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Research Article

Survival, Demography, and Growth of Gopher Tortoises (*Gopherus polyphemus*) from Three Study Sites with Different Management Histories

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ABSTRACT Recovery or sustainable management of wildlife populations often entails management of habitat on which they depend. In this regard, turtles pose unique conservation challenges because of their life histories. The combination of late maturity, low survival when young, and dependence on high adult survival suggests they may be slow to respond demographically to conventional habitat management. Thus, long-term studies are necessary to understand population dynamics and recovery potential in these species. We used 5–11 years of mark-recapture data from 3 populations to evaluate survivorship, demography, and somatic growth of gopher tortoises (*Gopherus polyphemus*). Green Grove and Wade Tract (southwest GA) are ecological reserves with a history of land management compatible with tortoises. In contrast, Conecuh National Forest (south-central AL) is a closed-canopy pine plantation with prior intensive site preparation but where management intervention improved habitat for tortoises during the study. Apparent survival was high for mature tortoises (87–98%) compared to immature tortoises (70–82%). Adults comprised 57–79% of individuals captured, with Green Grove and Wade Tract populations dominated by larger individuals but Conecuh having a more uniform size distribution. The largest adults captured at Conecuh (297 mm maximum carapace length [CL]) were smaller than the largest adults from Green Grove (337 mm CL) or Wade Tract (341 mm CL), although characteristic growth constants from von Bertalanffy models were similar among sites. We suggest these results indicate a recovering population at Conecuh, where habitat conditions for gopher tortoises have improved despite a legacy of intense predation by humans and reduced habitat quality at the inception of this national forest. Further, we recommend using a combination of short-term and long-term monitoring metrics to assess population recovery in such long-lived species.

KEY WORDS demography, gopher tortoise, *Gopherus polyphemus*, growth, habitat management, population recovery, survivorship.

Turtles are among the most imperiled vertebrate group globally, with nearly 66% classified as "vulnerable to extinction" or worse (International Union for the Conservation of Nature [IUCN] 2012). Turtles offer a unique set of conservation challenges due to their slow life history strategies. The combination of high hatchling and early juvenile mortality, high adult survivorship and longevity, delayed sexual maturity, and low reproductive output (Gibbons 1987, Iverson 1991) makes them vulnerable to demographic perturbations (Brooks et al. 1991, Congdon et al. 1993, but see Fordham et al. 2007). Likewise, these traits also limit the ability of turtle populations to recover even after threats have abated (Bailey and Guyer 1998, Hall et al. 1999, Tucker et al. 2001, Troëng and Rankin 2005).

The gopher tortoise (*Gopherus polyphemus*) is restricted to the Coastal Plain physiographic province in the southeastern United States and was historically associated with the longleaf pine (*Pinus palustris*) ecosystem. Less than 3% of the original longleaf pine ecosystem remains, mostly as small, isolated fragments (Ware et al. 1993, Means 2006). Because of this habitat loss, many of the more than 200 associated vertebrate species, including the gopher tortoise, have also experienced dramatic declines (Means 2006). In 1987, the western population of the gopher tortoise was federally listed as threatened, and in 2011, the United States Fish and

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Wildlife Service (USFWS) determined that listing in the rest of the range was warranted, with habitat loss and degradation cited as primary contributing factors (USFWS 1987, 2011, 2013).

High quality habitat for gopher tortoises includes deep, well-drained sandy soils that support extensive burrows, an open canopy that provides optimal thermal conditions, and an understory of abundant herbaceous vegetation for forage (Auffenberg and Franz 1982). Although federal, state, and privately managed forest lands can harbor significant numbers of tortoises, pine plantations with high tree densities can become unsuitable as understory becomes increasingly shaded and groundcover species are eliminated (Wilson et al. 1997, Hermann et al. 2002, Jones and Dorr 2004). In addition, intensive soil disturbance from some silvicultural and agricultural practices destroys herbaceous groundcover, and many plant species, including wiregrass (*Aristida beyrichiana*), fail to re-establish (Outcalt et al. 1999, Aschenbach et al. 2010). Frequent (every 1–4 yr) prescribed fires have maintained open canopy and contributed to the high plant diversity of the longleaf pine ecosystem (Walker and Peet 1983, Kirkman et al. 2001), a management practice that mimics the historical frequent, low-intensity, growing-season fires that likely shaped this habitat (Robbins and Myers 1992). Prescribed fire has been eliminated in much of the gopher tortoise's range—either being suppressed completely or occurring infrequently (Van Lear et al. 2005). Thus, much of the remaining potential habitat for gopher tortoises has become degraded or unsuitable (USFWS 2011, 2013).

Longevity of gopher tortoises and their ability to persist in suboptimal habitats (Berish et al. 2012) can mask demographic changes that can precipitate population declines, such as persistent lack of recruitment or low reproductive output. Likewise, the lag time between improved habitat conditions and associated demographic responses makes detecting population recovery equally challenging. Line-transect distance sampling recently has proven to be a promising technique for estimating current population size and density of tortoises, which can then be used to compare populations or to monitor a single population over time (Smith et al. 2009, Stober and Smith 2010). Widespread adoption of this standardized monitoring technique represents a critical step in assessing the status of this species across its range (USFWS 2013). However, line-transect distance sampling does not identify which demographic processes (e.g., mortality, recruitment, dispersal) are exerting the most influence on a population's trend—information that is critical for assessing population viability. Mark-recapture data sets, when available, allow us to examine demography to better understand the extent to which populations are affected by local habitat quality, rather than relying on changes in abundance (Van Horne 1983, Todd and Rothermel 2006). Such analyses aid not only the design of appropriate management interventions but also help evaluate whether prior implementation has improved conditions suitably. We used several years of mark-recapture data to investigate the population ecology of gopher tortoises at 3 sites at similar latitudes. Our primary objective was to compare apparent survival, demography, and somatic growth of gopher tortoises that inhabit sites of varying habitat quality and management history. In addition, we also sought to identify demographic signs of population recovery at a site where habitat conditions improved during the study.

STUDY AREA

We conducted our study at 3 sites that occur at similar latitude with similar climatic conditions but which vary in management history and habitat quality. Conecuh National Forest is located in Covington and Escambia Counties of south-central Alabama, USA (Fig. 1) and occurs on deep sandy soils dominated by the Troup and Fuquay series. During the 1960s, the forest was composed of a few large longleaf pines retained to encourage natural regeneration. During the 1970s, the longleaf pine stands were clearcut, raked, plowed, and replanted in closely spaced slash pine (*P. elliottii*) seedlings (Aresco and Guyer 1999*a*). Plantations were treated with winter burns every 3–4 years from 1986 until 1995, during which time the forest was composed of a mature, closely spaced slash pine canopy, a distinct mid-story layer of shrubs and scrub oaks (*Quercus* spp.), and an understory with sparse herbaceous cover and low plant species richness. In 1995, the forest stand was thinned, and during 1997–2008, the prescribed fire regime was altered to growing season fires applied every 3–4 years (Guyer et al. 2012). The Conecuh tortoise population was historically subjected to predation by humans (Aresco and Guyer 1999*a*). Of our 3 study sites, Conecuh had the lowest tortoise density (0.6 tortoises/ha; based on a 43.3 ha study site), with an estimated sex ratio of 0.8 M:1 F (Guyer et al. 2012). Additional information about the Conecuh study site can be found in Aresco and Guyer (1999*a*, *b*) and Waddle (2000).

Green Grove is a 100-ha site located on the Jones Ecological Research Center, an 11,700-ha ecological reserve in Baker County, southwest Georgia, USA (Fig. 1). The reserve is dominated by mature longleaf pine forest interspersed with live

Figure 1. Location of 3 study populations in relation to the geographic distribution of the gopher tortoise (shaded area).

oaks (*Q. virginiana*) and small agricultural food plots (Guyer et al. 2012). Since the 1920s, the longleaf pine forest has been managed as a quail-hunting plantation through the application of winter fires (Kirkman et al. 2001). More recently, periodic growing season fires have also been used. The plantation is characterized by a sparse overstory canopy and a diverse, relatively undisturbed, herbaceous understory dominated by wiregrass. Green Grove occurs on well-drained soils of the Norfolk, Wagram, Suffolk, Orangeburg, Lucy, and Bonneau series (Stoner 1986). It is surrounded by dirt roads and by similar habitat in all directions. Gopher tortoise density on Green Grove was 1.5 tortoises/ha, nearly 3 times the density of Conecuh (Guyer et al. 2012). The Green Grove population also had a slightly male-biased sex ratio (1.5 M:1 F). More site information can be found in Drew et al. (1998) and Eubanks et al. (2002, 2003).

The Wade Tract is an 81.5-ha private ecological preserve in Thomas County, southwest Georgia, USA (Fig. 1) and is managed by Tall Timbers Research Station. The preserve lies in the Red Hills physiographic region (Hermann et al. 2002), with underlying soils of the Faceville, Lucy, Norfolk, and Orangeburg series. The Wade Tract and Green Grove have similar soils and vegetation. The Wade Tract is composed of old-growth longleaf pine forest that has never been in agriculture (Guyer et al. 2012). The Wade Tract has been managed for bobwhite quail (*Colinus virginianus*) with annual or biennial fires for more than 100 years, with fires in the last 20 years occasionally applied during the growing season (Guyer et al. 2012). The diverse understory includes wiregrass and more than 400 species of groundcover plants (Platt et al. 1988). More site information is provided in Platt et al. (1988), Guyer and Hermann (1997), Waddle (2000), and Hermann et al. (2002). Wade Tract had an estimated tortoise density of 0.8 tortoises/ha, similar to that of Conecuh and half that of Green Grove (Guyer et al. 2012). The sex ratio was approximately 1.2 M:1 F (Guyer et al. 2012).

METHODS

We sampled gopher tortoises primarily by placing Tomahawk (Hazelhurst, WI) live traps at the entrances of active burrows, including those used by juveniles, although we incidentally captured a few tortoises by hand when we encountered them while checking traps. We shaded traps with burlap cloth and checked them twice daily. Trapping effort varied among sites and among years because of personnel and funding constraints. We trapped tortoises at 6 sub-sites at Conecuch, totaling 78.0 ha in June–September each year during 1992–2003 except 1996, although we sampled only 1 sub-site (site 4; 43.3 ha) in each of those years. We used only the more extensive mark-recapture data from site 4 to estimate apparent survival and growth; we used data from all 6 sub-sites at Conecuh to construct size frequency histograms. We set traps for an average of 24.4 ± 6.7 days (mean $\pm$ 1 SE; range = 6–75 days) each year at Conecuh. We trapped gopher tortoises at Green Grove annually May–October during 1995–1999 for an average of 164.4 ± 48.0 days (range = 47–289 days) each year. We trapped tortoises at Wade Tract annually May–October during 1997–2002 except in 1998 for an average of 149.8 ± 38.6 days (range = 63–267 days) each year. We could not calculate the number of days we set traps for 1 year at Conecuh and Wade Tract. In addition, we did not record number of traps set each day during sampling, thus we could not calculate total number of trap days.

We assigned individual identifications to captured tortoises by notching or drilling unique combinations of marginal scutes (Cagle 1939). We recorded morphometric measurements for each individual, including maximum carapace length (CL), the only measurement we report here. We determined sex and maturity based on plastral concavity, length of gular projection, and size of anal notch width (Aresco and Guyer 1999*a*, per McRae et al. 1981). To standardize across study sites, we classified tortoises $\geq$220 mm CL with conspicuous plastral concavities and elongated gulars as adult males. We classified tortoises that lacked secondary sexual characteristics as adult females when CL $\geq$230 mm. We classified all other tortoises as immatures. We handled animals according to Institutional Animal Care and Use Committee procedures approved through Auburn University (PRN 9612-R-0598).

Statistical Analyses

We used Program MARK (White and Burnham 1999) to implement Cormack–Jolly–Seber open population models (CJS) to examine tortoise apparent survival. For each site, we used a multi-model approach to examine all combinations of group (i.e., male, female, or immature tortoises) and either time-varying or constant apparent survival (Φ) and recapture probabilities (p). Sampling effort varied among years, but we could not quantify total trap-days, thus we could not explicitly model recapture probabilities as a function of sampling effort. Few of the individuals in our mark-recapture analysis transitioned from the immature stage to mature adult (none at Conecuh, 3 at Green Grove). Thus, we placed animals into a group (male, female, or immature tortoise) based on their size and group assigned at first capture. This allowed us to examine whether males and females differed in apparent survival or recapture probabilities and also whether animals first captured as immature tortoises had apparent survival or recapture probabilities that differed from those of adult males or females over the course of the study. We used corrected Akaike's Information Criterion (AIC_c) to evaluate the relative support for competing models and to identify the most parsimonious model for each site. We generated parameter estimates using the model-averaging feature in Program MARK. We used yearly time intervals in Program MARK to reflect our yearly sampling and we adjusted the interval spacing between capture periods to account for 1 missed sampling year at both Wade Tract and Conecuh.

We used Program RELEASE within Program MARK to assess goodness of fit of the general model (time- and group-dependent apparent survival and recapture probabilities) to data from each study site. For Conecuh and Green Grove, goodness-of-fit tests suggested no problems with the fit of the general CJS model to the data. However, for Wade

Tract, goodness-of-fit testing revealed violations of important assumptions about equal catchability and likelihood of recapturing individuals depending on prior capture history. Examination of encounter histories revealed that many adult tortoises were captured and not seen again during later sampling, possibly owing to differences in spatial extent or intensity of sampling effort among years. Also, because of a recent burn that cleared understory vegetation just before the final sampling occasion, many new immature tortoises and their burrows were visible during sampling, whereas they were less detectible during earlier sampling. Thus, we deemed it inappropriate to fit mark-recapture analyses to Wade Tract data.

We tabulated size frequencies of all captured tortoises based on each tortoise's CL at first capture. To compare size frequencies among sites, we plotted separate frequency histograms for each site of size at first capture. Sampling duration extended several years longer at Conecuh than the 5 years at both Green Grove and Wade Tract. Thus, we included first captures from the complete data sets for Green Grove and Wade Tract but only the first 5 years of data (all sub-sites) for Conecuh.

Previous studies of temperate reptiles, including gopher tortoises, have successfully fit von Bertalanffy growth models to size and interval data (Aresco and Guyer 1999*a*, Stanford and King 2004). These models are often a better fit in long-lived reptiles than are other models such as logistic models (Andrews 1982). Therefore, for each site we fit data from recaptured tortoises to von Bertalanffy growth models using an iterative model-fitting procedure to estimate the characteristic growth constant (k) and asymptotic body sizes (A) of males and females. For animals with more than 2 captures, we used body sizes at first and last capture to encompass the greatest time interval. If tortoises reached maturity during the study period and their sex could be conclusively identified in later captures, we classified them as male or female regardless of their size at first capture. We included data from immature tortoises that did not reach sexual maturity in analyses for both sexes, following Aresco and Guyer (1999*a*). Although this may preclude comparisons between sexes, characteristic growth constants and asymptotic sizes can be compared among sites because we followed the same procedure for all sites. A previous study by Aresco and Guyer (1999*a*) analyzed growth and body sizes of gopher tortoises at Conecuh; our analyses incorporate a larger data set that includes longer capture intervals of more animals.

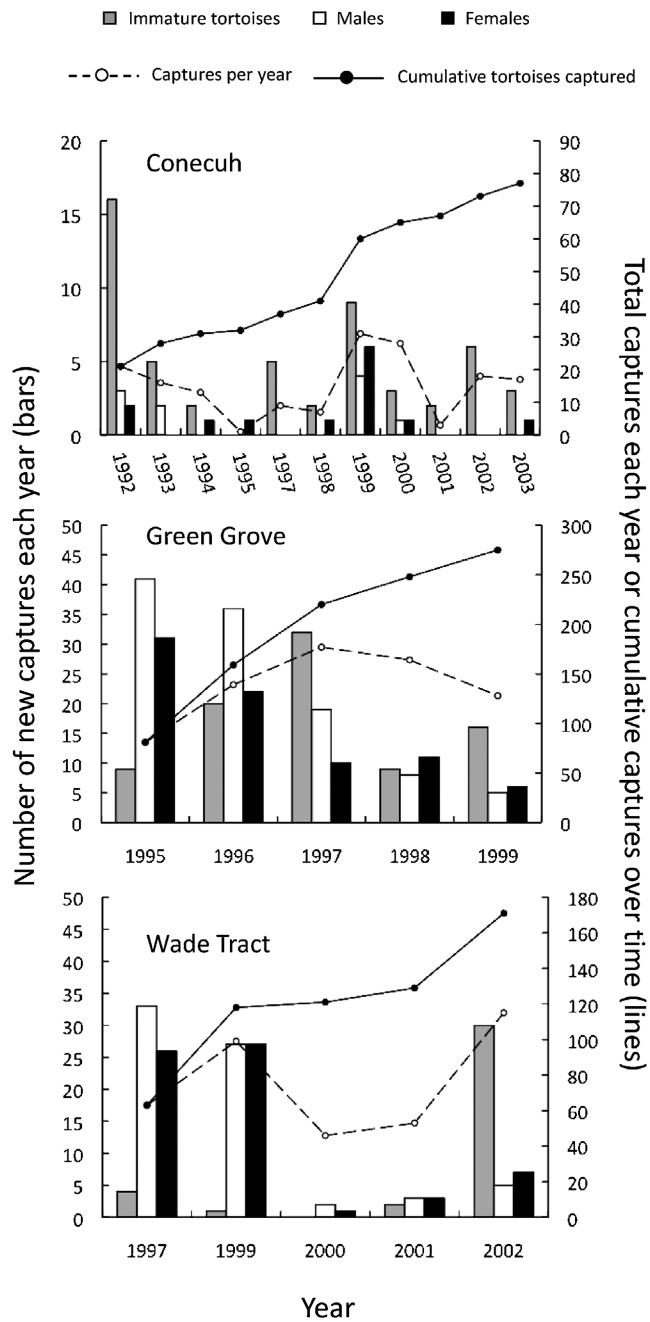

Figure 2. Bar graphs depicting the number of new captures in each gopher tortoise group each year (bars) as well as total number of tortoises captured each year (left y-axes; dashed lines with open circles) and the cumulative number of tortoises captured (right y-axes; solid lines with filled circles) at each site (Conecuh, Green Grove, Wade Tract) in the southeastern United States. Note that scales of axes differ. The figure for Conecuh (top) includes data from only the single sub-site sampled during each sampling event.

RESULTS

Total tortoises captured varied among sites (Fig. 2). In 5 capture periods, we had 689 captures of 276 individuals at Green Grove and 855 captures of 171 individuals at Wade Tract. Among the 6 Conecuh sub-sites, we had 536 captures of 194 individuals over 11 capture periods, with 164 captures of 76 individuals coming from the single sub-site (site 4) sampled during all capture periods (only the latter data are depicted in Fig. 2).

The number of tortoises we captured per sampling period (Fig. 2) also varied among years and among sites (17.91 ± 3.79 tortoises at Conecuh, 62.5 ± 18.17 at Wade Tract, and 137.6 ± 18.53 at Green Grove), in part because of variation in number of traps set or the number of days traps were deployed. The coefficient of variation for the number of tortoises captured among years within a study site was similar and low for Conecuh and Wade Tract (1.49 and 1.54, respectively) and higher for Green Grove (3.71). Most captures of new males and females occurred in the first 2–3 years of sampling, although we continued to capture new adults in later sampling periods (Fig. 2). Immatures dominated captures at Conecuh, representing an average of 69.4% of new captures and 64.0% of all captures across capture periods. On average, immatures represented only 19.8% of all tortoises captured at Green Grove and 8.8% of tortoises captured at Wade Tract.

Estimates of overall apparent survival were high for mature tortoises at Conecuh (males, 94.6 ± 3.9%; females, 98.0 ± 2.8%) and Green Grove (males, 86.8 ± 3.8%; females, 95.5 ± 2.2%). Males and females had similar apparent survival estimates with overlapping confidence intervals at Conecuh but not at Green Grove, where apparent survival of males on average was 8.7% lower than females. At both study sites, apparent survival of immature tortoises was significantly lower than for adult tortoises, averaging 82.4 ± 3.8% at Conecuh and 69.7 ± 9.1% at Green Grove. Population models at both sites demonstrated unambiguous support (i.e., all other models $\Delta AIC_c \geq 5$) for constant apparent survival through time and a group effect on apparent survival (Tables 1 and 2).

Mark-recapture models at both Conecuh and Green Grove identified strong support for time-varying recapture probabilities (Tables 1 and 2). Although the likelihood of recapturing tortoises may truly vary from year to year, this variation likely also stems from differences in the number of traps used each year and the number of days traps were deployed. Estimated recapture probabilities at the 2 sites varied from 21% to as high as 97% in some years. We found support for a time-by-group interaction on recapture probabilities at Green Grove. However, no group at Green Grove had consistently lower or higher recapture probabilities than any other. Additionally, no group showed a trend toward increasing or decreasing recapture probability over time at Green Grove. Rather, recapture probabilities were variable from year to year and depended on the group in question.

Table 1. Model selection table identifying the most parsimonious Cormack–Jolly–Seber model of gopher tortoise survival during 1992–2003 (except 1996) for the Conecuh study site in south-central Alabama. We modeled apparent survival (Φ) and recapture probability (*p*) by group (g; i.e., male, female, immature), as constant probabilities (.), as functions of time (t), or as interactions of these covariates. AIC_c is Akaike's Information Criterion corrected for small samples sizes.

Model	AIC_c	ΔAIC_c	AIC_c weights	Number of parameters
Φ(g) *p*(t)	362.39	0	0.97	13
Φ(.) *p*(t)	369.37	6.98	0.03	11
Φ(t) *p*(t)	382.76	20.37	0.00	19
Φ(.) *p*(g × t)	399.95	37.56	0	31
Φ(g) *p*(g × t)	401.05	38.66	0	33
Φ(g) *p*(.)	407.86	45.47	0	4
Φ(g) *p*(g)	408.42	46.03	0	6
Φ(.) *p*(g)	410.24	47.85	0	4
Φ(.) *p*(.)	414.67	52.28	0	2
Φ(t) *p*(g)	417.93	55.54	0	13
Φ(g × t) *p*(t)	420.59	58.20	0	38
Φ(t) *p*(g × t)	421.61	59.22	0	39
Φ(t) *p*(.)	421.76	59.37	0	11
Φ(g × t) *p*(.)	460.30	97.91	0	31
Φ(g × t) *p*(g)	463.30	100.91	0	33
Φ(g × t) *p*(g × t)	482.82	120.43	0	56

Table 2. Model selection table identifying the most parsimonious Cormack–Jolly–Seber model of gopher tortoise survival during 1995–1999 for the Green Grove study site in southwest Georgia. We modeled apparent survival (Φ) and recapture probability (*p*) by group (g; i.e., male, female, immature), as constant probabilities (.), as functions of time (t), or as interactions of these covariates. AIC_c is Akaike's Information Criterion corrected for small samples sizes.

Model	AIC_c	ΔAIC_c	AIC_c weights	Number of parameters
Φ(g) *p*(g × t)	795.29	0	0.89	15
Φ(g × t) *p*(g)	801.08	5.79	0.05	15
Φ(g) *p*(t)	802.33	7.04	0.03	7
Φ(g × t) *p*(.)	804.13	8.85	0.01	13
Φ(g × t) *p*(g × t)	804.73	9.44	0	21
Φ(.) *p*(g × t)	805.42	10.13	0	13
Φ(g × t) *p*(t)	806.84	11.55	0	15
Φ(t) *p*(g)	807.12	11.83	0	7
Φ(t) *p*(g × t)	807.55	12.26	0	15
Φ(g) *p*(g)	822.61	27.32	0	6
Φ(g) *p*(.)	823.77	28.48	0	4
Φ(.) *p*(g)	831.81	36.53	0	4
Φ(t) *p*(.)	834.93	39.64	0	5
Φ(t) *p*(t)	837.66	42.37	0	7
Φ(.) *p*(t)	838.80	43.51	0	5
Φ(.) *p*(.)	855.25	59.96	0	2

Size frequency histograms revealed important differences among sites. Both Green Grove and Wade Tract had a large cluster of sexually mature tortoises in larger size classes as well as a separate cluster of smaller tortoises with few tortoises in intermediate size classes, leading to a bimodal distribution (Fig. 3). In contrast, the distribution of first captures from the first 5 years at Conecuh was unimodal (Fig. 3). A large cluster of sexually mature tortoises in the larger size classes still occurred, but the size distribution of immature tortoises was more uniform (Fig. 3). At all 3 sites, mature females tended to be larger than mature males (Fig. 3). Also, average size of mature tortoises increased from Conecuh to Green Grove to Wade Tract (Fig. 3).

Our estimates of asymptotic body sizes at each site mirrored the pattern we observed in size frequency histograms, particularly for females (Table 3). Male tortoises at Conecuh were the only group whose estimated asymptotic sizes differed significantly from both Green Grove and Wade Tract. Female tortoises from Conecuh were smallest but had overlapping confidence intervals compared with larger estimates for females at both Green Grove and Wade Tract (Table 3). Characteristic growth constants did not differ significantly among any of the study sites.

DISCUSSION

Gopher tortoise populations play an increasingly important role in conservation planning for the southeastern United States because monitoring surveys suggest that populations continue to decline on some of the best remaining habitat (McCoy et al. 2006), and because humans have a special

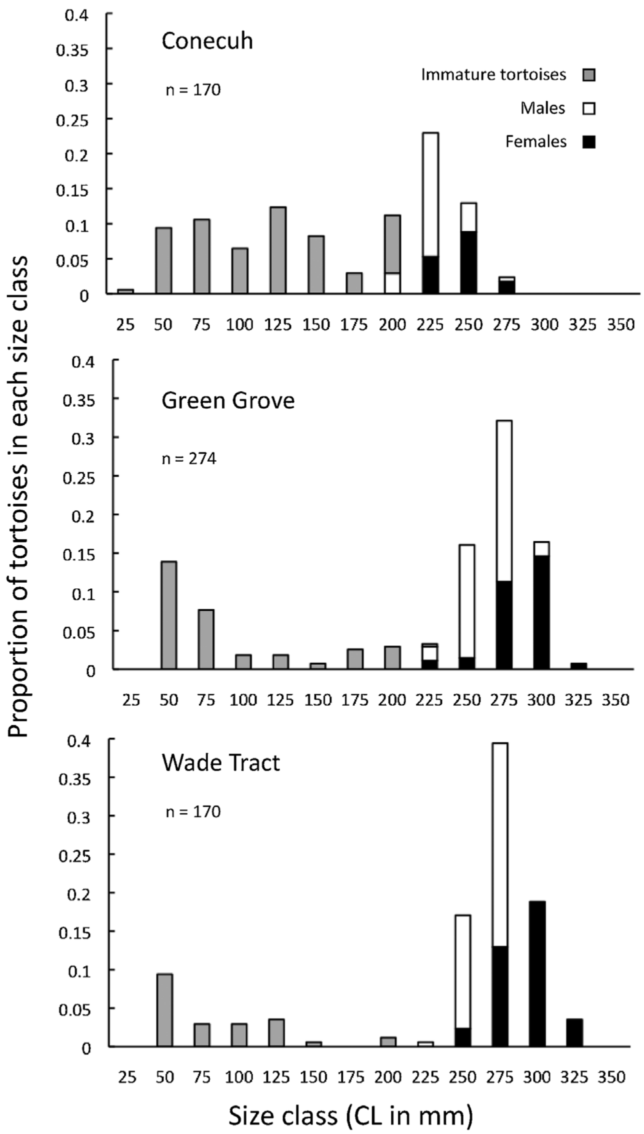

Figure 3. Size frequency histograms for maximum carapace length (CL) of gopher tortoises at first capture during the first 5 years of sampling at each of the 3 study sites in the southeastern United States: Conecuh (1992–1997, except 1996), Green Grove (1995–1999), and Wade Tract (1997–2002, except 1998).

affinity for these long-lived vertebrates (Hiaasen 2006). Conservation efforts have been hampered because key demographic variables are lacking for this species, leading to population models that rely largely on expert opinion (Miller 2001, Tuberville et al. 2009). Our research fills some important voids by providing estimates of survivorship. Additionally, our sites include 2 that are of exceptionally high habitat quality (Wade Tract and Green Grove), which we interpret to represent demographic patterns (size distributions or survival estimates) that conservation efforts elsewhere should strive to achieve, and 1 site representative of the types of managed lands where conservation efforts might lead to recovery of population viability (Conecuh). We discuss our data in terms of evaluating estimates of key demographic variables relative to tortoise conservation and compare variation among sites in terms of anticipated demographic changes as management efforts alter sites from currently heavily managed conditions (e.g., Conecuh) to sites restoring conditions of the old-growth forests to which gopher tortoises are adapted (e.g., Wade Tract and Green Grove).

A comparison of the size frequency distributions of individuals among our study populations reveals that the highest peak in the distributions corresponds to adults in all 3 populations, that remaining individuals are more evenly distributed among smaller size classes at Conecuh compared to either Green Grove or Wade Tract, and that the overall size distribution of tortoises is truncated at Conecuh compared to the other sites. Juveniles are frequently underrepresented in tortoise population studies (Hellgren et al. 2000), likely because of both high mortality rates on nests, hatchlings, and small juveniles, and because of lower detectability of smaller individuals and their burrows (Diemer 1992). In addition, the high survivorship of adults and reduced post-maturity growth rates (Medica et al. 1975) should result in an accumulation of adults of similar size even though they may represent multiple age cohorts (Alford 1980). Thus, a preponderance of adults would be expected in stable populations. In a comparison of habitat conditions and population demography at 51 sites across Florida, McCoy and Mushinsky (1988) found that large, undisturbed sites supported gopher tortoise populations "with a strong

Table 3. Estimated asymptotic body size (mm), characteristic growth constant, and standard errors derived from fitting von Bertalanffy growth models to maximum carapace length of gopher tortoises from 3 study sites in the southeastern United States (Conecuh, 1992–2003 except 1996; Green Grove, 1995–1999; Wade Tract, 1997–2002 except 1998). The 95% confidence intervals are shown in parentheses. Model-fitting procedures included an additional 10 immatures of unknown sex for Conecuh estimates, an additional 28 immatures for Green Grove estimates, and an additional 2 immatures for Wade estimates.

Site and sex	*n*	Asymptotic body size (*A*)	Characteristic growth constant (*k*)
Conecuh			
Males	17	240.9 ± 12.7 (214.7–267.1)	0.069 ± 0.018 (0.034–0.106)
Females	10	279.0 ± 27.2 (221.8–336.2)	0.049 ± 0.016 (0.017–0.083)
Green Grove			
Males	81	289.3 ± 4.1 (281.1–297.5)	0.061 ± 0.004 (0.053–0.069)
Females	63	306.5 ± 4.9 (296.8–316.3)	0.056 ± 0.004 (0.049–0.064)
Wade Tract			
Males	42	283.6 ± 1.9 (279.7–287.5)	0.064 ± 0.007 (0.050–0.078)
Females	46	318.4 ± 5.2 (307.9–328.9)	0.077 ± 0.013 (0.051–0.103)

representation of large individuals." In fact, a lack of animals in the larger size classes would be cause for concern, indicating unsustainable losses of adults through mortality or dispersal, possibly due to deteriorating habitat, which can in turn suppress recruitment (McCoy and Mushinsky 1988, Berish et al. 2012).

The distribution of smaller sized individuals can also provide insight into the demographic history of a population. Although the proportion of juveniles can vary from year to year because of variation in rates of recruitment or reproduction (Berish et al. 2012), sustained lack of recruitment would result in low abundance or large gaps in the distribution of smaller tortoises. Both Green Grove and Wade Tract gopher tortoise populations had bimodal size distributions with the second, smaller peak attributable to small immature tortoises (50–74 mm CL) and some representation in intervening size classes. However, the low relative abundance of intermediate-sized tortoises may be cause for concern and merit further monitoring (Smith et al. 1997). Alternatively, it may represent a population close to carrying capacity, with limited individuals appearing in the intermediate size classes because they disperse out of the study population or cannot compete for resources. In contrast, the Conecuh population had relatively uniform representation of tortoises across many smaller and intermediate size classes, demonstrating sustained recruitment in recent years. In support of this, immature tortoises comprised the highest proportion of captures at Conecuh (43%) compared with Green Grove (31%) and Wade Tract (21%).

In addition to the more uniform size distribution of gopher tortoises at Conecuh, maximum adult body sizes at Conecuh were truncated compared to the other 2 sites, with only 4 tortoises having CL $\geq$275 mm and none having CL $\geq$300 mm. In contrast, a large proportion of the Wade Tract and Green Grove tortoises had CL $\geq$275 mm (62.7% and 52.4%, respectively). Based on a smaller subset of our data (1991–1996), Aresco and Guyer (1999*a*) previously concluded that the smaller adult body sizes and lower characteristic growth constants for Conecuh gopher tortoises compared to a central Florida population (Mushinsky et al. 1994) were due to the low quality habitat and limited abundance of forage plants at Conecuh, which presumably limited somatic growth once Conecuh tortoises reached the subadult stage. They suggested that although intensive soil disturbance had not occurred at Conecuh for 20–25 years prior to their study, the legacy effects of that soil disruption as well as the dense pine canopy and lack of prescribed fires contributed to poor groundcover (Aresco and Guyer 1999*a*). In response to the findings by Aresco and Guyer (1999*a*, *b*), the United States Forest Service conducted tree thinning and initiated growing season burns at Conecuh in 1997, thus improving habitat management during the latter stages of our study (i.e., 1997–2003). During the 6 years of sampling after management improvements were initiated, adult body size distributions at Conecuh remained truncated compared to the Green Grove and Wade Tract populations, despite characteristic growth constants at Conecuh improving to match those of the higher quality sites.

We suspect that the large number of intermediate-sized tortoises and small adult body sizes at Conecuh reflect improving habitat conditions during the course of our study. That is, truncated adult body sizes reflect historically poor habitat conditions, whereas the accumulation of individuals in intermediate size classes represents increased recruitment and growth rates associated with improved habitat. Although indeterminate growth (growth after reproductive maturity) is a widespread phenomenon in turtles (Congdon et al. 2013), adult growth is significantly lower than that of immature animals. In addition, individuals that have reached reproductive maturity are less likely than immature individuals to exhibit renewed growth in response to increased resource availability; adult body size in turtles largely reflects resource availability when individuals are young (Gibbons 1967, Congdon et al. 2013). Consequently, changes in resource availability or habitat quality over time could take decades to manifest in adult body size in long-lived species such as turtles (Gibbs and Amato 2000), and may only do so when individuals that have experienced good quality habitat early in life eventually attain sexual maturity.

Growth rates in juvenile turtles have been shown to respond quickly in response to changing habitat or populations densities (Dodd and Dreslik 2008, Spencer and Janzen 2010), highlighting the potential utility of growth rates as a short-term monitoring metric. Frazer et al. (1991) noted a shift in the size distribution of a Michigan population of painted turtles (*Chrysemys picta*) between the 1960s and 1980s and attributed the increase in adult body size to an increase in juvenile growth rates between the early and late 1980s (Frazer et al. 1993). The longer duration of their study and the earlier age at maturity in painted turtles (4–5 yr in males, 7–13 yr in females; Congdon et al. 2003) compared to gopher tortoises (up to 20 yr; Landers et al. 1982, Aresco and Guyer 1999*a*) could explain why a shift in adult body size was detected in their study but has not yet been seen in gopher tortoises at Conecuh. However, if habitat quality and resource availability at Conecuh have improved sufficiently to support recruitment of tortoises across many age classes and to support growth on par with those in other populations (as suggested by the similar characteristic growth constants observed in our 3 study populations), we predict that the asymptotic body sizes at Conecuh will increase over time, with body sizes of recently recruited individuals eventually surpassing those of their parents.

Our study is among the first to report long-term survivorship estimates for naturally occurring populations of gopher tortoises based on mark-recapture data. Two previous studies of translocated populations reported 98.5% adult annual survival at Okeehellee County Park, Florida, USA (Ashton and Burke 2007), and 98% adult and 84% immature apparent annual survival at St. Catherines Island, Georgia, USA (Tuberville et al. 2008). Of the populations we studied, Conecuh tortoises exhibited apparent survival most similar to those at St. Catherines Island, with adult male and female annual apparent survival equal, immature apparent survival slightly lower than that of adults, and annual apparent survival estimates consistently high among years. Interestingly, both populations could be considered recovering populations—St. Catherines from translocation of tortoises to a previously unoccupied site, Conecuh from past tortoise harvesting and poor habitat conditions with a dense forest canopy that was not thinned until 1995. The high apparent survival we report for tortoises at Conecuh is in sharp contrast to the previously high rates of burrow abandonment (22% per year) documented prior to stand thinning and application of growing-season fires (Aresco and Guyer 1999*b*).

Apparent survival of male tortoises was nearly 9% lower than that of females at Green Grove. Additionally, apparent survival of immature tortoises at Green Grove was markedly lower than those at Conecuh (69.7% and 82.4%, respectively), or those reported for immature tortoises at St. Catherines Island (84%; Tuberville et al. 2008). Given that apparent survival is a measure of both site fidelity and true survivorship, the lower apparent survival rates in males and immatures at Green Grove could be due to either higher mortality or greater dispersal from the study area. We know of no differences among sites in mortality factors (e.g., disease, roads) that would explain the lower apparent survival of larger immatures and adult males at Green Grove compared to the other 2 study sites. However, overall tortoise density, total number of males, and the ratio of males to females at Green Grove are much higher than at either Conecuh or Wade Tract (Guyer et al. 2012). Widespread density-dependent phenomena have only recently been documented in gopher tortoises. In a comparison of 6 sites, including the 3 in our study, Guyer et al. (2012) reported higher incidences of shared burrows, greater home range overlap, and increased mating attempts with increasing population density—all factors increasing opportunity for social interactions. Although burrow sharing is common and could be interpreted as tolerance for conspecifics, both male and female gopher tortoises frequently chase or displace resident tortoises, particularly other males, from their burrows (Johnson et al. 2009). Thus, we suspect that the lower apparent survival in both male and immature tortoises at Green Grove indicate that this high quality site has reached carrying capacity, forcing subordinate individuals of both these groups to disperse because of social factors or competition for resources (McRae et al. 1981).

MANAGEMENT IMPLICATIONS

Our work demonstrates that adult body size or population density may not accurately reflect the current status of a population. Although small adult body size may indicate past disturbance to a population, high survival of all groups, somatic growth rates on par with those of viable populations, and the presence of an even distribution of tortoises of intermediate size all likely represent promising signs of recovery. Presumably, once populations recover and reach carrying capacity, a bimodal size distribution results, showing evidence of successful reproduction each year with a preponderance of sexually mature adults with density-dependent factors eventually forcing intermediate-sized tortoises to disperse or fail to establish residence. The combination of demographic data, estimates of vital rates, and long-term trends in population size or density, such as those derived from line-transect distance sampling, will yield the most complete assessment of population status to inform management of gopher tortoises.

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