
	Site D12	2.5	10.4	5.2	"
	Site D17	3.8	2.1	1.6	"
	Site F1	4.6	3.3	0.7	"
	Site G2	3.5	9.1	3.1	"
	Site K20	9.9	3.7	1.3	"
	Site O11	1.3	10.0	3.1	"
	Site O14	7.4	3.4	1.2	"

Third, we expanded the boundaries of an ORIGINAL reserve to include the remainder of home ranges for those tortoises that only partly occupied the reserve (we refer to these as an EXPANDED reserve because the number of burrows required is expanded beyond that of the ORIGINAL reserve). We then counted all active and inactive burrows within EXPANDED reserves to estimate the number of burrows required to enclose all inhabitants.

As a final set of analyses, we used linear regression to evaluate the influence of burrow density (burrows/ha) on two key variables, home range overlap (ha) and tortoise density (tortoises/ha). This was done to determine whether alterations to the Cox et al. (1987) model are needed. We examined regressions of burrow density on home range overlap within MAXIMUM, MINIMUM, and EXPANDED reserves.

We created three regressions to determine the relationship between burrow density and tortoise density. The first two used the area within 80-burrow reserves in the calculation of burrow density and the two different methods of calculating tortoise density (MAXIMUM versus MINIMUM reserves). In the third regression, we used the EXPANDED reserve area. Finally, we examined the relationship between burrow density and tortoise density based on accumulated literature values (see Table 1). This analysis was included to document whether patterns observed at a

Table 2. Reserve area estimates for populations of gopher tortoises from published data. Overlap category denotes the number of tortoises sharing a polygon and the proportion of total area represents the proportion of Green Grove occupied by that number of tortoises. For each study, we calculated critical areas (CA) using Equation 3 [$RA = \sum((CA * N * O_i)/i)$, where i indicates the overlap category and the summation is from 1 to 13].

Overlap Category	Proportion of Total Area	Silver Lake Station (McRae et al., 1981)	Lochloosa WMA (Diemer, 1992)	Kennedy Space Center (Smith et al., 1997)	Green Grove (present study)
1	0.5157	18.05	30.94	59.31	43.83
2	0.2521	4.41	7.56	14.50	10.71
3	0.1329	1.55	2.66	5.10	3.77
4	0.0543	0.48	0.81	1.56	1.15
5	0.0219	0.15	0.26	0.50	0.37
6	0.0105	0.06	0.10	0.20	0.15
7	0.0032	0.02	0.03	0.05	0.04
8	0.0028	0.01	0.02	0.04	0.03
9	0.0033	0.01	0.02	0.04	0.03
10	0.0017	0.01	0.01	0.02	0.01
11	0.0009	0.003	0.005	0.01	0.01
12	0.0006	0.002	0.003	0.01	0.005
13	0.0001	0.0003	0.001	0.001	0.001
Reserve Area (ha)		**24.8**	**42.4**	**81.3**	**60.1**
Critical Area (ha)		**0.7**	**1.2**	**2.3**	**1.7**

single site (Green Grove) reflect range-wide patterns. From these regressions, we then estimated reserve sizes necessary to contain 50 adult gopher tortoises for burrow densities between 2 and 7 burrows/ha.

RESULTS

Estimating Reserve Area from Home Range Size. — Critical area was 1.0 ha for females and 2.3 ha for males. The ratio of females to males was not different from 1:1 (sex ratio = 1:1.3; $\chi^2 = 2.4$, df = 1, $p > 0.05$). Thus, the critical area per tortoise was 1.7 ha. About half (52%) of the average home range of a tortoise was used only by the resident; as the number of overlapping neighbors increased, progressively smaller proportions of the average home range were shared among tortoises (Table 2).

Using Equation 3, we estimated that a population of 50 adult gopher tortoises on Green Grove required 60 ha of habitat. Values for reserve size were similar when calculated for other sites for which home range data were collected (assuming patterns of overlap were similar to those observed on Green Grove); such reserves ranged from 25–81 ha (Table 2). All reserve estimates were greater in size than the values recommended by Cox et al. (1987).

Estimating Reserve Area from Burrow Counts. — For MAXIMUM reserves, the mean number of tortoises known to use each reserve was 47.1 ± 0.31 (range: 36–67), with a mode of 40 tortoises (Fig. 2). Over 66% of simulated reserves (n = 210) contained fewer than 50 tortoises. The mean number of tortoises within MINIMUM reserves was 19.0 ± 0.19 (range: 10–28; Fig. 2). All estimates were less than the target of 50 animals. Within EXPANDED reserves, an average of 157.0 ± 1.68 burrows (range: 138–206) was required to capture all burrows used by a population of at least 50 tortoises over a one year period (Fig. 3). All estimates were above the 80 burrows used by Cox et al. (1987) as a target sample size likely to contain 50 animals.

Variation in tortoise density accounted for only 8% of the variance in total overlap area within MAXIMUM reserves ($F_{1,314}$ = 29.4; $p < 0.0001$; Fig. 4a). Variation in MINIMUM tortoise density accounted for 12% of the variance in total overlap area ($F_{1,314}$ = 41.1; $p < 0.0001$; Fig. 4b). However, variation in tortoise density accounted for 30% of the variance in total overlap area within EXPANDED reserves ($F_{1,314}$ = 135.6; $p < 0.0001$; Fig. 4c).

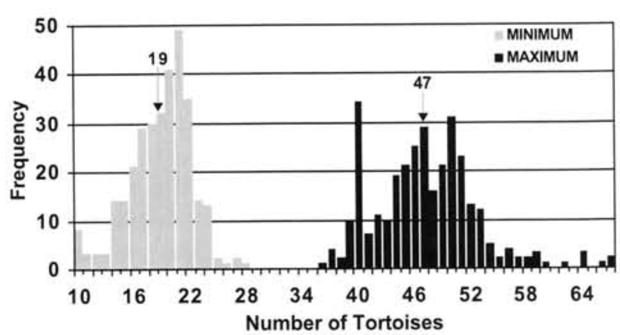

Figure 2. Range and frequency of population sizes that occurred in 315 simulated gopher tortoise (*Gopherus polyphemus*) reserves at Green Grove, Georgia. Data are based on home range estimates for all reserve occupants (MAXIMUM) or for only those tortoises whose entire home range occurred within reserve boundaries (MINIMUM). Arrows indicate mean population size for each set of reserves.

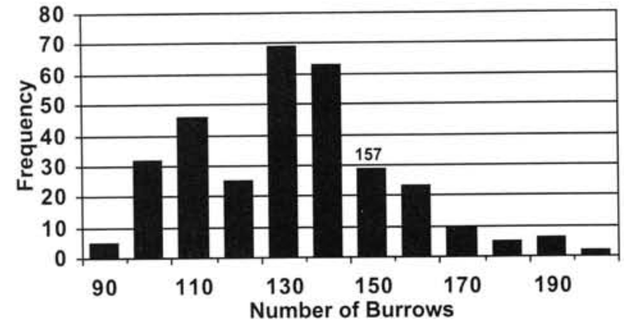

Figure 3. Range and frequency of burrow counts that occurred in 315 simulated reserves at Green Grove with boundaries expanded to include 100% home range areas for all gopher tortoises occupying the reserve (EXPANDED). Number above bar indicates the mean number of burrows required to completely enclose 50 gopher tortoises.

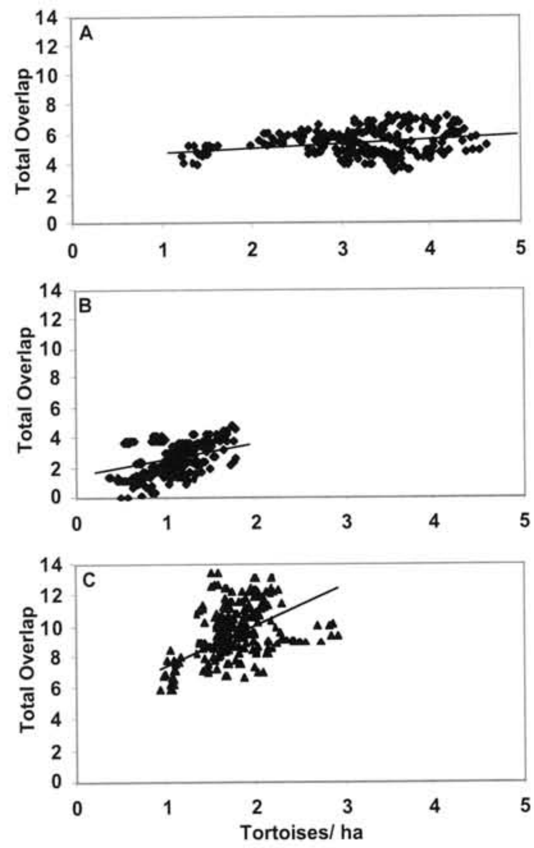

Figure 4. Relationship between total overlap area (ha) and tortoise density (tortoises/ha) at Green Grove in 315 simulated gopher tortoise reserves with (A) tortoise density determined by occurrence of animals in at least one burrow (MAXIMUM; $r^2 = 0.08$, $y = 0.288x + 4.557$), (B) tortoise density determined using only tortoises whose home range occurred within a reserve (MINIMUM; $r^2 = 0.12$, $y = 1.072x + 1.533$), and (C) reserves adjusted to include 100% home range areas for all tortoises occupying the ORIGINAL reserve (EXPANDED; $r^2 = 0.30$, $y = 2.621x + 4.832$).

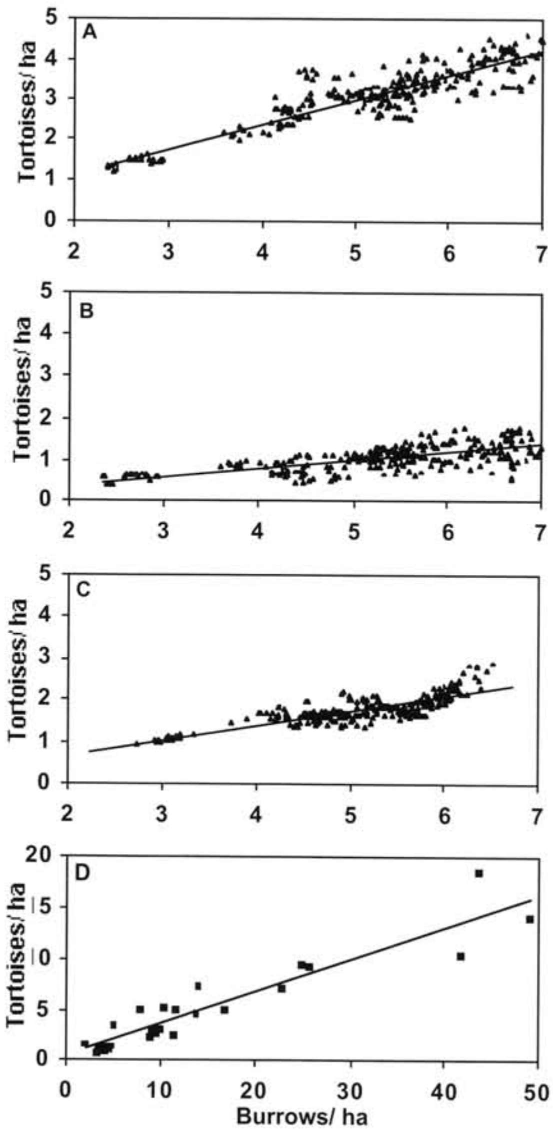

Figure 5. Relationship between tortoise density (tortoises/ ha) and burrow density (burrows/ ha) in 315 simulated gopher tortoise reserves with (A) tortoise density determined by occurrence of animals in at least one burrow (MAXIMUM; $r^2 = 0.84$, $y = 0.619x - 0.133$), (B) tortoise density determined using only tortoises whose home range occurred within a reserve (MINIMUM; $r^2 = 0.58$, $y = 0.206x - 0.042$), (C) reserves adjusted to include 100% home range areas for all tortoises occupying the ORIGINAL reserve (EXPANDED; $r^2 = 0.78$, $y = 0.352x - 0.027$), and (D) existing gopher tortoise reserves located throughout the southeastern United States ($r^2 = 0.88$, $y = 0.321x + 0.373$; see Table 1 for list of sites).

Variation in burrow density accounted for 84% of the variance in tortoise density in MAXIMUM reserves ($F_{1,314} = 1609$; $p < 0.0001$; Fig. 5a) and 58% of the variance in tortoise density within MINIMUM reserves ($F_{1,314} = 506$; $p < 0.0001$; Fig. 5b). In EXPANDED reserves, variation in burrow density accounted for 78% of the variance in tortoise density ($F_{1,314} = 1088$; $p < 0.0001$; Fig. 5c). For all sites in the southeast (Table 1), variation in burrow density accounted for 88% of the variance in tortoise density ($F_{1,25} = 184$; $p < 0.0001$; Fig. 5d).

Using the above regression equations, predicted reserve sizes for burrow densities of 2–7 burrows/ha ranged from 12–135 ha (Table 3). For each regression, reserve sizes required to contain 50 tortoises decreased with increasing burrow density.

DISCUSSION

Based on home range analyses, reserve sizes required to conserve 50 adult gopher tortoises vary between 25 and 81 ha. These data indicate that current models of minimum reserve size based on tortoise movements (Cox et al., 1987) must be revised upward. Current literature indicates that differences in home range size between sites are sufficient to question the blanket use of average values of home range size. Thus, before a reserve could be established, extensive home range data would need to be collected at the site. This would be time-consuming, difficult, and often expensive. Further, our analysis of density-dependent effects on overlap values questions the validity of applying a single set of overlap values to multiple sites. Finally, the use of home range area in reserve design would be best suited to situations in which large areas of habitat containing established gopher tortoise populations will be developed and small reserves are to be established within these areas for small, but viable populations of gopher tortoises. However, most reserves likely are to be established in areas of suitable habitat that lack gopher tortoises at the time of establishment and to which animals will be moved for conservation purposes. Thus, estimation of reserve size using home range area seems unfeasible at this time.

Area estimates based on burrow counts appeared more accurate in determining reserve size. Cox et al. (1987) recommended that reserves for 40–50 gopher tortoises contain 80 active or inactive burrows and be 10–20 ha is size. In our MAXIMUM reserves, mean population size was well within these predicted ranges. We used the value of 50 adult tortoises as the target size of viable populations and the majority of reserves contained fewer than this number of animals. However, only 17 of 315 reserves (< 1%) contained populations smaller than 40 individuals, the lower value for

Table 3. Estimated reserve area (in ha) required for 50 adult gopher tortoises based on the following formula: RA = T/ ((S * D) + I), where T = the target population size, S = the slope of the regression line, D = burrow density, and I = the intercept of the regression line. Column headings are for varying tortoise densities and the resultant reserve areas needed based on the four regression equations in Fig. 5 (A = MAXIMUM, B = MINIMUM, C = EXPANDED, D = existing reserves in southeastern USA).

Burrow Density	Reserve Area A	Reserve Area B	Reserve Area C	Reserve Area D
2.0	45.2	135.1	73.9	49.3
3.0	29.0	86.8	48.6	37.4
4.0	21.3	63.9	36.2	30.2
5.0	16.9	50.6	28.9	25.3
6.0	14.0	41.9	24.0	21.7
7.0	11.9	35.7	20.5	19.1

a viable population considered by Cox et al. (1987). Thus, at first glance, reserves established using 80 active and inactive burrows appeared to preserve adequate habitat for the target population sizes.

Because home range data were used to establish tortoise locations, a tortoise was included within a reserve population if it occupied at least one burrow within the reserve over a one year time period. If such a reserve were established in the real world, it is likely that some tortoises would be located in portions of their home range outside the reserve boundaries when the reserve was established. Therefore, the actual population size within a reserve would be smaller than predicted for an 80-burrow reserve. To determine minimum population sizes, only those animals whose entire home range occur within reserve boundaries (MINIMUM) should be counted, increasing the likelihood that individuals considered to be part of the reserve would be able to carry out all of their annual activities within the reserve. Mean population size decreased to 19.0 ± 0.19 tortoises within MINIMUM reserves, with the largest population containing only 28 tortoises. These population sizes are substantially lower than current estimates of viable population size. Thus, reserves created using a target of 80 burrows may be too small to sustain viable populations. Based on burrow counts in EXPANDED reserves, our study suggests that at least 157 burrows are necessary to ensure that 50 adult tortoises are conserved by those burrows, assuming that tortoises throughout the geographic range move similarly to those at Green Grove.

When Cox et al. (1987) calculated minimum viable population size, insufficient reproductive data were available for use in creating models of population viability. Instead, estimates of life history traits were used. Minimum viable populations based on more recent data may indicate that population sizes should be larger than previously predicted, requiring even larger reserves to accommodate additional tortoises. Estimates should be recalculated with current data and models of population viability to ensure that effective population size can be calculated accurately. Further, although current estimates of minimum viable population are between 40 and 50 individuals, only 50–75% of a gopher tortoise population is composed of breeding adults (Alford, 1980). Thus, to account for non-breeding individuals, effective populations would need to contain 50 to 80 gopher tortoises. Even within EXPANDED reserves, the largest population at Green Grove contained only 67 tortoises. If current guidelines continue to be used, the number of burrows added to reserves should be adjusted to reflect area requirements for effective populations and not merely viable populations.

An alternative method to those suggested by Cox et al. (1987) might be to use the strong relationships between burrow density and tortoise density to predict reserve area. The similarity of regressions between Green Grove and data gathered from the literature suggests that a common equation might be applicable across the entire gopher tortoise range. The regression equation for data from the literature probably is the best predictor of reserve area because it utilizes data from a broad geographic distribution. Thus, to predict the required reserve area (RA) for a target number of animals, the following formula could be used:

$$RA = T/((0.321 * D) + 0.373) \quad [5]$$

where T = the target population size and D = burrow density. This equation could be used for any area where the expected burrow density was known or could be inferred from surveys of surrounding areas. From this equation, a population of 50 gopher tortoises would require between 19 and 41 ha of habitat, depending on burrow density within a site (Table 3, regression D). However, habitat type and quality likely influence burrow density within a particular site. Therefore, before this formula is implemented range-wide, additional data should be gathered to test the accuracy of the relationship between burrow density and tortoise density at multiple sites and within the entire range of habitat types found in the geographic range. Otherwise, similar problems to those associated with the study by Cox et al. (1987) could result that would underestimate required area for some gopher tortoise reserves.

Although the guidelines created by Cox et al. (1987) were initiated because of increasing development pressures in Florida, these recommendations provide the only source for estimating gopher tortoise reserve size throughout the entire geographic range of the species. We argue that these recommendations underestimate the amount of habitat necessary to sustain populations of gopher tortoises. Regression analyses provide one alternative to existing methods, but additional alternatives also should be explored to assure that the most accurate estimates of reserve area are calculated. Furthermore, factors such as habitat connectivity, site quality, forage availability, and land use history vary considerably both within and around potential reserve sites. These factors are likely to affect the number of tortoises that a particular reserve can sustain. Refinement of the methods explored in this paper and exploration of alternative models are needed to improve estimation of reserve requirements. Unfortunately, expansion of human activities within the ancestral habitat of gopher tortoises demands that these refinements occur rapidly. Otherwise, it is clear that conservation decisions will have to be made from the extremely restricted data currently available. We suggest that future reserve size estimates be larger than current methods predict to ensure that existing populations are maintained over time, especially if new models expand current estimates of minimum viable population size or of reserve areas necessary to support viable populations.

ACKNOWLEDGMENTS

We thank Sharon Hermann, Whit Gibbons, and an anonymous reviewer for their insightful comments on early drafts of this manuscript. This research was supported by funding from the Robert Woodruff Foundation through the J.W. Jones Ecological Research Center.

LITERATURE CITED

ALFORD, R.A. 1980. Population structure of *Gopherus polyphemus* in northern Florida. J. Herpetol. 14:177-182.

AUFFENBERG, W. AND FRANZ, R. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). In: Bury, R.B. (Ed.). North American Tortoises: Conservation and Ecology. U.S. Dept. Int. Fish Wildl. Serv. Wildl. Res. Rep. No.12, pp. 95-126.

BREININGER, D.R., SCHMALZER, P.A., AND HINKLE, C.R. 1991. Estimating occupancy of gopher tortoise (*Gopherus polyphemus*) burrows in coastal scrub and slash pine flatwoods. J. Herpetol. 25:317-321.

BURKE, R.L. 1989. Florida gopher tortoise relocation: overview and case study. Biol. Conserv. 48:295-309.

BURKE, R.L. 1991. Relocations, repatriations, and translocations of amphibians and reptiles: taking a broader view. Herpetologica. 47:350-357.

BURKE, R.L. AND COX, J. 1989. Evaluation and review of techniques used to study and manage gopher tortoises. Proceedings of the symposium on the management of amphibians, reptiles, and small mammals in North America. Flagstaff, AZ.

COX, J., INKLEY, D., AND KAUTZ, R. 1987. Ecology and habitat protection needs of gopher tortoise (*Gopherus polyphemus*) populations found on lands slated for large-scale development in Florida. Tallahassee, FL: Florida Game and Fresh Water Fish Commission, Non-Game Wildlife Tech. Report No. 4, 75 pp.

DIEMER, J.E., JACKSON, D.R., LANDERS, J.L., LAYNE, J.N., AND WOOD, D.A. 1987. Gopher tortoise relocation symposium proceedings. Florida Game and Freshwater Fish Commission, Nongame Wildlife Technical Report 5, Gainesville, FL.

DODD, C.K. AND SEIGEL, R.A. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica. 47:336-350.

DOUGLASS, J.F. 1990. Patterns of mate-seeking and aggression in a southern Florida population of the gopher tortoise, *Gopherus polyphemus*. Proceedings from the Annual Meeting of the Desert Tortoise Council, 1986, pp. 155-199.

DREW, M.B., KIRKMAN, L.K., AND GHOLSON, A.K., JR. 1998. The vascular flora of Ichauway, Baker County, Georgia: a remnant longleaf pine/ wiregrass ecosystem. Castanea. 63:1-24.

ERNST, C.H., LOVICH, J.E., AND BARBOUR, R.W. 1994. Turtles of the United States and Canada. Washington, DC: Smithsonian Institution Press, 578 pp.

HERMANN, S.M., GUYER, C., WADDLE, J.H., AND NELMS, M.G. 2002. Sampling on private property to evaluate population status and effects of land use practices on the gopher tortoise, *Gopherus polyphemus*. Biol. Cons. 108:289-298.

HOOGE, P.N. AND EICHENLAUB, B. 1997. Animal movement extension to ArcView. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK.

KIE, J.G., BALDWIN, J.A., AND EVANS, C.J. 1996. CALHOME: a program for estimating animal home ranges. Wildl. Soc. Bull. 24:342-344.

MCCOY, E.D., AND MUSHINSKY, H.R. 1995. Demography of *Gopherus polyphemus* (Daudin) in relation to size of available habitat. Florida Game and Freshwater Fish Commission, Nongame Wildlife Program Project Report GFC-86-013, Tallahassee, FL, pp. 1-71.

MCRAE, W.A., LANDERS, J.L., AND GARNER, J.A. 1981. Movement patterns and home range of the gopher tortoise. Am. Midl. Nat. 106: 165-179.

NOSS, R.F. 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. Nat. Areas J. 9:211-213.

OTT, J.A. 1999. Patterns of movement, burrow use, and reproduction in a population of gopher tortoises (*Gopherus polyphemus*): implications for the conservation and management of a declining species. M.S. Thesis, Auburn University, Alabama.

TESII. 1995. U. S. Threatened and Endangered Species. Volume 1: Animals. Golden, CO: Threatened and Endangered Species Information Institute.

Received: 22 May 2000
Reviewed: 4 August 2002
Revised and Accepted: 28 August 2002