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Authors: Guyer, Craig, Goessling, Jeffrey M., and Folt, Brian

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Annual and Lifetime Home Ranges Reveal Movement Patterns Within and Among Local Populations of Gopher Tortoises (*Gopherus polyphemus*)

CRAIG GUYER^{1,*}, JEFFREY M. GOESSLING², AND BRIAN FOLT³

¹Department of Biological Sciences, Auburn University, Auburn, Alabama 36849 USA [guyercr@auburn.edu];

²Natural Sciences Collegium, Eckerd College, St Petersburg, Florida 33711 USA [goessljm@eckerd.edu];

³Conservation Science Partners, Inc, 11050 Pioneer Trail, Suite 202, Truckee, California 96161 USA [brian@csp-inc.org]

*Corresponding author

ABSTRACT. – To explore patterns of emigration of gopher tortoises (*Gopherus polyphemus*), we examined movements at a study site in south-central Alabama that consisted of 2 distinct aggregations of burrows located on adjacent north and south sandhills separated by a mesic depression wash. We collected telemetry data from 41 individuals over a complete season of activity (2000–2001) and capture-mark-recapture data of those same individuals during 14 trapping sessions from 1992 to 2020. We observed a bimodal distribution of telemetry fixes, with 1 mode created by individuals with few fixes ($n = 9$) who also were recaptured infrequently, which we interpreted to represent emigrants. Thus, our data suggest that the proportion of a local population that emigrates each year is on the order of 20%. To characterize the degree to which resident tortoises (those recaptured ≥ 5 times over the 29-yr period) used space across the entire study site, we used 100% minimum convex polygons to examine the proportion of annual home ranges (based on telemetry data) and lifetime home ranges (based on capture-mark-recapture and telemetry data) that involved both sandhills. For annual home ranges, only a single individual (of 14 residents) occupied burrows on both hills over 1 yr. For lifetime home ranges, 9 individual residents used burrows on both hills. Lifetime home ranges were 6 times larger than annual home ranges, with longest distances between vertices of lifetime home ranges approaching distances ascribed to emigration in previous studies. A model generated from the lifetime recapture data indicated a tendency for greater apparent survival of adults compared with juveniles on the study site and for juveniles and adult females to be more likely to move from the south hill to the north hill than the opposite direction. When added to 5 additional sites for which telemetry data were gathered, we argue that emigration rate is strongly and negatively correlated with local tortoise density. We conclude that current individual-based population models correctly separate movements of animals within a local population (residents) from emigration of animals among local populations, such models require addition of density dependence when addressing emigration rate, and dispersal distances are longer than those based on studies of movements within a single season of activity.

KEY WORDS. – *Gopherus polyphemus*; dispersal; migration; demography; telemetry; density dependence

Long-term management of sensitive species in the face of habitat loss and a changing environment is among the greatest challenges in conservation science. Risk assessments for imperiled species often involve predictive population models that seek to project how populations might respond to plausible future scenarios of environmental change (e.g., DeAngelis and Grimm 2014; Smith et al. 2018). In the absence of detailed data describing demographic rates or anthropogenic effects on populations, models are often characterized by substantial uncertainty (Runge et al. 2011). However, such uncertainty can be reduced by accumulation of novel field data, especially when these data improve estimates of key demographic vital rates and allow modification of model structure to include previously unknown effects.

The rate at which individuals emigrate from a local population is among the most difficult demographic variables to characterize because exploratory movements of individuals within populations must be separated from dispersal between populations (McMahon and Matter 2006). Despite this difficulty, emigration from a local population and eventual immigration to another local population is known to be a key variable in characterizing population dynamics (Millon et al. 2019). For example, Folt et al. (2022) used demographic models to demonstrate that population persistence of gopher tortoises (*Gopherus polyphemus*), a long-lived but declining species associated with longleaf pine (*Pinus palustris*) forests of the southeastern United States, is highly sensitive to immigration. These authors concluded that improved knowledge of dispersal

rates and distance between local populations are key to making predictions for how gopher tortoises will respond to anthropogenic threats in a future changing world. However, estimates of dispersal for gopher tortoises emerge largely from Eubanks et al. (2003), who estimated that 2% of a population monitored via radiotelemetry emigrated from a local population, moving 1.2–1.5 km from the population along paths of 4.8–6.4 km. Based on characteristics described in Berry (1986), movements associated with emigration were separated from those associated with exploratory movements within a home range by being successively farther from the home range and involving moves of at least 2 km.

Improved estimates of emigration distances and rates are warranted for understanding gopher tortoise spatial ecology. As noted by Berry (1986), estimates of emigration distance typically are based on movement studies lasting a single season of activity rather than being representative of a lifetime of movements. Additionally, published values of emigration distance are likely to be underestimates because telemetered animals emigrating long distances can move beyond the detection distance of the receiver. Such observations frequently are attributed to equipment failure rather than emigration. Additionally, replicate studies of emigration rate of gopher tortoises are desirable given that this variable might be density dependent, a feature known for other aspects of tortoise movements (Guyer et al. 2012). A plausible hypothesis is that emigration rate will be greater at low-density, poor-quality sites because an emigrant has an improved probability that a neighboring local population is of better quality (McMahon and Matter 2006).

Here, we explore patterns of movement within a local population of gopher tortoises and emigration from it, using a unique study site where individuals were monitored with telemetry for a complete field season and using mark–recapture over a 29-yr period. First, to estimate the discrepancy between movement patterns measured at annual and lifetime scales, we measured the difference between home range size over a single year of activity and that representing long-term capture localities of resident tortoises. Second, to understand exploratory movements within a population, we used a multistate population model to estimate the probability that individuals will explore adjacent sandhills, while accounting for stage-specific apparent survival probabilities and imperfect detection. Last, we used telemetry data gathered at our primary study site and 5 additional sites to estimate emigration rates and to test whether emigration is influenced by local population density.

METHODS

Primary Study Site. — Our primary study site was a 54-ha tract in the Conecuh National Forest in southwestern Covington County, AL, near the rural town of Bradley. The physiography of the study site included 2

adjacent sandhills formed by soils of the Troup series; the sandhills each contained an aggregation of burrows used by tortoises over time, 1 covering the north hill and the other covering the base of the south hill (Fig. 1). Blackwater Creek formed a northern and western border to the study site, a private agricultural field formed the eastern boundary, and altered habitat structure associated with a border between management units formed the southern boundary. Initially, the study site was within a US Forest Service compartment managed for longleaf pine restoration starting in 1987. During that year, harvest of some slash pine (*Pinus elliottii*) occurred, and the site received a prescribed fire during the winter to allow natural regeneration of longleaf pine. In the subsequent 35 yrs, the site received prescribed fire approximately every 2.5 yrs, typically in winter, but with spring burns in 1994 and 1997; harvest of some pines (thinning) also occurred in 1993 and 2007. In 2011, the area containing the south hill was cleaved to a separate management area. This new management area was clear-cut in 2011, planted with longleaf pine in 2014, and treated with herbicide (to reduce competing understory vegetation) in 2015 (Pudner et al. 2021). These management activities created an overstory dominated by pines (equivalent abundance of longleaf and slash pines) with scattered hammocks of water oak (*Quercus nigra*), Darlington oak (*Quercus hemisphaerica*), and flowering dogwood (*Cornus florida*). The understory was a mosaic of areas dominated by grasses (primarily *Andropogon gerardia* and *Aristida beyrichiana*), blueberry and yaupon (*Vaccinium* spp. and *Ilex vomitoria*), or runner oaks (*Quercus geminata* and *Quercus minima*). Bluejack (*Quercus incana*), sand post (*Quercus margaretta*), and turkey (*Quercus laevis*) oaks created a midstory.

We used capture-mark-recapture methods to sample tortoises at the study site during 14 trapping events (1992, 1993, 1994, 1997, 1998, 1999, 2000, 2001, 2002, 2003, 2016, 2017, 2019, and 2020). We captured individuals in wire live traps placed at the entrance of active burrows. Traps were shaded with burlap or vegetation and checked daily at ca. 1000 and 1400 hrs. Typically, individuals were identified based on previous file marks on marginal scutes (filed if newly captured), measured for body size (carapace length, plastron length, body mass), characterized as to sex (deep plastral depression in males; plastral depression shallow or lacking in females), and released to the burrow of capture. However, for some individuals successive recapture intervals were separated long enough in time to require identification by other means because file marks can erode. These additional identification marks included scute anomalies, epoxy residues from detached transmitters, unusual color markings, and records of broken toenails. Recorded as sketches or notes on data sheets or digital images, these additional markings served to identify some individuals. For such animals, we refreshed file markings to maintain the primary method of identification. Burrows at which tortoises were captured were

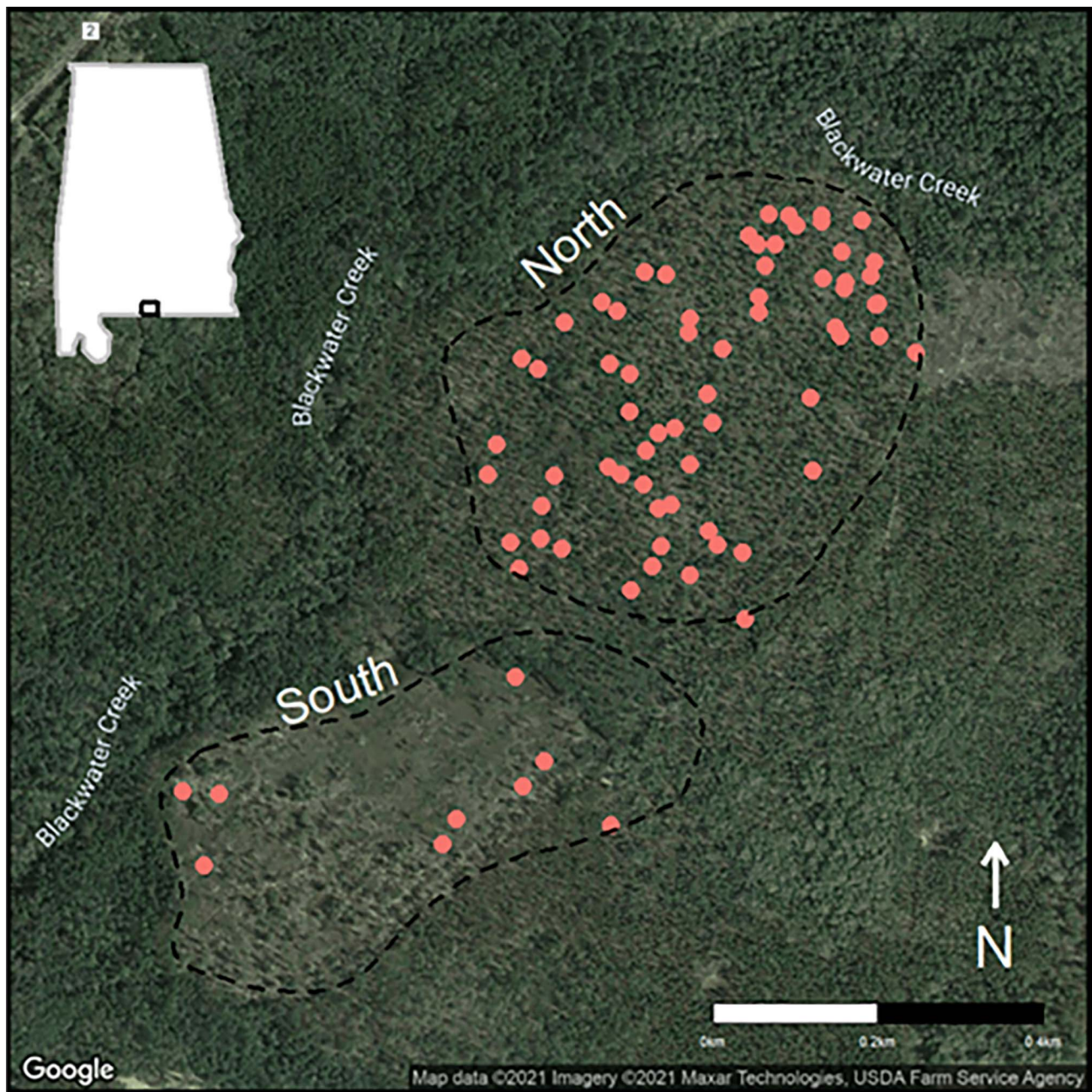


Figure 1. Map of primary study site showing its location within Alabama (top left inset) and the distribution of gopher tortoise (*Gopherus polyphemus*) burrows found to be occupied during 1992–2021. Dashed ellipses delimit a sand hill that forms the northern portion of the study site (“North”) and the base of an adjacent sand hill that forms the southern portion of the study site (“South”).

georeferenced to within 3 m with handheld global positioning system units (Garmin 64st®).

We collected telemetry data on adult tortoises during 2000 and 2001. Two-part putty epoxy (Oatey®) was used to attach a radio transmitter (American Wildlife Enterprises, Inc) to a posterior costal scute, with the antenna being epoxied to lateral and anterior costal scutes. We trapped 20 adult females, 20 adult males, and 1 additional individual (sex unknown) during 15 July–4 October 2000 and attached transmitters at this time. Relocations of transmitter-equipped tortoises occurred 3–5 times per week from 31 August 2000–19 October 2001. This period

covered peak mate seeking (September–November 2000), brumation (November 2000–April 2001), nesting (May–June 2001), and early mate seeking (July–October 2001). Use of a radio receiver (Communications Specialists, Inc.) and antenna (Yagi handheld) allowed us to relocate individuals within georeferenced burrows.

Secondary Study Sites. — We explored data gathered at 5 additional sites. Two of these, Green Grove and the Wade Tract in Georgia, represented high-quality habitat containing an overstory dominated by old (> 80 yrs) longleaf pine and an understory maintained by frequent fire, including growing-season burns; tortoise density was

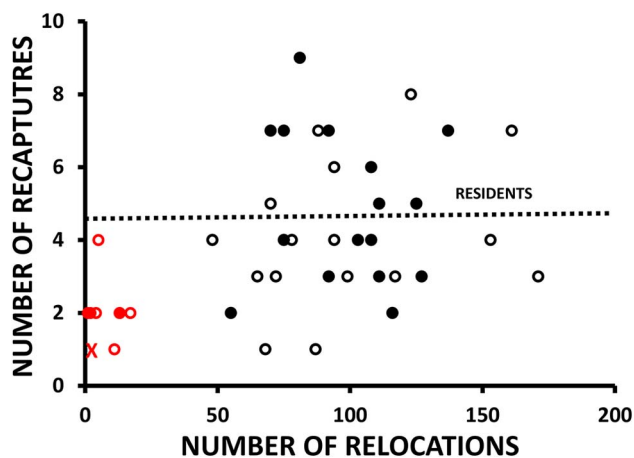


Figure 2. Bivariate plot of radiotelemetry fixes (x axis) and number of long-term captures (y axis) of gopher tortoises (*Gopherus polyphemus*) from a population in southern Alabama. Points are: females (open circles), males (filled circles), and an individual of unidentified sex (X). Dashed line separates individuals defined to be residents (above line) from those defined to be emigrants (below line). Presumed emigrants during year 2000 are indicated in red.

high at these sites. Two sites represented poor-quality habitat associated with active, short-rotation pine production (Mobile County, AL) and infrequent fire (Dixon Center, AL); tortoise density was low at these sites. The fifth site (Camp Shelby, MS), like our primary study site, was of intermediate quality, being managed by thinning and use of dormant-season prescribed fire; tortoise density was intermediate at these 2 sites (see Guyer et al. 2012 for details of each site). At each site, preliminary surveys were conducted to locate burrows, which were then examined with a burrow scope, with occupants being trapped as described above. Each individual received a radio transmitter and was monitored for an entire season of activity. From these telemetry data, we categorized an individual as being an emigrant if telemetry detections ceased at least 1 mo before the end of the tracking period.

Analyses. — We performed all analyses in the statistical program R (R Core Team 2021) and, where appropriate, evaluated significance with $\alpha = 0.05$. As a preliminary analysis, we tested the null hypothesis that the number of telemetry fixes for the 41 monitored tortoises was unimodal (Hartigan's dip test [Hartigan and Hartigan 1985] as implemented with package 'dipTest' [Maechler 2021]). Telemetry relocations differed significantly from a unimodal distribution ($D = 0.08$; $p = 0.05$) and instead conformed to a bimodal distribution (Fig. 2) with a small mode ($n = 9$) centered on 5 relocations and a large mode ($n = 32$) centered on 80 relocations. We defined individuals within the small mode to be emigrants (long-distance migrants unlikely to return to the study site) because no transmitter was ever recovered from these individuals, an expectation if members of the small mode represented equipment failure. The conclusion that emigration may occur annually suggests that some individuals for which telemetry locations were recorded for a complete year emigrated in

subsequent years while others did not (residents). Inclusion of emigrants to assess lifetime home range area would dilute area estimates generated for the target group of residents. For this reason, we arbitrarily chose 4.5 captures as a cutoff below which we considered individuals to be potential emigrants and above which we considered individuals to be residents. This cutoff divided individuals into 2 groups of roughly equivalent size, 1 characterized by the high number of recaptures expected of residents and 1 characterized by low numbers of captures expected of emigrants (Fig. 2). We performed home range analyses on the 6 females and 8 males judged to be residents, a group that represented 34% of the local population monitored via telemetry.

We calculated home range area as 100% minimum convex polygons for individuals on the primary study site. Annual home ranges were estimated from telemetry records of each individual, while lifetime home ranges were estimated from all burrows comprising the annual home range and all additional occupied burrows identified from the long-term capture records. The same tortoises were used to estimate both annual and lifetime home ranges. We used repeated-measures analysis of variance to test for differences in home range area by sex and home range type (annual or lifetime). We calculated home range area (m^2) in Excel from the formula in Jennrich and Turner (1969) for adjacent polygon vertices (Universal Transverse Mercator values for burrow locations); home ranges comprising a single burrow were assigned a value of $1 m^2$ and home ranges comprised of 2 burrows were assigned values equal to the distance between those burrows. To characterize lifetime movements, we calculated the longest distance between all pairs of vertices for each lifetime home range and used the mean and maximum values to evaluate published values for dispersal distance against longest lifetime movements of resident tortoises.

To estimate annual variation in survival and relocation between sandhills, we compiled detection histories for each individual marked in the study area where, upon capture, we classified individuals as juveniles (sex unknown), adult females, or adult males and as occupying the north sandhill or the south sandhill. Folt et al. (2021) built a multi-state mark-recapture model (Lebreton et al. 2009; Kéry and Schaub 2012)—an extension of the generalized Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965)—to estimate stage-specific apparent survival probability for 6 distinct populations of gopher tortoises in southern Alabama, including the north sandhill from our present study. Here, we adapted that model to estimate 5 parameters: apparent annual survival probability (ϕ_t^j , the probability that an individual in stage j that is alive and in the population in year t survives and is in the population in year $t + 1$), recapture probability (p_t^j , the probability of an individual in stage j being recaptured, if alive and present in the population), transition probability (τ_t , the probability of a juvenile in year t being a female in year $t + 1$), female probability (f_t , the probability of a juvenile transitioning to

an adult female state in year t), and sandhill relocation probability (ψ^{ab} , the probability of an individual previously detected in sandhill a being detected in sandhill b during any given year). Only individuals in the juvenile state transitioned to adult states (adult female or adult male), therefore the transition probability, τ , represented an average maturation rate for both sexes. Because patterns of gopher tortoise demography and movement are thought to vary by habitat (Howell et al. 2020) and management history

differed between the north and south sandhills, we modeled ϕ and ψ to vary between sandhills.

The state process (survival, relocation, and transition probabilities) was represented as a matrix describing the probability of transition from the row index state to the column index state in a single year with seven distinct states (north juvenile, south juvenile, north adult female, south adult female, north adult male, south adult male, or dead):

$$\begin{bmatrix} \phi^{jn}(1 - \psi^{ns})(1 - \tau) & \phi^{jn}\psi^{ns}(1 - \tau) & \phi^{jn}(1 - \psi^{ns})\tau f & \phi^{jn}\psi^{ns}\tau f & \phi^{jn}(1 - \psi^{ns})\tau(1 - f) & \phi^{jn}\psi^{ns}\tau(1 - f) & 1 - \phi^{jn} \\ \phi^{js}\psi^{sn}(1 - \tau) & \phi^{js}(1 - \psi^{sn})(1 - \tau) & \phi^{js}\psi^{sn}\tau f & \phi^{js}(1 - \psi^{sn})\tau f & \phi^{js}\psi^{sn}\tau(1 - f) & \phi^{js}(1 - \psi^{sn})\tau(1 - f) & 1 - \phi^{js} \\ 0 & 0 & \phi^{fn}(1 - \psi^{ns}) & \phi^{fn}\psi^{ns} & 0 & 0 & 1 - \phi^{fn} \\ 0 & 0 & \phi^{fs}\psi^{sn} & \phi^{fs}(1 - \psi^{sn}) & 0 & 0 & 1 - \phi^{fs} \\ 0 & 0 & 0 & 0 & \phi^{mn}(1 - \psi^{ns}) & \phi^{mn}\psi^{ns} & 1 - \phi^{mn} \\ 0 & 0 & 0 & 0 & \phi^{ms}\psi^{sn} & \phi^{ms}(1 - \psi^{sn}) & 1 - \phi^{ms} \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

We represented the detection process as a matrix describing the probability of detecting an individual in the column index state (observation outcome; detected as juvenile in the north, juvenile in the south, adult female in the north, adult female in the south, adult male in the north, adult male in the south, or not detected); given that it is truly in the row index state:

$$\begin{bmatrix} p^{jn} & 0 & 0 & 0 & 0 & 0 & 1 - p^{jn} \\ 0 & p^{js} & 0 & 0 & 0 & 0 & 1 - p^{js} \\ 0 & 0 & p^{fn} & 0 & 0 & 0 & 1 - p^{fn} \\ 0 & 0 & 0 & p^{fs} & 0 & 0 & 1 - p^{fs} \\ 0 & 0 & 0 & 0 & p^{mn} & 0 & 1 - p^{mn} \\ 0 & 0 & 0 & 0 & 0 & p^{ms} & 1 - p^{ms} \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

We modeled p as varying between the north and south sandhills because those sites experienced different management histories and were characterized by different habitat structure, in ways that might influence the detection process during mark-recapture surveys. During 2 years with low sampling at both sandhills (1995 and 1998), we constrained state-specific recapture probabilities to equal 0.

This model conditioned on first capture and assumed that individuals within the population were sampled randomly, marks were not lost and were detected perfectly, the population was closed to mortality within sampling periods, and the population was closed to emigration and

immigration during the study (Williams et al. 2002; Kéry and Schaub 2012). Additionally, we assumed that state assignment was made perfectly, individuals within states were identical with respect to apparent survival, recapture, and maturation probabilities, and states had identical relocation probabilities between sandhills. While we acknowledge that population closure during the study was likely violated due to emigration that we observed, we believe this model is still useful for estimating state-specific movement rates of individuals that were present in the study area, especially for movements between sandhills.

We estimated demographic parameters using a state-space formulation of the multistate model in JAGS (Plummer 2003; Kéry and Schaub 2012), implemented using the ‘jagsUI’ package (Kellner 2016). We ran 3 independent chains of 50,000 iterations with a burn-in period of 25,000 iterations and an adaptation period of 10,000 iterations. We thinned chains by 10, which gave us 1500 samples from the posterior distribution. We used uninformative uniform prior distributions for all our parameters. We assessed model convergence by evaluating the \hat{R} statistic and by visual examination of the chains for convergence (Kéry and Schaub 2012); we considered convergence on the posterior distribution adequate when all structural parameters had $\hat{R} < 1.1$. We summarized the posterior distribution of parameters estimated by our multistate model using mean values and 95% credible intervals (CI); we considered parameter estimates from the model as statistically significant when 95% CI did not overlap 0.

To estimate emigration rate, we counted emigrants for all 6 study sites based on loss of telemetered individuals

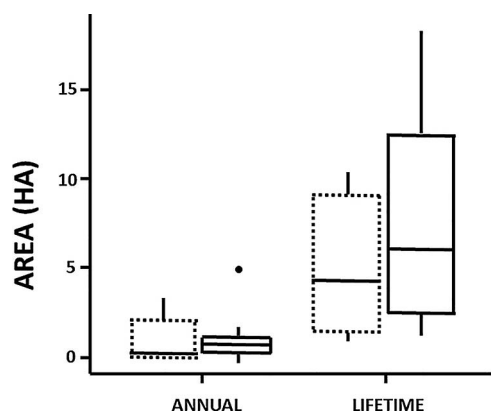


Figure 3. Box-and-whisker plots describing annual and lifetime home range size (ha) of adult female (dotted-line boxes) and adult male (solid-line boxes) gopher tortoises (*Gopherus polyphemus*) at a population in southern Alabama. Horizontal line shows median, boxes show upper and lower quartiles, vertical line shows range, and solid dark dot shows an outlier.

(see above). We assumed that all individuals were detected on each site and divided number of emigrants by the total number of individuals to calculate annual emigration rate. We then regressed these estimates on tortoise density of each site (from Guyer et al. 2012) which allowed us to assess density-dependence of emigration rate via linear regression.

RESULTS

We found home ranges to vary considerably among individuals; 1 female occupied a single burrow as her annual home range, while 1 male occupied a lifetime home range of 18.2 ha. Annual home range area was approximately 6 times smaller than lifetime home range area (Fig. 3), a difference that was statistically significant ($F_{1,12} = 8.20$, $p = 0.009$). Home range area did not vary significantly by sex ($F_{1,12} = 1.21$, $p = 0.28$) nor was there a sex-by-type interaction ($F_{1,1} = 1.19$, $p = 0.29$). The longest distance between vertices of the lifetime home range averaged 567 m and ranged up to 1014 and 1075 m for females and males, respectively. Annual home ranges of residents were centered on the north hill (Fig. 4), with only 1 (a male) of 14 residents displaying movements extensive enough to include the south hill. However, 9 of 14 residents (5 males and 4 females) had lifetime home ranges that were extensive enough to include both hills.

We found that apparent annual survival on the primary study area tended to be greater for adult females and males than juveniles (mean estimates of adults greater than 95% CI of juveniles) (Table 1; Fig. 5). Our estimates suggest greater apparent annual survival on the north sandhill relative to the south sandhill, a pattern characterizing adult females and juveniles but not adult males (Table 1), although wide 95% CI indicate additional data will be required to ascribe statistical significance to this pattern. The probability that an individual would move from one sandhill to the other was greater for the south-

to-north direction than for north-to-south (Table 1; Fig. 6). State-specific recapture probabilities (p) also were greater for juveniles than for adults and were greater on the north sandhill than the south for all age and sex groups (Table 1).

The proportion of individuals inferred to have emigrated during 2000–2001 (9 of 41) included similar numbers of each sex ($n = 4$ males; $n = 5$ females) and represented 22% of the cohort of animals affixed with a radio transmitter in 2000. None of these individuals was recaptured during the 5 subsequent sample events. When examined across 5 additional study sites, we observed a negative relationship between emigration rate and population density ($Y = -0.20 X + 0.33$; $F_{1,4} = 36.46$; $p = 0.002$; Fig. 7).

DISCUSSION

Our data estimate the degree to which parameters based on movement patterns gathered over a single season of activity underestimate the likely extent of space use over a gopher tortoise's lifetime, a desired parameter for population models based on activities of individuals. We found that movement estimated from a single season of activity was 6 times less than movement estimates using a longer time series of captures. This difference likely results from annual home range centroids shifting over time, which generates significantly larger dimensions to the lifetime home range compared to home ranges used during individual years. Whether this results from expansion expected of Brownian motion models of movement or nonrandom changes in the distribution of key resources (see Börger et al. 2008) remains to be determined for gopher tortoises. Nevertheless, our values for lifetime home ranges still underestimate the true values, despite being based on recaptures over a 29-yr period, because we have only a single location within each year for nearly all samples of lifetime home ranges of each resident. Use of lifetime telemetry devices (e.g., Curry 2018) will provide an opportunity to improve estimation of both annual and lifetime home ranges in gopher tortoises relative to the values that we provide here.

In addition to estimations of geographic area represented by location data, our multistate model reinforces the concept that resident tortoises move extensively in their lifetimes. Our analysis estimates that 20%–40% of individuals move between adjacent sandhills each year. The model also suggests that tortoises occupy some areas (north sandhill) of the local population preferentially over others (south sandhill). These observations, along with our home range analyses, suggest that the extent of lifetime movements of residents within a local population commonly approach distances previously attributed to emigration from a local population (e.g., Eubanks et al. 2003). Such movements within our study site indicate that panmixis of resident adults within our local population is possible given the large size and wide overlap of

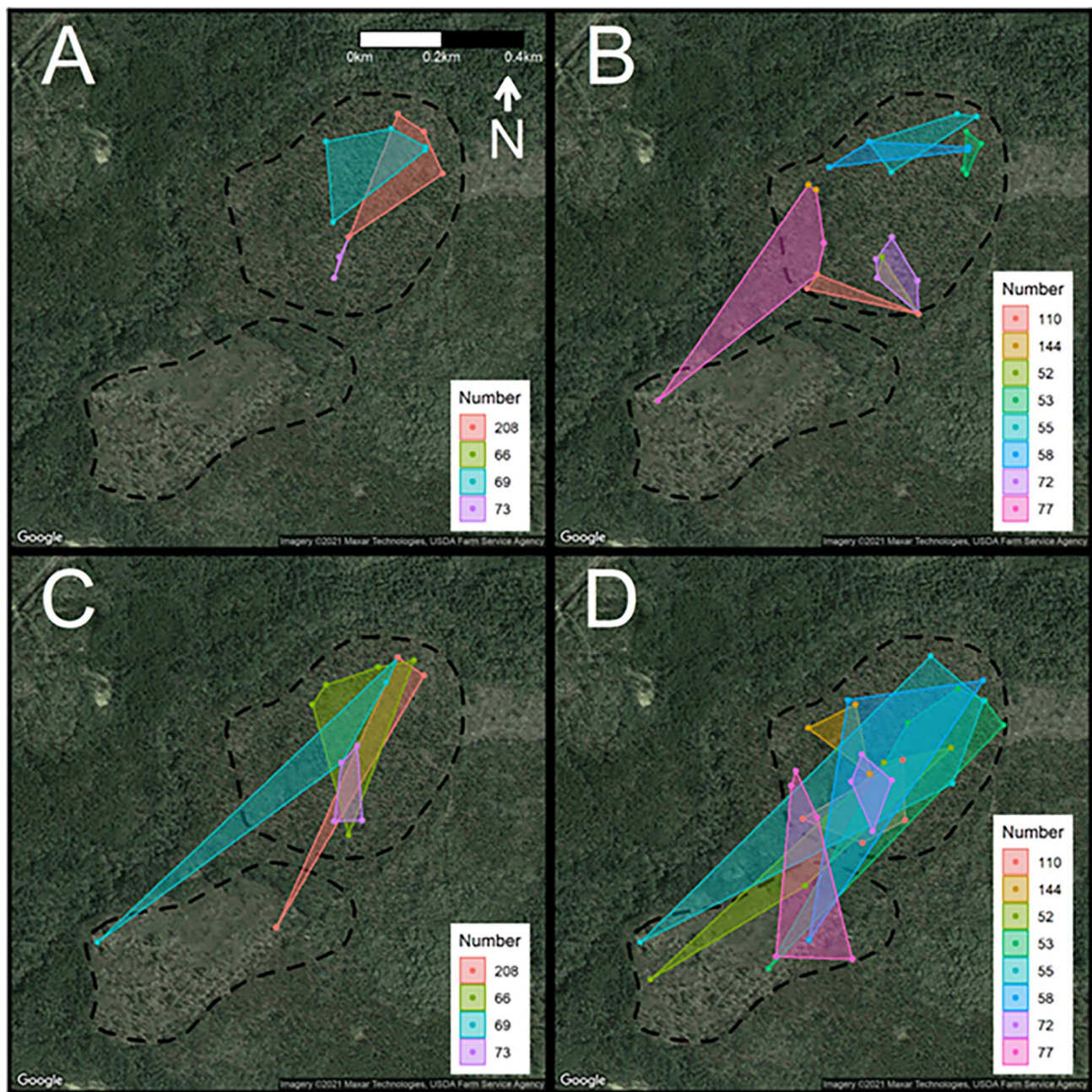


Figure 4. Annual home ranges of resident female (A) and male (B) gopher tortoises (*Gopherus polyphemus*) during 2000–2001 and lifetime home ranges of those same resident female (C) and male (D) tortoises during 1992–2020.

lifetime home ranges, a propensity of many individuals, especially adult males, to explore the entire extent of the local population, and known long-term sperm storage in females (Palmer and Guillette 1988; Moon et al. 2006).

Our observations allowed us to separate extensive movement of individuals that remain within the local population from emigrants who move an undetermined distance to occupy a different local population or die in transit. Based on the number of individuals that disappeared during our telemetry study and assuming that transmitter failure did not occur, we estimated that the proportion of individuals to have emigrated during 1 yr at this site to be ca. 0.20, a value an order of magnitude

larger than that observed by Eubanks et al. (2003). However, our local population increased in size over the entire study period (Goessling et al. 2021), indicating that immigration and/or recruitment were large enough to offset losses due to emigration. Based on an estimate of 0.95 apparent annual survival of adults (Folt et al. 2021, Goessling et al. 2021), 2–3 emigrating tortoises likely survived to 2020, providing ample opportunity for emigrants to leave the local population and then return to it in subsequent years. None of the putative long-distance migrants was documented to return to the site in subsequent years, but an individual from a preliminary sample of tortoises affixed with transmitters in 1999 immediately vanished

Table 1. Mean and 95% credible intervals (lower credible limit [LCL], upper credible limit [UCL]) for parameter estimates from a multistate mark–recapture model used to estimate demographic rates (apparent annual survival [ϕ], maturation [τ], and female sex probabilities), migration probability [ψ], and recapture probability [p] for gopher tortoises (*Gopherus polyphemus*) living on 2 adjacent sandhills in south Alabama during 1992–2004. Parameter superscripts are: juvenile (*j*), adult female (*f*), adult male (*m*), north sandhill (*n*), and south sandhill (*s*).

Parameter	Mean	LCL	UCL
ϕ^{jn}	0.75	0.31	0.98
ϕ^{js}	0.67	0.18	0.98
ϕ^{fn}	0.93	0.76	1.00
ϕ^{fs}	0.85	0.28	1.00
ϕ^{mn}	0.95	0.83	1.00
ϕ^{ms}	0.92	0.58	1.00
τ	0.08	0.01	0.23
f	0.47	0.04	0.94
ψ^{ns}	0.18	0.02	0.60
ψ^{sn}	0.39	0.11	0.75
p^{jn}	0.48	0.24	0.81
p^{js}	0.40	0.11	0.83
p^{fn}	0.70	0.41	0.99
p^{fs}	0.41	0.15	0.85
p^{mn}	0.64	0.41	0.94
p^{ms}	0.40	0.13	0.89

from the site, and then was detected on it because the transmitter was functional for much of 2001. Thus, we know that individuals can emigrate beyond the range of a telemetry receiver for periods of over a year and then return to a local population.

Transmitter failure is a well-documented problem in telemetry studies. This factor has been used by others to censor data associated with individuals characterized by truncated relocation records (e.g., Eubanks et al. 2003). We argue such truncated records may identify emigration rather than equipment failure. Our principal evidence is that the 9 adult tortoises presumed to have emigrated during 2000 were never seen again despite 5 sample periods over which they might have been recaptured had they remained residents. High adult recapture probability (0.4–0.7), high adult apparent survival (0.85–0.95), and

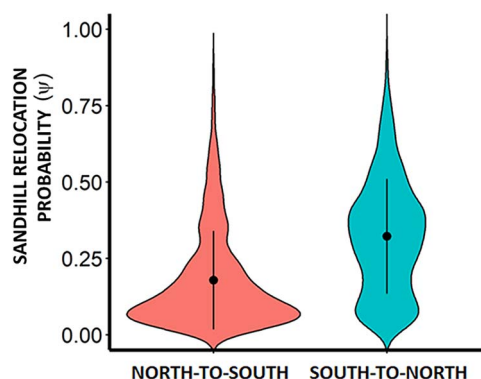


Figure 6. Sandhill relocation probability (i.e., migration probability, ψ) for gopher tortoises (*Gopherus polyphemus*) between the north and south sandhills. Solid dot shows mean, vertical line shows 95% credible interval, and outer boundaries show data distribution smoothed by a kernel density estimator. Individuals occupying the north sandhill have a lower mean probability of relocating to the south sandhill in a given year (pink) than the probability of individuals moving from south to north (blue).

retention of epoxy residue on transmitter residents decades after the telemetry study ended suggest that some of the putative emigrants would have been detected had they remained on site with faulty transmitters. We argue that truncation of such data in studies of demography may prevent discovery of important parameters such as emigration rate. However, given that failure of radio telemeters does occur, we acknowledge that our estimate of emigration of up to 20% of individuals in a local population each year likely is an overestimate. We cannot estimate the degree to which emigration rate was overestimated in that year but note that uncertainty around estimates of apparent survival on the north and south sandhills leaves room for values of emigration rate of at most 5%–15%.

We found that emigration is density dependent, with local populations at low-density, low-quality sites experiencing annual emigration rates approaching 40% of the local population and local populations at high-density, high-quality sites experiencing annual emigration rates of about 2%. Hunter and Rostal (2021) recovered a similar

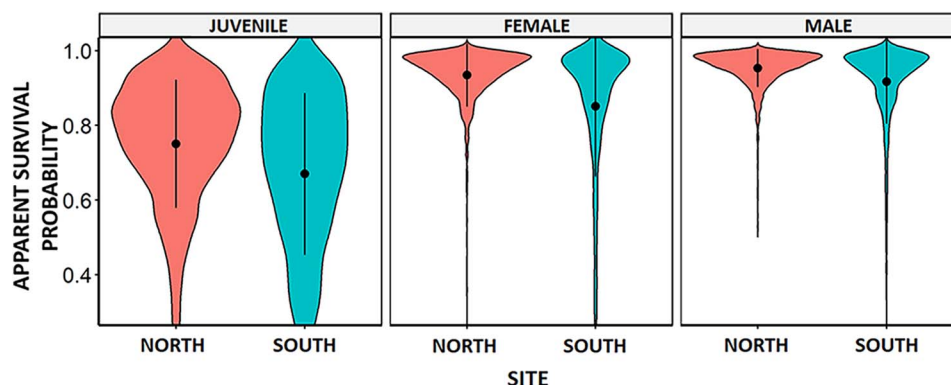


Figure 5. Apparent annual survival probability estimates for gopher tortoises (*Gopherus polyphemus*) occupying the north (pink) and south (blue) sandhills. Solid dot shows mean, vertical line shows 95% credible interval, and outer boundaries show data distribution smoothed by a kernel density estimator.

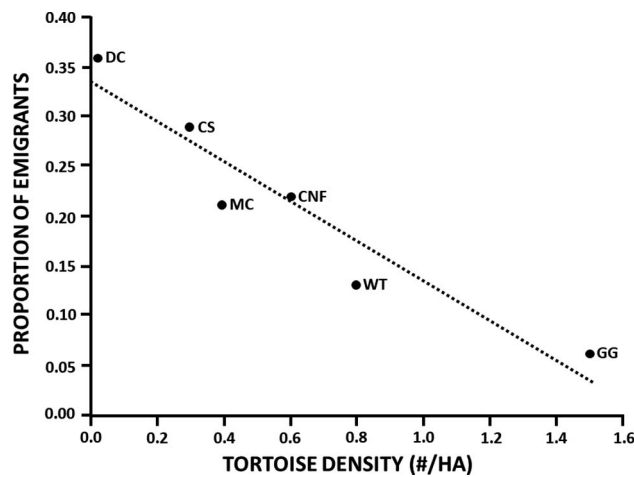


Figure 7. Regression of how local population density influences emigration rate for 6 sites described in Guyer et al. (2012). Dashed line represents ordinary least-squares regression line ($y = -0.20x + 0.33$; $R^2 = 0.91$). Lower-density sites have higher emigration rates. Site abbreviations and sample sizes (total number of individuals transmitted) are Camp Shelby, MS (CS; 38), Conecuh National Forest, AL (CNF; 41), Dixon Center, AL (DC; 13), Mobile County, AL (MC; 40), Green Grove, AL (GG; 132), and Wade Tract, GA (WT; 66).

pattern of reduced habitat quality leading to increased emigration, with habitat quality increasing due to reduced time since last burn. Individual tortoises moving to low-density sites within a metapopulation are likely to continue annual emigration until a high-density/high-quality site is encountered. At such sites, continued emigration is reduced. However, recent immigrants to a high-density site may experience reduced reproductive opportunities while they integrate into the local social structure (Tuberville et al. 2011); additionally, subadult emigrants may experience reduced apparent survival relative to similar-aged residents (Tuberville et al. 2008). Nevertheless, negative density dependence of emigration rate provides a mechanism for extensive gene flow among local populations achieving high density. In the Conecuh National Forest, areas of low local density are extensive and areas of high density are rare (Goessling et al. 2021). Low-density sites typically are of low quality because they lack adequate fire-return intervals, leading to hardwood encroachment (Hermann and Kush 2020). In such areas, tortoises occupy rare open patches, which frequently are found along roadside habitat (Rautsaw et al. 2018). Roads associated with our primary study site include a main access road maintained by the US Forest Service extending north from Covington County Road 4 and branching to provide access to the 2 sandhills (ca. 1.8 km road distance along each branch). An extension of the branch leading to the north sandhill continues east to provide access to a private farm. No tortoise burrow was detected along the main access road during the entire study, suggesting that any tortoise emigrating along this route traveled greater than 2 km within an annual cycle of activity. The closest known local population to our study site is ca. 6.3 km away by road (3.8 km straight-line

distance) to the east. Eubanks et al. (2003) document that tortoises can move 4.8–6.4 km over a period of a few days, indicating that individual tortoises could move between the 2 local populations. However, none of the 226 tortoises marked within the 2 local populations has ever appeared in the other (Folt et al. 2021). Given the high proportion of individuals estimated to emigrate annually and high apparent adult survival, it may be surprising that no individual has been sampled at both sites. From this we infer that 1) additional estimates of emigration rate are necessary to characterize this parameter, 2) there are more local populations than have been detected, 3) roadside habitat absorbs many more individuals than are detected by the cursory searches of roadside habitat that we conducted (see Rautsaw et al. 2018), 4) tortoises disperse along many more routes than dirt roads, or 5) dispersing tortoises experience significantly increased mortality.

Our examination of tortoise movements supports the modeling approach of Westervelt and MacAllister (2012) in which emigration is considered a separate factor from density-dependent movements of resident individuals. Density-dependent movement of residents appears to be a reasonable mimic of our observation of expanded lifetime home ranges relative to annual home ranges. Comparison of lifetime and annual home ranges of individuals within computer models would provide a valuable test of the degree to which models reflect field observations. For future modeling efforts, the proportion of individuals emigrating annually should be modeled as a density-dependent factor constrained to 2% of the local population for the highest-quality sites and 40% of the local population for the lowest-quality sites. Emigration distances within population models could be increased to account for the distances that resident tortoises move during their lifetimes. Unfortunately, our data do not provide information on maximum annual emigration distance or the distribution of such distances. However, the longest distance between burrows at our primary study site was 1.2 km, a distance that resident tortoises appear to traverse during their lives within this local population, sometimes repeatedly. Our telemetry receiver detected transmitters up to 300 m. Thus, we infer dispersing tortoises at this site traveled at least 1.8 km to reach an adjacent local population where we were unlikely to detect them and from which they were unlikely to return to the primary study site. This represents the minimum distance moved by an emigrant during a season of activity. Because the longest path followed by an emigrating tortoise reported by Eubanks et al. (2003) was 6.4 km, we recommend that models select values between 2 and 6.5 km for emigrating tortoises within a season of activity. Additionally, we recommend models include effects of fire frequency (Hunter and Rostal 2021) and habitat quality (Guyer et al. 2012) on likely emigration distances.

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