Contrasting Patterns of Demography and Population Viability Among Gopher Tortoise Populations in Alabama

BRIAN FOLT (ID),[1] *Alabama Cooperative Fish and Wildlife Research Unit, 3305 School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*

JEFFREY M. GOESSLING (ID), *Eckerd College, 075 James Center for Molecular and Life Sciences, St. Petersburg, FL 33711, USA*

ANNA TUCKER (ID), *U.S. Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD 20708, USA*

CRAIG GUYER, *Department of Biological Sciences and Auburn University Museum of Natural History, 331 Funchess Hall, Auburn University, Auburn, AL 36849, USA*

SHARON HERMANN, *Department of Biological Sciences, 331 Funchess Hall, Auburn University, Auburn, AL 36849, USA*

ERICHA SHELTON-NIX, *Alabama Department of Conservation and Natural Resources, 64 Union Street, Montgomery, AL 36130, USA*

CONOR McGOWAN, *U.S. Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*

ABSTRACT Population viability analyses are useful tools to predict abundance and extinction risk for imperiled species. In southeastern North America, the federally threatened gopher tortoise (*Gopherus polyphemus*) is a keystone species in the diverse and imperiled longleaf pine (*Pinus palustris*) ecosystem, and researchers have suggested that tortoise populations are declining and characterized by high extinction risk. We report results from a 30-year demographic study of gopher tortoises in southern Alabama (1991–2020), where 3 populations have been stable and 3 others have declined. To better understand the demographic vital rates associated with stable and declining tortoise populations, we used a multi-state hierarchical mark-recapture model to estimate sex- and stage-specific patterns of demographic vital rates at each population. We then built a predictive population model to project population dynamics and evaluate extinction risk in a population viability context. Population structure did not change significantly in stable populations, but juveniles became less abundant in declining populations over 30 years. Apparent survival varied by age, sex, and site; adults had higher survival than juveniles, but female survival was substantially lower in declining populations than in stable ones. Using simulations, we predicted that stable populations with high female survival would persist over the next 100 years but sites with lower female survival would decline, become male-biased, and be at high risk of extirpation. Stable populations were most sensitive to changes in apparent survival of adult females. Because local populations varied greatly in vital rates, our analysis improves upon previous demographic models for northern populations of gopher tortoises by accounting for population-level variation in demographic patterns and, counter to previous model predictions, suggests that small tortoise populations can persist when habitat is managed effectively. © 2021 The Wildlife Society.

KEY WORDS demography, *Gopherus polyphemus*, hierarchical model, mark-recapture analysis, minimum viable population, population structure, population viability analysis, survival.

Population viability analysis (PVA)—a form of predictive modeling used to estimate future population trends for imperiled species—has become an important tool in population ecology and conservation biology (Beissinger and McCullough 2002). Population viability analysis can project abundance and population growth, estimate extinction risk, and understand the sensitivity of populations to changes in demographic parameters (Ralls et al. 2002, Chaudhary and Oli 2020). Population viability analyses can be extended to

evaluate how threats or management actions may influence persistence of populations, among other uses (Converse et al. 2013). Like any model-building process, PVAs may be limited for myriad reasons. For uncommon and imperiled species, models often are constructed with limited data, rely on expert judgment, and produce predictions that are imprecise or incorrect. As monitoring continues and more information becomes available, models are best revised and updated. Therefore, a valuable step of the PVA framework is to periodically revisit PVAs with new data, update models, and verify that management strategies are based on the strongest models (Beissinger and Westphal 1998, Ralls et al. 2002).

In southeastern North America, the gopher tortoise (*Gopherus polyphemus*) is an ecologically important species that has declined significantly (Auffenberg and Franz 1982, McCoy et al. 2006) and has, therefore, been the subject of multiple PVAs assessing tortoise demography and extinction risk. Gopher tortoises are large, long-lived terrestrial turtles that occur in uplands with well-drained sandy soils in Coastal Plain physiographic regions (Nussear and Tuberville 2014). Gopher tortoises dig long subterranean burrows that create habitat for >365 commensal species (Jackson and Milstrey 1989, White and Tuberville 2017); because diversity of associated commensal species is positively linked to the abundance of tortoise burrows across the landscape, gopher tortoises are a hypothesized keystone species with a significant role in regulating diverse animal assemblages in the longleaf pine (*Pinus palustris*) ecosystem (Catano and Stout 2015)—an ecosystem that contributes to a globally significant biodiversity hotspot in southeastern North America (Noss et al. 2015).

Given the ecological significance of gopher tortoises and their associated conservation risk, researchers have built numerous predictive models to understand population growth and extinction risk for tortoises (Cox et al. 1987, Cox 1989, Seigel and Dodd 2000, Miller 2001, Tuberville et al. 2009). Sensitivity analyses of these models suggested that survival of adult females is important for population growth (Miller 2001) and hatchling survival may be important as well (Miller 2001, Tuberville et al. 2009). Some models have suggested that small populations (20–40 individuals), although sensitive to stochasticity, can persist for long time periods under high-quality habitat conditions (Cox 1989, Miller 2001). Two models suggested that northern populations have greater extinction risk than central and southern populations in peninsular Florida, USA (Miller 2001, Tuberville et al. 2009); however, 1 analysis predicted that all populations throughout the geographic range of the species will experience population declines and that central and northern populations that are small (20–40 individuals) have extremely high extinction risk when projected over the next 100 years (Tuberville et al. 2009).

Previous tortoise PVAs have provided useful insights for management, but a common challenge throughout was that models lacked long-term estimates for adult survival. Although previous researchers have described many demographic parameters, including fecundity (Landers et al. 1980, Smith 1995), nest survival, hatching success (Landers et al. 1980, Smith 1995, White et al. 2018), and hatchling survival (Perez-Heydrich et al. 2012), published survival rates for juveniles and adults have been uncommon until recently (Tuberville et al. 2014, Howell et al. 2020, Goessling et al. 2021). Because the gopher tortoise is a long-lived species and population growth of long-lived species is often most sensitive to adult survival relative to other vital rates (Heppell et al. 1996, Heppell 1998), using robust estimates for stage-specific survival should be an important component when assessing population viability of the species. To this end, new iterations of PVAs can be validated or updated with new datasets describing long-term trends in survival and abundance. For long-lived species that occur in low densities and are difficult to detect (e.g., tortoises), long-term datasets are often necessary to obtain sufficient sample sizes to estimate how demographic parameters vary by age or state, to estimate transition probabilities between states, and to observe important temporal variation in population processes (Reinke et al. 2019).

One notable long-term study of tortoise demography occurred at Conecuh National Forest in southern Alabama, USA, where researchers monitored 6 local tortoise populations for 30 years to better understand demography (Tuberville et al. 2014), spatial ecology (Guyer et al. 2012), social structure (Guyer et al. 2014), and habitat management (Aresco and Guyer 1999a, b). Of particular interest for PVA efforts is a recent analysis emerging from the Alabama tortoise study that has estimated trends in abundance and survival from multiple populations over a multidecadal time period (Goessling et al. 2021). The goal of Goessling et al. (2021) was to determine whether population stability was possible at the highest-quality remaining populations on public lands within the state. At 3 local tortoise populations ($N = 20–50$ individuals/population) in the Conecuh National Forest, Goessling et al. (2021) reported that population size was stable or increased in abundance over 27 years. Their results suggested that small tortoise populations may be more stable than was predicted by previous PVAs (Tuberville et al. 2009) and that it may be useful to revisit the model of population viability for tortoises, given new data and analytical tools. Goessling et al. (2021) also demonstrated that sampling scale was an important determinant for inferences about population stability; landscape-scale population estimates indicated that gopher tortoises on Conecuh National Forest were substantially below a density threshold (<0.4 adults/ha) hypothesized to be important for movement, social structure, and potentially population viability (Guyer et al. 2012; Gopher Tortoise Council 2013, 2014).

We estimated patterns of demography and extinction risk of gopher tortoises using 30 years of mark-recapture data from 6 local populations in Conecuh National Forest. Three of the study populations are hypothesized to be stable and characterized by demographics of viable tortoise populations (Goessling et al. 2021), whereas 3 other populations appear to represent declining populations because recent surveys have suggested decreases in adult abundance. It is currently unclear to what degree the study populations are at risk of extinction in the future. Our objectives in this study were to estimate and compare component vital rates between stable and potentially declining populations to better understand demographic mechanisms determining population stability of gopher tortoises and build a revised PVA for northern populations of gopher tortoises using demographic estimates from the study populations and other recently published demographic data. Given the hypothesized nature of the study populations as stable or declining, we predicted to observe different patterns of apparent survival and population structure reflecting altered demographic processes between stable and declining populations, with declining

populations characterized by decreased survival and decreased proportions of juveniles or adult females relative to stable populations.

STUDY AREA

We studied population dynamics of gopher tortoises at 6 study sites in Conecuh National Forest, Alabama during 1991–2020 (Fig. 1). Conecuh National Forest is a 33,000-ha area in Covington and Escambia counties in southern Alabama (elevation = 100–300 m) and possesses deep sandy soils of the Lower Coastal Plain physiographic region (Mount 1975). The climate is characterized by mild winters with a mean low of 2.4°C during January and hot, humid summers with a mean high of 33.1°C during July; rainfall averages 1.5 m/year, peaking during winter (Jan–Mar) and summer (Jun–Aug). Typical land cover types in the area includes upland sand ridges dominated by the longleaf pine-turkey oak (*Quercus laevis*) ecosystem, which slopes gently toward dense hardwood forests and broad floodplains. In particular, recent management efforts in Conecuh National Forest have worked to restore the longleaf pine ecosystem to upland areas by removing slash pine (*Pinus elliottii*), planting longleaf pine, and managing the forest with prescribed fire.

We selected study sites (Fig. 1) that contained suitable soils for gopher tortoises (Troup, Bonifay, or Fuquay series; Nussear and Tuberville 2014) and that possessed dense clusters of burrows during 1991–1992; therefore, our sites were representative of the best local tortoise habitat at the beginning of long-term monitoring of the populations. All 6 sites contained sandy soils, plant assemblages in the understory (e.g., wiregrass [*Aristida beyrichianum*], gopherweed [*Baptisia lanceolata* var. *tomentosa*], dogtongue buckwheat [*Eriogonum tomentosum*], slender blazing star [*Liatris gracilis*], gopher apple [*Licania michauxii*], dollarleaf [*Rhynchosia reniformis*], weak leaf yucca [*Yucca flaccida*]) and midstory (bluejack oak [*Quercus incana*], turkey oak, sand post oak [*Q. margaretta*]), and a sympatric vertebrate assemblage (e.g., bobcats [*Lynx rufus*], nine-banded armadillo [*Dasypus novemcinctus*], red-shouldered hawk [*Buteo lineatus*], black racer [*Coluber constrictor*], green anole lizards [*Anolis carolinensis*]) expected for habitat occupied by gopher tortoises in the Lower Coastal Plain of southern Alabama. Historically, longleaf pine was the dominant canopy tree at each site, until those trees were harvested on all sites during the 1970s, followed by root raking and planting of closely spaced slash pine (Aresco and Guyer 1999*a*). All sites then received prescribed fire during winter on a 3–4-year fire-return interval.

We selected study sites with the intention of performing a landscape-scale experiment examining the effects of stand-thinning and growing-season fire on survival, growth, and reproduction of gopher tortoises. Following a burrow census in 1991–1992 to establish study plots, we randomly assigned sites to 1 of 2 treatment groups. In 1 group (sites 1, 4, 5), we intended to enhance habitat quality for gopher tortoises (reduced midstory hardwoods, reduced canopy cover, increased ground forage) through a single overstory thinning and a growing-season (Apr–Jul) prescribed fire in 1993. In the other group (sites 2, 3, 6), we intended to decrease habitat quality by conducting no initial thinning or growing-season fire. Periodic (3–4 yr) dormant-season (Dec–Mar) prescribed fire continued on all sites. Over time, the original study design was undermined by variation in the implementation of treatments, variation in soil characteristics among sites, and early termination of the experiment (we provide additional details of the experimental design and implementation history in Supporting Information).

The experimental treatments were too brief and insufficiently replicated to yield reliable inference on effects of treatments on long-term demographic patterns; thus, we excluded treatment as a factor in our analytical design. By 2020, each site except site 6 had received ≥1 instance of stand thinning, and all had received persistent prescribed fire.
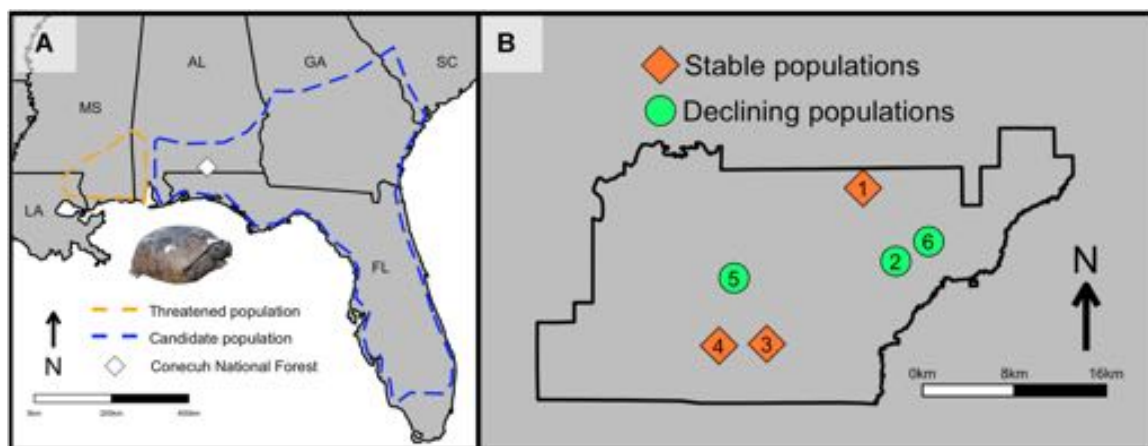

Figure 1. A) Approximate geographic distribution of the gopher tortoise (pictured) in southeastern North America. The orange dotted lines indicate the population that receives federal protection as threatened under the Endangered Species Act; the blue dotted lines indicate the candidate population for federal protection. The white diamond indicates the study area, Conecuh National Forest, in southern Alabama, USA. B) The study area, Conecuh National Forest, Alabama, USA, during 1991–2020. Numbers 1–6 designate study populations (i.e., sites 1–6). Previous research hypothesized that populations at 3 sites (sites 1, 3, 4) have been stable during 1991–2017 (orange diamonds; Goessling et al. 2021), whereas populations at 3 other sites (sites 2, 5, 6; green circles) are hypothesized to be in decline.

Three sites (2, 5, 6) experienced ≥10 years of hardwood succession that reduced habitat quality for tortoises. Sites varied in overstory composition, from slash pine-dominated to longleaf pine-dominated. Thus, although the 6 study sites all have suitable soils for gopher tortoises, sites varied in management practices common across public conservation properties that resulted in differing habitat quality ranging from high quality (i.e., widely spaced overstory longleaf pine, sparse midstory; e.g., site 3) to low quality (i.e., dense understory and midstory and abundance of emergent oak trees that minimize light penetration to the soil layer; e.g., site 5).

We formally delimited the spatial extent of each study site in 1991–1992 by performing a preliminary survey for tortoise burrows until we found no new burrows within 50 m of other identified burrows (Fig. 2). We marked each burrow with a uniquely numbered aluminum tag, measured burrow width (mm; at 50 cm depth), and mapped burrow location. After this preliminary survey, we constructed a minimum-convex polygon containing all burrows to define the spatial extent of the study area (Fig. 2), and sampled populations in the study area repeatedly during 1991–2020 (Table S1, available online in Supporting Information).

Goessling et al. (2021) described demographic data from 3 apparently stable study populations (sites 1, 3, 4; Fig. 1), and that study included detailed descriptions of those study sites. We report and analyze 3 additional years of data from those 3 sites and data from 3 apparently declining populations (sites 2, 5, 6; Fig. 1) spanning 1991–2020. Sites 2 and 5 were approximately 7 ha each; loamy fine sands of the Bonifay soil series dominated both sites (47% at site 2; 55% at site 5). Site 6 was 11.8 ha and the dominant soil type was Troup (loamy sand; 87%). Sites 2 and 6 received no thinning and developed a closed canopy. Forest managers thinned site 5 in 1991, but the site received sporadic, ineffective fire that allowed heavy hardwood encroachment that created canopy closure from 1994–2020. Each of the study sites was relatively isolated from the other sites (nearest neighbor distances were >3 km) and separated by significant barriers to dispersal, such as bottomlands, creeks, and paved roads.

METHODS

Sampling Methods
We sampled gopher tortoises at the study sites (Fig. 2) during 1991–2020 using mark-recapture methods. Our sampling protocol included the following steps during a given year of sampling. First, we performed a burrow survey at each site to assess burrow status as active (fresh tracks, plastral skid, scat on the burrow apron), inactive (half-moon shape of a tortoise carapace but lacking footprints, plastral skids, or scat), abandoned (loss of half-moon shape but hole still present), or filled (hole no longer present; Mushinsky
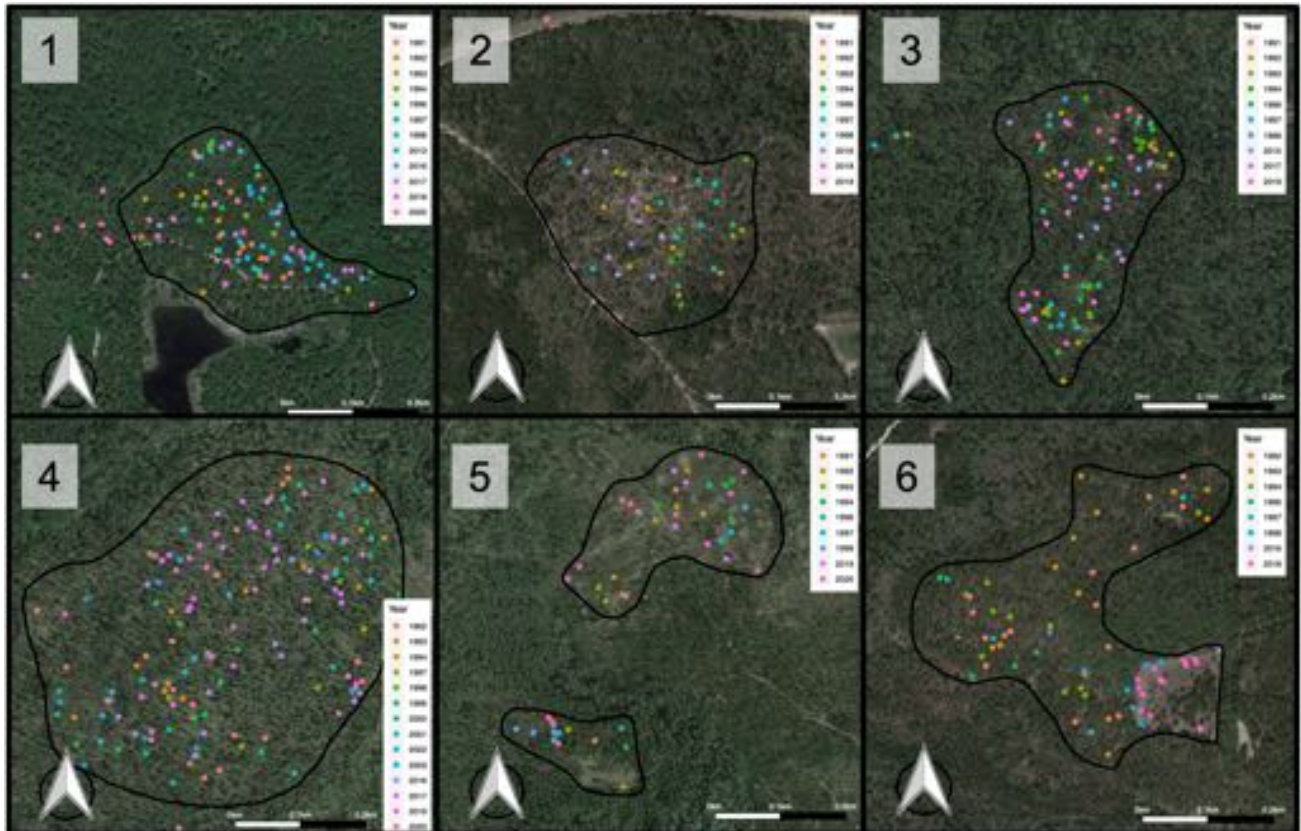

Figure 2. Captures of gopher tortoises from 6 study populations (inset numbers) in Conecuh National Forest, Alabama, USA, 1991–2020. Black lines indicate the spatial extent searched for tortoise burrows during each sampling session at each study site; we did not include captures outside of the study area in analyses. Maps courtesy of Google (Mountain View, CA, USA) and Maxar Technologies (Westminster, CO, USA).

and McCoy 1994, Guyer and Hermann 1997, Waddle et al. 2006). During surveys, we revisited burrows from previous sampling events and recorded their status, and we tagged new burrows. During 1991–2014, we identified burrows likely to contain a tortoise (active burrows), and then attempted to catch tortoises from these burrows using live traps (Tomahawk, Hazelhurst, WI, USA). During 2015–2020, we used a burrow-scope camera to verify the presence of tortoises in burrows before trapping. We covered traps using burlap and native vegetation to provide shade and then checked traps twice daily (~1000 and 1400). We measured all captured individuals for standard (midline) carapace length (CL; mm), plastral length (PL; mm), plastral concavity (PC; mm), and mass (g). When possible, we estimated age by counting annuli on abdominal scutes; when scutes were too worn to estimate age from annuli, we recorded individuals as adults. We classified individuals as juveniles, adult females, or adult males following Landers et al. (1982): juveniles were all individuals <18 cm CL, adult females were individuals >22 cm CL with PC ≤ 5 mm, and adult males were >18 cm CL with PC > 5 mm. We marked each individual uniquely by filing v-shaped notches into the marginal scutes (Cagle 1939). Because notch markings occasionally erode with time, particularly for small tortoises, we sketched or photographed notable scute characteristics, color patterns, and shell irregularities to aid later identification of individuals. Additionally, starting in 2018, we injected a unique passive-integrative transponder (8 mm FDX-B, Oregon RFID, Portland, OR, USA) approximately 0.5 cm deep into each tortoise between the cloaca and the median suture of the anal scutes as a third form of unique identification; using these 3 lines of evidence allowed us confidence in identifying individuals with little error. During recaptures, we re-filed external markings to maintain clarity in marks. After processing an individual and recording all relevant data, we released it into the burrow from which it was captured. Field sampling methods were authorized under Alabama Scientific Collection Permits (number 2019128031068680) and Auburn University Institutional Animal Care and Use Committee (number 2017-3102) protocols.

Mark-recapture sampling sessions at each site generally lasted 2–3 weeks. We did not sample each site every year during the study; we sampled sites an average of 10 years (range = 8–13 yr; Table S1). We sampled no sites in 1995, 2004–2012, and 2014.

Population Structure and Demographic Estimation

We used the 2004–2012 sampling gap to divide our dataset into 2 time periods, 1991–2003 and 2013–2020. To better understand temporal and spatial patterns of population structure, we summarized the number of individuals observed in each population within each time period. We evaluated whether hypothesized stable and declining populations differed in patterns of observed population structure by testing whether adult:juvenile and male:female ratios varied from 1:1 at each site within and between time periods using Fisher's exact tests with $\alpha = 0.05$.

We used annual trapping data to compile detection histories for each individual marked in each population during 1991–2020. Upon encounter, we classified individuals as juveniles (sex unknown), adult females, or adult males. We used a multi-state mark-recapture model (Lebreton et al. 2009, Kéry and Schaub 2012) to estimate age- and sex-specific survival and growth rates (Fig. 3A). Using this framework, we estimated 3 types of parameters from the data: apparent annual survival probability ($\varphi_{i,t}^{j}$; the probability of an individual in stage j at site i and surviving from year t to year $t+1$), recapture probability (p^{j}; the probability of an individual in stage j being recaptured, if alive and present in the population), transition probability ($\tau_{i,t}$; the probability of a juvenile at site i in year t transitioning to an adult stage), and female probability ($f_{i,t}$; the probability of a juvenile transitioning to an adult state at site i in year t to be female). Only individuals in the juvenile state could transition to adult states (adult female or adult male); therefore, the transition probability (τ) represents an average maturation rate for both sexes. Because patterns of gopher tortoise behavior and movement vary ontogenetically and intersexually in ways that might influence survival and capture probabilities (Tuberville et al. 2014, Howell et al. 2020), we modeled apparent survival probability as fixed effects of stage and site. To account for temporal stochasticity, we incorporated a random effect of time (yr) on apparent survival, transition, and female probabilities estimated by the model. We included temporal random effects that varied independently among sites within each year. We hypothesized populations had fixed demographic differences in φ, τ, and f among sites. Each of the 6 study sites was relatively isolated from other sites, and we did not detect any individuals migrating between local populations. Each study site had a unique management history before and during the study period, which we hypothesized caused distinct demographic effects. Therefore, we modeled fixed effects of state and site on φ, τ, and f because we wanted to better understand differences rather than averages among sites. We represented the state process (survival and transition probabilities) as a matrix describing the probability of transition from the row index state to the column index state in a single year (juvenile [^{j}], adult female [^{f}], adult male [^{m}], or dead):

$$\begin{bmatrix} \varphi^{j}(1-\tau) & \varphi^{j}\tau f & \varphi^{j}\tau(1-f) & 1-\varphi^{j} \\ 0 & \varphi^{f} & 0 & 1-\varphi^{f} \\ 0 & 0 & \varphi^{m} & 1-\varphi^{m} \\ 0 & 0 & 0 & 1 \end{bmatrix}.$$

Because males reach sexual maturity at younger ages than females in the study area (Aresco and Guyer 1999a), we derived sex-specific transition probabilities by multiplying τ by f to estimate juvenile-female transition probability (i.e., τ^{jf}) and multiplied τ by $1-f$ to derive a juvenile-male transition probability (i.e., τ^{jm}).

We represented the detection process as a matrix describing the probability of detecting an individual in the column index state (observation outcome; detected as
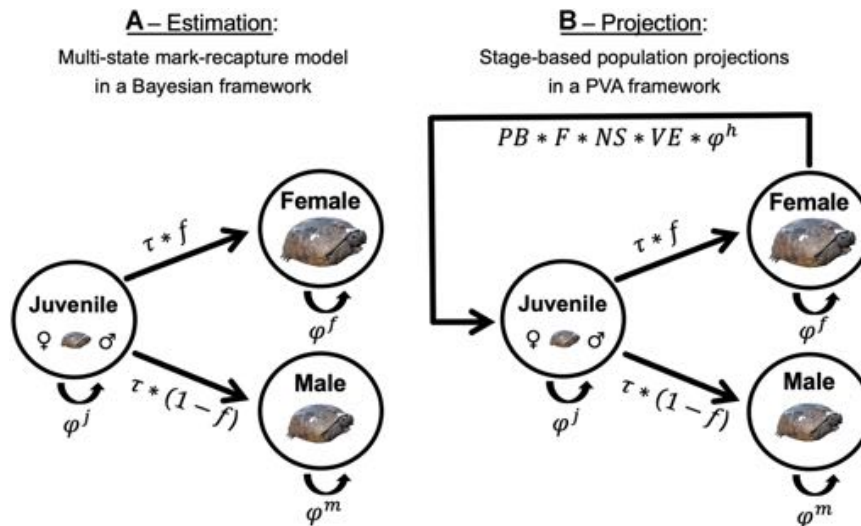
Figure 3. Conceptual models for demographic estimation and population projection (i.e., population viability analysis; PVA) of gopher tortoise demography in Conecuh National Forest, Alabama, USA. A) A multi-state population model used to estimate stage-specific apparent survival (juveniles $= \varphi^j$; females $= \varphi^f$; males $= \varphi^m$) and transition probabilities (juvenile-adult transition, τ; probability of being female, f) from mark-recapture data collected at the 6 study populations during 1991–2020. We modeled juveniles (both sexes) as a single state within which individuals have a probability of transitioning to adulthood (τ) as either a female (f) or male ($1 - f$). In any year, individuals in all 3 states can also transition to a dead state (not pictured). B) A stage-based population model used to project population size into the future. The projection model is structurally similar to the estimation model but includes a recruitment component. We derived estimates of φ, τ, and f from analysis of mark-recapture data at study populations; we obtained estimates of probability of breeding (PB), fecundity (F), probability of nests surviving predation (NS), egg viability probability (VE), and hatchling survival for the first year (φ^h) from the literature.

juvenile, adult female, adult male, or not detected), given that it is truly in the row index state:

$$\begin{bmatrix} p^j & 0 & 0 & 1 - p^j \\ 0 & p^f & 0 & 1 - p^f \\ 0 & 0 & p^m & 1 - p^m \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

Because we had no *a priori* reason to suspect that p varied among sites, we modeled p as varying among states but invariant among sites. For any site-year combination in which no sampling occurred (Table S1), we constrained state-specific recapture probabilities at that site and year to equal zero.

This model conditions on first capture and assumes that individuals within populations are sampled randomly, marks are not lost and are detected perfectly, and populations are closed to mortality within sampling periods (Williams et al. 2002). Additionally, we assumed we made state assignments perfectly and that individuals within states were identical with respect to apparent survival, recapture, and transition probabilities.

We estimated demographic parameters using a state-space formulation of the multi-state model in JAGS (Plummer 2003, Kéry and Schaub 2012), implemented using the statistical Program R and the jagsUI package (Kellner 2016, R Core Team 2018). We ran 3 independent chains of 100,000 iterations with a burn-in period of 50,000 iterations and an adaptation period of 25,000 iterations. We thinned chains by 10, which gave us 5,000 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 visually examining 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 by mean values and 95% credible intervals (CrI).

Population Viability Analysis

We sought to better understand extinction risk associated with the study populations in a PVA (Beissinger and McCullough 2002). We built a stage-based population model (Lefkovitch model; Caswell 2001) and used the model to project population size and structure forward in time using simulations. For the PVA, we conceptualized local demography of tortoises in a multi-stage, 2-sex model with 3 discrete age-sex stages: juveniles (both sexes), adult females, adult males (Fig. 3B). During a given time-step, each stage had a probability of individuals surviving and staying within the stage (φ), and the juvenile stage had a probability of maturing (τ) to 1 of 2 adult sexes, given the female probability (f; or, conversely, males: $1 - f$).

We built a 2-sex, pre-breeding census, stage-structured population model for each of the 6 gopher tortoise populations in Conecuh National Forest. We used the model to predict future abundance of populations using a first-order Markovian process in which adult abundance of each stage at time t was a function of abundance at time $t - 1$ with vital rates stochastically drawn from distributions estimated from the mark-recapture model. Specifically, we estimated the abundance of adults by:

$$A_t^s = A_{t-1}^s \times \varphi_{t-1}^s + J_{t-1} \times \varphi_{t-1}^j \times \tau_{t-1}^s, \tag{1}$$

where A and J are the abundances of adults and juveniles, respectively, φ is survival, and τ is a transition probability

from juvenile to adult, and the superscripts denote sex specificity, s (either female or male) or j (juvenile). In the case of τ, the superscript s denotes sex-specific transition probabilities to either adult female (i.e., τ^{jf}; a product of adult transition probability, τ, and female probability, f) or adult male (i.e., τ^{jm}; a product of adult transition probability, τ, and male probability, $1-f$) states. At each time step t (yr), we drew values of τ and φ from their estimated posterior distributions. Similarly, we projected the abundance of juveniles by:

$$J_t = J_{t-1} \times \varphi_{t-1}^{j} \times \left(1 - \tau_{t-1}^{jf} - \tau_{t-1}^{jm}\right) + R_{t-1}, \quad (2)$$

where J is the abundance of juveniles, φ^{j} is the survival rate of juveniles, τ^{jf} and τ^{jm} are sex-specific transition probabilities from juvenile to adult female or male stages, respectively, and R is recruitment (below) during each time step t (yr).

For individuals to recruit into local populations by reproduction, adult females must lay eggs that hatch and survive until the next survey period (i.e., time step). Therefore, to estimate annual recruitment by reproduction, we modeled the probability of females breeding (PB), the mean number of eggs laid by females (fecundity; F), the probability of nests surviving predation (NS), the proportion of eggs that are viable and hatch (VE), and the survival probability of hatchlings through the first year to the next survey period (φ^{h}) at time t. We modeled probabilities (PB, NS, VE, φ^{h}) as beta-distributed random variables, and we modeled fecundity as a log-normal random variable. Together, we modeled recruitment (R) at time t as a product of:

$$R_t = PB_t \times F_t \times NS_t \times VE_t \times \varphi_t^{h}, \quad (3)$$

where the superscript h denotes hatchling.

To construct empirical models for each study population (Fig. 3B), we used population-specific estimates of φ and τ obtained from the mark-recapture model described above. We have few data describing recruitment in the focal populations (e.g., reproductive rate, nest survival, hatchling survival), and we were, therefore, unable to produce site-specific estimates of recruitment. We reviewed the literature to compile estimates of recruitment from northern populations of gopher tortoise (Table 1). We modeled the proportion of breeding females (oviposition; PB) in a given year as 95% with an expert-elicited value from Miller (2001). To estimate fecundity (F) in Alabama, we compiled haphazard observations from Conecuh National Forest and

other sites in Alabama, which generated a mean regional clutch size of 5.4 ± 0.5 (SE) eggs/clutch. We modeled the probability of nests that survive predation (NS) as 0.35 (Smith et al. 2013). We modeled the probability of eggs being viable and hatching (VE) as 0.85, an average from a review of field hatching rates (Landers et al. 1980, Rostal and Jones 2002). We modeled hatchling survival (φ^{h}) from nest emergence until the following survey period as 0.13 (95% CI = 0.04–0.34), given results from a meta-analysis of hatchling survival of gopher tortoises (Perez-Heydrich et al. 2012). For each recruitment parameter, we modeled parameters using appropriate statistical distributions (below) and randomly estimated the parameter using stochastic draws with variance each year.

We estimated initial abundance for each population (site 1 = 26, site 2 = 18, site 3 = 22, site 4 = 42, site 5 = 10, site 6 = 22) based on results from Goessling et al. (2021) and by evaluating recent survey data. We assumed an even sex ratio and a 3:1 adult:juvenile ratio to further specify initial population age structure. We simulated future population trajectories over 100 years with 1,000 replicates. During simulations, we applied an uncertainty structure that accounted for parametric uncertainty (among replicates) and temporal stochasticity (within replicates; McGowan et al. 2011). For each replicate, we drew mean values (and an associated error term) to model parametric uncertainty; we then modeled temporal stochasticity by drawing stochastically from the mean (given its error) during each time step within the replicate. For parameters estimated in our empirical analysis (φ^{j}, φ^{f}, φ^{m}, τ^{if}, τ^{jm}), we drew replicate-level means from the posterior distribution along with the associated error term corresponding to the temporal random effect. For parameters for which we lacked empirical estimates, we drew replicate-level means stochastically from either beta distributions (e.g., PB, NS, VE, φ^{h}) with shape parameters calculated from mean and standard deviation estimates (Morris and Doak 2002) or a log-normal distribution (e.g., F). To understand future abundance and extinction risk at the study populations, we summarized projection results for population size (N) and extinction risk. We evaluated extinction risk with a quasi-extinction probability (P_e), where we estimated P_e by the proportion of simulations resulting in <3 females or no males alive at the end of the simulation period.

To better understand the sensitivity of population growth (λ) to different demographic parameters, we expressed our population projection model in a stochastic matrix form, which allowed us to perform an elasticity analysis

Table 1. Demographic parameters used to predict recruitment in demographic projection models for populations of the gopher tortoise in Conecuh National Forest, Alabama, USA during simulated population projections.

Parameter	Notation	Estimate	SE	Reference(s)
Proportion of females breeding	PB	0.95	0.04	Expert elicitation; Miller (2001)
Fecundity	F	5.40	0.50	This paper
Nest survival from predation	NS	0.35	0.10	Smith et al. (2013)
Probability of viable eggs (i.e., hatching success)	VE	0.85	0.05	Landers et al. (1980), Rostal and Jones (2002)
Hatchling (true) survival	φ^{h}	0.13	0.03	Perez-Heydrich et al. (2012)

(Crouse et al. 1987, Caswell 2001) and estimate other relevant demographic parameters. We used elasticity analysis to assess the relative sensitivity of λ to differences in demographic parameters. We compiled the component demographic vital rates into a matrix (A) describing the probability of transition from column index state to row index state in a single year:

$$A = \begin{bmatrix} \varphi^j(1 - \tau^{jf} - \tau^{jm}) & PB \times F \times NS \times VE \times \varphi^h & 0 \\ \varphi^j\tau^{jf} & \varphi^f & 0 \\ \varphi^j\tau^{jm} & 0 & \varphi^m \end{bmatrix}$$

To simulate and project future population dynamics at study populations, we multiplied the matrix (A) by a vector of initial population size (N^i) for stage classes in each study population i at each time step t:

$$N^i = \begin{bmatrix} N^j \\ N^f \\ N^m \end{bmatrix}$$

We simulated parameters in the population vital rate matrix by drawing from the posterior distribution of parameters estimated from study populations (φ^j, φ^f, φ^m, τ^{jf}, τ^{jm}) or by using stochastic, random variables with beta distributions for other probabilities (e.g., φ^h) and log-normal distributions for fecundity. For each study population, we used the matrix model to estimate elasticity of demographic parameters, λ, stable-stage distribution (SSD), generation time (G; yrs), and reproductive value (RV; offspring/individual) of life stages. We estimated each metric ($\bar{x} \pm 95\%$ CI) using 1,000 simulation replicates per population.

We built the predictive population model and performed the elasticity analysis using Program R. We used the package popbio (Stubben and Milligan 2007) to perform the elasticity analysis and to estimate other population demographic values (λ, SSD, G, RV). We used the package lognorm (Wutzler 2019) to estimate log-normal parameters when sampling values of fecundity. The data, JAGS code, and R scripts to perform all analyses described here are available on GitHub (https://github.com/brianfolt/tortoise-population-model).

RESULTS

Population Structure and Demographic Estimation

During 1991–2020, we realized 846 captures of 369 individuals across the 6 study populations. The sample size was dominated by observations from 3 populations (sites 1, 3, 4), where we marked and recaptured substantially more individuals (618 captures of 256 individuals) relative to the other populations (228 captures of 113 individuals; Table 2). Observed population structure generally had similar proportions of adults and juveniles and adult sex ratios during 1991–2003 and 2013–2020, but site 5 shifted from a male-biased population with many juveniles to a population lacking juveniles across the study period (Fig. 4). Across all individuals in the study, we captured 11 adults

Table 2. Summary of mark-recapture efforts for gopher tortoises at 6 sites (populations) in Conecuh National Forest, Alabama, USA, 1991–2020.

Site	Captures	Individuals	Captures/individual ($\bar{x}$)
1	201	69	2.9
2	54	27	2.0
3	162	66	2.5
4	255	121	2.1
5	70	31	2.3
6	104	55	1.9
Total	846	369	2.3

during 1991–1993 that survived and stayed within study populations until at least 2017–2020.

We found recapture probability (p) to be comparable among juveniles (0.54; 95% CrI = 0.43–0.64), adult females (0.50; 95% CrI = 0.43–0.58), and adult males (0.46; 95% CrI = 0.39–0.52). Annual apparent survival and transition probabilities varied by age, sex, and site. Average apparent survival probabilities for juveniles (φ^j) varied between 0.67–0.72 among sites and were generally lower than estimates for adults (Fig. 5; Table S2, available online in Supporting Information). Estimates of average apparent survival (Table S2) for adult females (φ^f) ranged between 0.96–0.97 at the 3 apparently stable sites (sites 1, 3, 4) but were much lower at the 3 apparently declining sites (0.63–0.90; sites 2, 5, 6; Table S2). Average apparent survival for adult males (φ^m) was less variable and ranged between 0.92–0.97 among the populations (Table S2); however, mean male apparent survival was lower in declining populations (0.92–0.93) than in the 2 stable populations (0.95, 0.97). Derived estimates of sex-specific transition probabilities also varied between females and males and among sites (Table S3, available online in Supporting Information). Juveniles had a higher probability of transitioning to become adult males (τ^{jm}) in a given year (among-site $\bar{x} = 0.073$), relative to juveniles transitioning to become adult females (τ^{jf}; among-site $\bar{x} = 0.049$); this pattern was consistent across 5 of 6 sites. Stable populations had substantially lower transition probabilities for both sexes when compared to declining populations (Table S3).

Population Viability Analysis

Simulated population projections predicted considerable variation in abundance and P_e among populations over the next 100 years. Projected abundance (Fig. 6) was greatest at site 1 (median = 19; 95% CI = 11–84) and site 4 (median = 18; 95% CI = 9–336) and these sites had the lowest P_e (0.001, 0.017, respectively). Projected abundance at site 3 (median = 16; 95% CI = 7–294) was similar to that at sites 1 and 4, but extinction risk at site 3 was higher ($P_e = 0.077$). Sites 2, 5, and 6 had the smallest projected abundance and highest P_e after 100 years: median abundance ranged between 5–9 individuals and P_e from 0.469–0.839 at those sites.

We estimated mean λ values over the next 100 years to range between 0.936–0.986 among populations (Table 3). For the 3 populations with highest λ (sites 1, 3, 4), stable-stage distributions and reproductive values indicated relatively even ratios of adult females and males and higher lifetime reproductive output of females, whereas
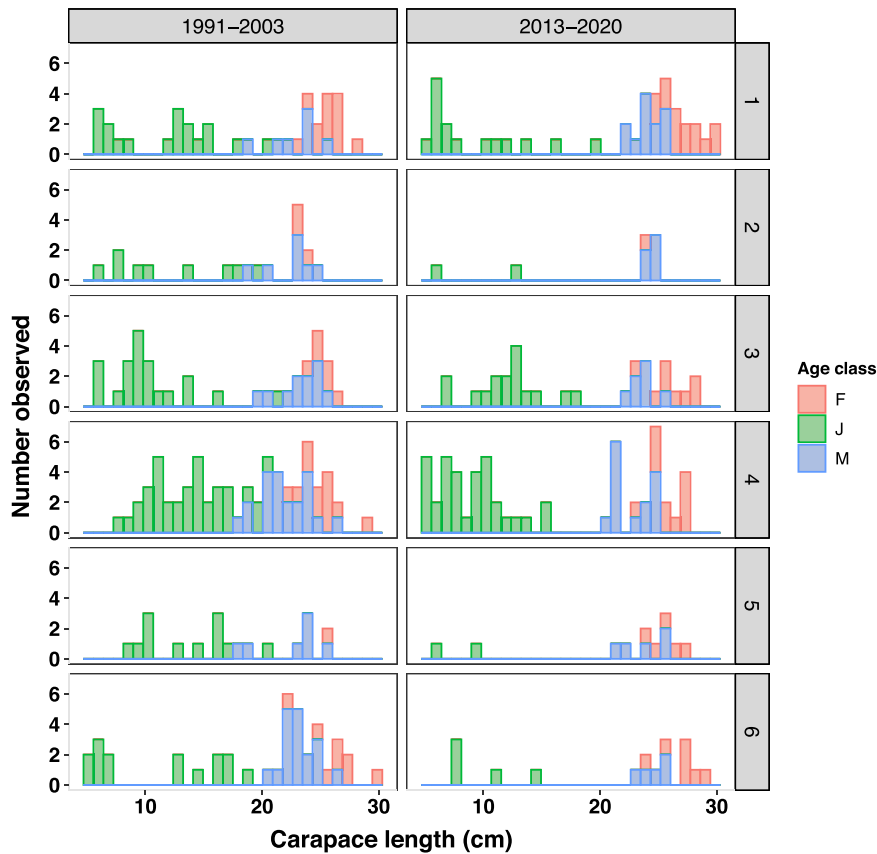
Figure 4. Temporal patterns in population structure (juveniles [J], adult females [F], and adult males [M]) of gopher tortoises at 6 populations (sites 1–6; right panels) in Conecuh National Forest, Alabama, USA, 1991–2020. We inferred population structure by taking the average body size (midline carapace length; cm) for each individual during 1991–2003 (left) and 2013–2020 (right) at each population (rows). Asterisks indicate adult sex ratios (*) and juvenile:adult ratios (**) that significantly deviated from 1:1 (Fisher's exact test: $P < 0.05$) during either 1991–2003 or 2013–2020; † indicates population structure that changed through time at site 5 (Fisher's exact test: $P < 0.05$).

populations with lowest λ (sites 2, 5, 6) had lower proportions of adult females in populations (approaching zero) and lower reproductive output of females. Similarly, populations with higher λ also had longer generation times than populations with lower λ (Table 3). Our elasticity analysis indicated that λ was sensitive to changes in demographic parameters in ways that varied among populations. Specifically, we found that 4 populations (sites 1, 3, 4, and 6) were highly sensitive to changes in φ^f, whereas

2 populations (sites 2 and 5) exhibited comparable sensitivity to both φ^j and φ^f (Fig. 7).

DISCUSSION

Using a multi-state analytical framework, we estimated demographic rates over 3 decades and projected future abundance for 6 populations of gopher tortoises in south Alabama. Our results suggested contrasting patterns of demography and viability among populations. We found that
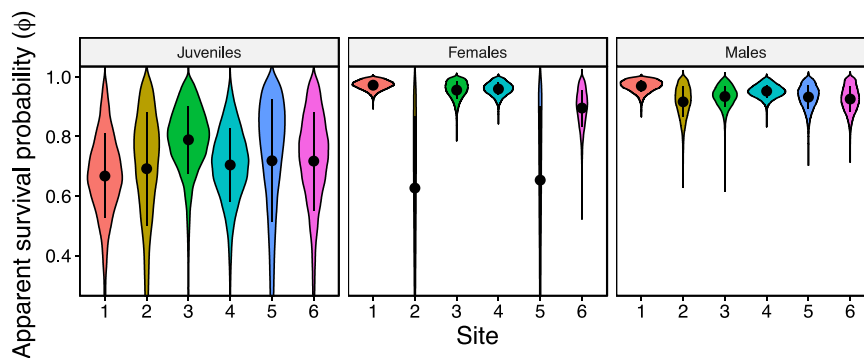

Figure 5. Posterior distributions (shaded area) estimating stage-specific apparent annual survival probability (φ) of gopher tortoises from 6 populations in Conecuh National Forest, Alabama, USA, 1991–2020. Life stages are separated by panels (see headers); we ordered populations (i.e., sites) numerically within life-stage panels.
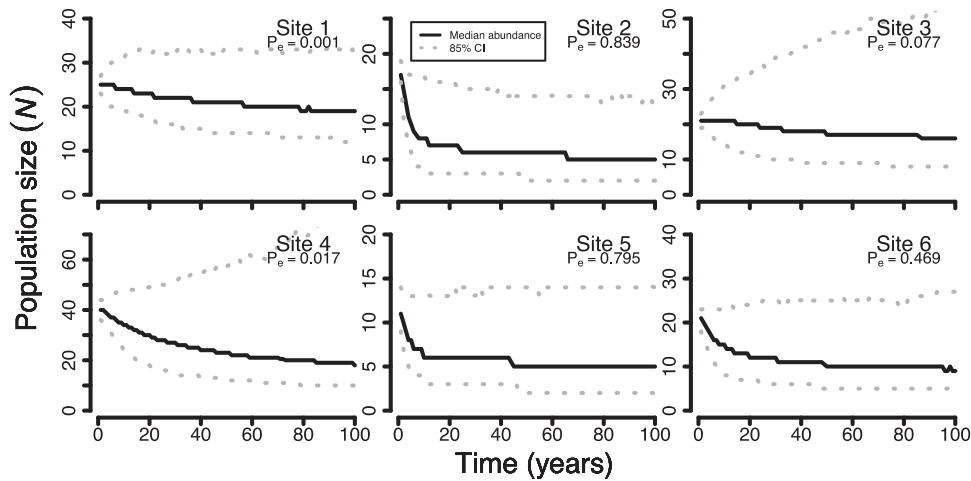
Figure 6. Simulated population size of gopher tortoises in 6 populations in Conecuh National Forest, Alabama, USA, during a 100-year population projection interval. Graphs illustrate the median (±85% credible interval) abundance of all individuals in the population over 100 years into the future. Graph panels are numbered by study population (sites 1–6). The quasi-extinction probability (P_e) is the probability of adult abundance decreasing to <3 females or to zero males after 100 years. To best illustrate patterns at each site, we varied the vertical axes among panels, and we used a smaller credible interval threshold than reported in the text.

Table 3. Simulated population growth rate (λ), stable-stage distribution (J = juvenile; F = adult female; M = adult male), female reproductive value, and generation time for 6 populations of gopher tortoises in Conecuh National Forest, Alabama, USA. Population growth, reproductive value (offspring per individual), and generation time (years) values are reported as the mean and 95% credible interval (CrI) of 1,000 replicates. We represented the stable-stage distribution by the mean proportion of individuals in each stage class projected to occur at 100 years.

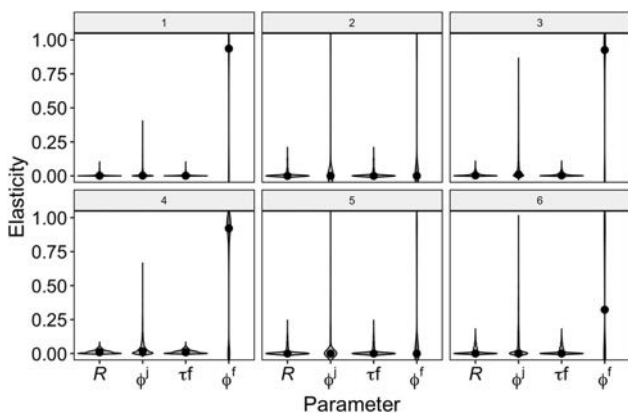| Site	λ		Stable-stage distribution			Reproductive value		Generation time	
	$\bar{x}$	95% CrI	J	F	M	$\bar{x}$	95% CrI	$\bar{x}$	95% CrI
1	0.986	0.96–1.02	0.20	0.27	0.44	22.9	4–1,020	122.0	33–1,050
2	0.936	0.82–1.02	0.00	0.00	1.00	0.9	0–114	46.3	11–680
3	0.975	0.92–1.03	0.39	0.32	0.17	20.0	2–1,480	73.9	21–532
4	0.980	0.94–1.02	0.25	0.34	0.36	13.6	3–238	53.0	23–256
5	0.949	0.86–1.06	0.00	0.00	1.00	1.0	0–44	43.2	9–437
6	0.957	0.87–1.05	0.04	0.03	0.93	4.7	1–260	40.2	12–506

Figure 7. The proportional sensitivity (elasticity) of population growth (λ) to changes in demographic parameters at 6 populations (sites) of gopher tortoises in Conecuh National Forest, Alabama, USA. Demographic parameters are recruitment (R), apparent survival probability of juveniles (φ^j) and adult females (φ^f), and transition probability of juveniles to adult females (τ^f). Recruitment is a function of fecundity, hatching success, and first-year survival of hatchlings. We described the 6 study populations numerically by grey panel headers (sites 1–6).

3 hypothesized-stable populations (Goessling et al. 2021) were characterized by high annual apparent survival of adult females (≥0.95) and were projected to have low extinction risk over 100-year population projections ($P_e < 0.10$). Conversely, we estimated 3 declining populations to have substantially lower female apparent survival rates and higher extinction risk ($P_e > 0.40$). Population structure of apparently viable populations maintained the presence of juveniles across the study period, whereas apparently unviable populations had lower juvenile survival and therefore lower recruitment of new breeding adults. If we take $P_e = 0.10$ as a maximum acceptable extinction risk for a viable population, then our results suggest that viable populations possess high apparent survival of females (≥0.95), whereas populations with lower female survival rates may be unviable during the next 100 years.

Previous PVAs for gopher tortoises have made contrasting predictions about population viability and conservation value of small populations in the northern area of the species' range (Miller 2001, Tuberville et al. 2009). An admitted limitation of these PVAs was that they lacked

data-driven estimates of survival for gopher tortoises, a parameter important to population growth of other large, long-lived turtles (Crouse et al. 1987, Cunnington and Brooks 1996, Mogollones et al. 2010, Páez et al. 2015, Folt et al. 2016). To be most accurate during site-specific projections, PVAs should incorporate demographic estimates from relevant populations of interest whenever possible (Ralls et al. 2002). Our PVA framework updated previous demographic models for gopher tortoises by estimating local, site-specific demographic rates and using site-specific parameter estimates to project future abundance, while accounting for parametric uncertainty and temporal stochasticity. Although our results are consistent with the hypothesis that small, northern populations of gopher tortoises can be viable over relatively long time periods (Goessling et al. 2021), other such populations are likely to decline and are at risk of local extinction. Given variation observed among local populations in our study, our PVA has improved upon previous efforts for gopher tortoises by accounting for important local, site-specific variation in population demographics and thereby avoiding over-generalizing demographic patterns at regional scales.

Habitat quality is likely a primary factor affecting variation in tortoise survival and growth and causing differences in demographic parameters between stable and declining populations in Conecuh National Forest. Our results are consistent with recent long-term studies of tortoise demographics suggesting that adult tortoises have higher survival than juveniles (Tuberville et al. 2008, 2014; Howell et al. 2020; Goessling et al. [2021] provides an alternative model). In a metapopulation in southern Florida, overall apparent survival of adults was higher than juveniles, but demographic rates varied by land cover type across the landscape: unmanaged landscapes supported significantly lower survival, growth, and abundance relative to a restored forest and, in particular, an open grassland landscape (Howell et al. 2020). At our study sites, habitat supporting stable populations had lower basal area and canopy cover, sparse midstory, and other features associated with high-quality habitat for gopher tortoises (Aresco and Guyer 1999b, McIntyre et al. 2019). During the study, managers performed habitat management to increase habitat quality for tortoises (stand thinning, prescribed fire) at 2 of 3 stable populations (sites 1 and 4), but 2 of 3 sites with declining populations did not receive such management (sites 2 and 6). Of the remaining 2 sites, 1 was likely stable because sandy soils were so deep that growth of a woody mid-story was limited despite no thinning and limited fire (site 3; C. Guyer, Auburn University, personal observation), evidently sufficient to sustain the tortoise population. Managers applied thinning and a growing-season fire at the other site (site 5), but so much debris from thinning was left on the soil layer that fire was ineffective, allowing hardwood encroachment that may have forced tortoises to disperse. Sites 2 and 6 received no thinning and developed a closed canopy that forced tortoises to move, one to a food plot (site 6) or to unknown areas (site 2).

Gopher tortoises construct burrows in open areas with low canopy closure and abandon burrows when canopy closure

increases (Aresco and Guyer 1999b). We observed decreased apparent survival of females on sites with increased canopy closure and decreased habitat quality relative to sites with higher habitat quality (Aresco and Guyer 1999b, McIntyre et al. 2019). We suggest this effect may not necessarily reflect increased mortality but is influenced in part by increased emigration of females from sites with declining habitat quality. We know that a small percentage of tortoises emigrate from local populations, even when habitat quality is high, and Ott-Eubanks et al. (2003) hypothesized that females disperse from low-quality habitat in search of areas with suitable nesting habitat. Conversely, apparent survival of males did not vary strongly among stable and declining sites. Our population projections predicted stable populations with high female survival to have population structure characterized by even adult sex ratios, whereas declining populations with decreased female survival became male-biased. In some cases, female survival was so low at declining populations that simulated stable-stage distributions became completely dominated by males and lacked any females. Model-predicted shifts to male-biased sex ratios are supported by data from 1 declining population in Conecuh National Forest (site 2; Fig. 3) and other small, declining populations at Fort Benning in Georgia, USA (Guyer et al. 1996). We hypothesize that small, declining populations become male-biased because females emigrate in search of more open, higher-quality habitat, but males are reluctant to vacate sites where at least a few females are present and are known to the males.

We suggest that habitat management can improve λ of gopher tortoises by increasing growth and maturation rates. Because variation in individual growth influences transition probabilities, survival probabilities, and lifetime reproductive outputs (Armstrong et al. 2018), depressed growth rates of tortoises in poorly managed habitat can have significant negative effects on survival, reproductive output, and ultimately population viability. Contrary to this hypothesis, we observed greater transition probabilities in declining populations relative to stable ones. This could be due to a density-dependent mechanism where declining populations at low densities may experience increased maturation rates relative to higher-density populations (but see below). We also observed greater maturation rates for males than females at most populations, which is likely a consequence of younger age and size at maturation for males (Aresco and Guyer 1999a).

An analysis of simulated data with known parameter values indicated that estimation was less accurate for populations with smaller N^i and lower φ (B. Folt, Auburn University, unpublished data). Similarly, we observed the greatest uncertainty in parameter estimation of survival and transition probabilities at 2 declining populations (sites 2 and 5) relative to other populations. Sites 2 and 5 had the fewest individuals and captures, and the paucity of data may have caused difficulty during parameter estimation and population projections. Although our field data indicate that those sites have in fact declined during the last 30 years, uncertainty and potential inaccuracy during the estimation process may have

caused inaccurate parameters to be used during population projections. We suggest caution when interpreting results at sites 2 and 5; future analyses could benefit from increased data collection at those sites in particular.

Previous analyses have suggested that λ of gopher tortoises may be sensitive to the survival of hatchlings (Tuberville et al. 2009) or juveniles (Miller 2001). Our elasticity analysis indicated that adult survival was more important to variation in λ than reproduction, juvenile survival, and female transition probabilities in stable populations; however, the rank importance of parameters changed for declining populations, for which adult survival was as comparably important as juvenile survival, female transition rate, and recruitment. This result supports the conclusion that high adult survival is important to maintaining and promoting long-term λ and population stability of gopher tortoises but also suggests that management actions to increase juvenile survival, such as head-starting, may be useful to increase λ of small, declining populations, particularly when such actions are performed along with management aimed to increase adult survival. Tuberville et al. (2009) did not consider adult survival in their elasticity analysis, citing a lack of field estimates of adult survival in the literature. Their analysis also specified a maximum reproductive age of 60 years; however, given the high adult survival rates and generation times we estimated in stable populations, a maximum reproductive age of 60 years may have led to underestimating the lifetime reproductive value of females and contributed to population declines in their model predictions. Other recent field studies have reported that North American turtles may remain reproductive until >60 years of age (Congdon et al. 2003). We captured 11 adults in 1991 that were still alive and present at the study sites 27–30 years later. Because age of adult gopher tortoises is estimated unreliably, it is impossible to know their true age upon first capture; however, the size and smoothing of the shell indicated a minimum age of 15 years at first capture. Therefore, these individuals were likely >45 years old upon recapture during 2017–2020. Given the estimated generation times of >70 years in viable populations in our study area and the great longevity of other tortoise species worldwide, maximum longevity of gopher tortoises may be greater than previously considered for wild populations. Continued long-term field studies could provide a better understanding of the upper limits of longevity and reproductive ages for gopher tortoises.

Studying and managing populations of long-lived species is difficult because it may take many years to robustly estimate population parameters and for the effects of management actions on populations to manifest. By analyzing 3 decades of data, we estimated demographic vital rates and projected populations in a PVA framework. Our simulation exemplifies why long-term studies are critical to permit demographic estimation and projection for long-lived species because without a long time series of mark-recapture data we would not have collected sample sizes large enough to permit accurate parameter estimation. Our results also demonstrate how updating population viability models as new data emerge is important to ensure that management strategies are based on the strongest available model predictions. Future research can strengthen models for tortoise demographics and predictions about population viability by collecting additional local-scale data on the reproductive biology (Table 1) and effective migration between populations. Our PVA assumed populations were closed to immigration, but future model iterations could explore how female immigration contributes to population growth and stability of gopher tortoises.

Conserving populations of gopher tortoises in Conecuh National Forest is a key goal of state and federal agencies. Conecuh National Forest is the largest tract of public property supporting tortoises in Alabama and is important to the long-term conservation of genetic diversity among western populations of tortoises (Gaillard et al. 2017). Although we observed and projected population stability at 3 populations, we projected the observed population vital rates to cause population declines at all study populations in Conecuh National Forest, and 3 populations are likely to be extirpated in the near future. Tortoises also experienced similar population declines on managed conservation lands in Florida that were linked to decreasing habitat quality (McCoy et al. 2006). Current habitat management in Conecuh National Forest may not be sufficiently aggressive to generate suitable conditions for tortoise populations, particularly at 3 sites experiencing the strongest declines. Increased management action (e.g., prescribed fire, stand thinning, midstory control) to improve habitat among sites could help increase survival, site fidelity, and population growth of gopher tortoises in declining and stable populations and help conserve populations in Alabama.

The gopher tortoise is currently a candidate species for federal protection under the United States Endangered Species Act (ESA) across the species' entire range (U.S. Fish and Wildlife Service 2011). Specifically, although populations west of the Mobile River are currently federally protected as threatened, the United States Fish and Wildlife Service is assessing all populations across the species' entire range for federal listing under the ESA as well. During this process, the United States Fish and Wildlife Service will perform a Species Status Assessment (Smith et al. 2018) to assess historical population trends and evaluate how threats may influence abundance in the future. In particular, the PVA framework presented here might be a useful tool to project future abundance of gopher tortoises during a Species Status Assessment. We could extend the model to simulate demography at other localities with emerging demographic data, at larger spatial scales (i.e., regions), or during analyses that evaluate positive and negative factors influencing tortoise persistence, such as conservation or management actions and emerging threats.

MANAGEMENT IMPLICATIONS

A sound definition of what constitutes a population of gopher tortoises will be important to effectively estimate population trends and manage for sustainable population growth. Management plans for gopher tortoises have recently conceptualized viable populations based on benchmarks of >250 adults occurring at a density of >0.4 tortoises/ha, evidence of

recruitment, and >100 ha of high-quality habitat. We observed the greatest number of juveniles in stable populations, suggesting that recruitment is important for population stability. Our results indicate that our study populations are substantially smaller in abundance and geographic area than minimum thresholds identified by the benchmarks for tortoise population viability, yet our populations have been stable over 3 decades and are projected to persist in the future. We suggest that an exclusive focus by wildlife managers on the number of tortoises present on a property may lead to overlooked conservation opportunities presented in smaller populations. Instead, managers may achieve conservation goals within small populations by focusing on habitat improvements that cause increases in demographic parameters—particularly female survival—that we have associated with stability in small populations. Similarly, population delimitation for conservation planning of gopher tortoises might assign greater conservation value to small, local populations than existing benchmarks for tortoise population viability. Our results suggest that maintenance of open areas with stand thinning or selection of conservation sites where plant growth is limited by deep sands are useful approaches that can contribute to the maintenance of small local populations. Last, we suggest that land managers work to support multiple local populations on properties and to manage habitat such that it permits dispersal and gene flow among local populations in a metapopulation context.

ACKNOWLEDGMENTS

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