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# Bog Turtle Demographics within the Southern Population

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**Turtles are among the most vulnerable vertebrate group to declines, extirpations, and extinctions, especially those species with specific habitat requirements. The Bog Turtle (*Glyptemys muhlenbergii*) is listed as federally Threatened in the United States, but the southern population of the species does not receive full habitat protection under the Endangered Species Act. To understand Bog Turtle demographics within the southern population, we applied Cormack-Jolly-Seber and multistate models in program MARK and calculated annual adult, sex-specific, and juvenile survival for intensively sampled (19–180 sampling days) Bog Turtle populations in North Carolina. The most parsimonious model indicated that adult survival remained constant over time for all populations, but was relatively low when compared to other species of turtles. Adult survival estimates varied between 0.86 and 0.94 among the sites, all below the 0.96 adult survival estimate documented for northern Bog Turtle populations. To evaluate variation in juvenile survival, we focused on three populations: the two largest known populations and an intensely studied, but critically declining population. The two largest populations had a greater proportion of juveniles than other populations and higher juvenile survival (0.68 and 0.67) than the declining population (0.50). Thus, conservation efforts targeting juvenile survival and recruitment, such as nest protection and habitat enhancement, are important to ensure population stability. Furthermore, our estimates of adult and juvenile survival indicate that North Carolina populations are likely declining and without stronger protection measures, local and regional extirpations of the species may occur.**

SIGNIFICANT reptile declines have been documented on a global scale (Gibbons et al., 2000; Böhm et al., 2013). Turtles surpass other major vertebrate taxa, such as birds, mammals, and amphibians, in terms of species recognized as Threatened and Endangered under IUCN criteria (e.g., approximately 51% of turtle species are considered Threatened compared to 41% of amphibian species, another highly at risk vertebrate group; Turtle Taxonomy Working Group, 2014). Certain life-history traits likely make turtles more sensitive than other taxa to anthropogenic disturbance. Turtles are characterized by delayed sexual maturity and typically high egg and juvenile mortality, necessitating high adult survival to maintain stable populations (Congdon et al., 1993; Pittman et al., 2011). Thus, implementing management plans that improve and maintain survival, such as preserving and restoring suitable habitat or protecting nests, could help to ensure the persistence of turtle populations (Sirois et al., 2014; Reid et al., 2016).

Bog Turtles (*Glyptemys muhlenbergii*) are small and cryptic semi-aquatic turtles that are federally listed as Threatened in the United States primarily as a result of habitat fragmentation and degradation (USFWS, 1997). They occupy small tracts of open canopy meadows, bogs, and fens conducive to basking and burrowing under mud (Herman and Tryon, 1997). Bog Turtles occur in the eastern U.S. in two geographically distinct population networks: a northern population network extending from New York and western Massachusetts to Maryland and a southern population network extending from Virginia to northern Georgia (Ernst and Lovich, 2009). While Bog Turtles in the northern U.S. receive full protection under the Endangered Species Act (ESA), Bog Turtles within the southern population network are listed as Threatened due to their "similarity in appearance" to the northern population network. Thus, federal regulations prohibit the collection of Bog Turtles throughout their range, but only Bog Turtles in the northern U.S. are federally protected from destructive activities affecting their habitat, such as wetland draining (USFWS, 1997).

In North Carolina, Bog Turtles are found in the western portion of the state, concentrated in a montane region known as the Blue Ridge, with the exception of a few isolated populations in the Piedmont. Wetland draining for agricultural use of land within the Bog Turtle's range has resulted in a 90% loss of North Carolina mountain bogs (Weakley and Schafale, 1994; Noss et al., 1995). In addition to habitat loss and fragmentation, poaching may be a factor contributing to declines of certain Bog Turtle populations (USFWS, 1997). Bog Turtles are highly sought after for the pet trade because of their rarity and are considered one of the most valuable turtle species native to the United States (Herman and Tryon, 1997; USFWS, 1997).

To create effective management strategies that improve Bog Turtle population viability and maintain stable populations, underlying demographic questions need to be addressed, especially for the less-intensely studied southern population network. Considering that North Carolina contains the majority (63.9%) of the Bog Turtle's geographic range in the southeast (G. Graeter, unpubl. data), the state's populations are likely fundamental to the overall viability of the southern network. Ultimately, key vital rates of well-studied populations known to be stable could serve as benchmarks for assessing the viability of other populations. Thus, our objective was to evaluate Bog Turtle demography at 11 sites in the mountains and Piedmont of North Carolina. Although measures of fecundity and recruitment are important to consider when evaluating the overall viability of populations, nesting studies have yet to be completed at these North Carolina populations. Considering the large contribution of adult and juvenile survival to population growth in freshwater turtles relative to the input from fecundity or recruitment (Congdon et al., 1993; Heppell, 1998), we believe that examining these vital rates is critical to begin understanding demographic differences among populations. Thus, we used open population modeling to calculate

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**Table 1.** Sampling data from 11 Bog Turtle sites in North Carolina, USA. Site name, site code from the NC Bog Turtle Database, total number of marked turtles, total number of turtle captures, total number of sampling events, and sampling period. Sites are labeled A–K, according to the number of marked turtles, from greatest to least.

| Site name | Site code | Total # of marked turtles | Total # of captures | Total # of sampling events | Sampling period |
|---|---|---|---|---|---|
| A | 108 | 228 | 496 | 40 | 1995–2014 |
| B | 110 | 156 | 483 | 72 | 1996–2014 |
| C | 26 | 144 | 187 | 79 | 1975–2012 |
| D | 131 | 72 | 155 | 37 | 2002–2014 |
| E | 88 | 57 | 335 | 180 | 1992–2014 |
| F | 113 | 47 | 126 | 45 | 1996–2013 |
| G | 69/75 | 40 | 58 | 24 | 1990–2013 |
| H | 87/91 | 32 | 110 | 30 | 1992–2014 |
| I | 76 | 33 | 158 | 64 | 1990–2013 |
| J | 136 | 29 | 72 | 20 | 2000–2014 |
| K | 141 | 29 | 60 | 19 | 2002–2014 |

adult, juvenile, and sex-specific survival, and examined age and sex structures to describe patterns in Bog Turtle captures over entire sampling periods.

## MATERIALS AND METHODS

We used individual mark-recapture records from a long-term dataset (>10 years) maintained by the North Carolina Wildlife Resources Commission and Project Bog Turtle (hereafter referred to as the NC Bog Turtle Database). Experienced researchers with Project Bog Turtle completed many of the Bog Turtle population surveys and worked closely with private landowners (Somers, 2000). We chose 11 well-studied sites from the NC Bog Turtle Database to examine age and sex structures and used the eight most-intensively sampled sites for modeling survival. The NC Bog Turtle Database contained records of all population surveys completed at the 11 sites between 1975 and 2014. We provided each site with a letter name based on the number of marked turtles (i.e., A is the site with the greatest number of marked turtles and K is the site with the fewest number of marked turtles) and did not disclose precise locations or exact site names because of concerns about the potential for poaching.

We used a combined total of 2,240 captures of 810 Bog Turtles at the 11 sites to determine demographic factors affecting Bog Turtle survival. The number of marked turtles, number of captures, number of sampling events, and sampling periods varied considerably among sites (Table 1). Active search methods, such as probing with wooden sticks and visual encounters, accounted for nearly all Bog Turtle captures. Population surveys varied in sampling time and effort, but surveys included an average of three hours per person, and 2–34 (median of 3) surveys occurred during sampling years. During population surveys, researchers typically searched an entire site area. Traps were used some years at Site E to supplement probing efforts. Consult Pittman et al. (2011) for a detailed description of sampling techniques at Site E.

To examine patterns of captures over the entire sampling history of a site, we described the sex and age structure as the proportion of males or females in the adult population and the proportion of juvenile or adult initial captures, respectively. Juvenile turtles were aged by counting scute rings, but because scute ring counts are inaccurate for mature individuals (Brooks et al., 1997; Litzgus and Brooks, 1998), adult ages were estimated (e.g., >7 years of age) or calculated from the NC Bog Turtle Database for recaptured turtles. We determined an age cutoff for the adult class by querying the NC Bog Turtle Database for the youngest gravid female, yielding several gravid females aged 7 years. Thus, we considered individuals aged 7+ years as adults. We used all captures for the sex and age structures for each site, and thus these structures may not reflect the sex and age distributions of the current populations. We used simple linear regressions to examine the relationship between the proportion of female captures and adult survival estimates, and the relationship between the proportion of juvenile initial captures and adult survival estimates. In other words, we examined whether the sex and age structures of the more robust populations (i.e., populations that harbored a greater number of turtles and exhibited higher survival) differed from populations exhibiting the lowest survival.

***Statistical analyses.***—To calculate adult and sex-specific survival, we used an open population Cormack-Jolly-Seber (CJS; Lebreton et al., 1992) model in MARK, a program which can estimate year-specific apparent survival ($\Phi$) and recapture (p) parameters using mark-recapture records (Version 6.2; White and Burnham, 1999). Each sampling interval was annual and included captures from all spring, summer, and fall sampling occasions because few turtles were captured during a given season at many sites. Each site was sampled with varying amounts of effort, with some sampled multiple times in a given year and others sampled more sparingly. Years with minimal effort (i.e., only one occasion in a year) were excluded from the capture histories because we did not consider one occasion sufficient to effectively sample a Bog Turtle population. Accordingly, we adjusted the intervals between sampling in program MARK to reflect any gaps in years sampled. Because most sites were sampled in different years, we first calculated survival for each Bog Turtle population individually. In MARK we considered four candidate models for each site, including the fully time-dependent global model $\Phi_{(t)}p_{(t)}$. We separately included sex as a factor in the adult survival model set to test for differences in survival between males and females (refer to Supplements 1–6 for descriptions of each sex-specific model; see Data Accessibility). We did not test for differences in apparent survival between male and female juveniles because sex was not known for all juveniles.

We focused on sites A, B, and E to identify key differences in demography among more robust Bog Turtle populations (such as sites A and B) and declining populations (such as Site

E). Sites A and B had the greatest number of marked turtles (i.e., A and B are most likely the largest populations), and Site E was the most intensively sampled (Fig. 1). However, the Site E Bog Turtle population has declined dramatically since the 1990s, with no new adult captures since 2006 (Pittman et al., 2011). In contrast, at Site A there was an average of $15.6 \pm 6.8$ new turtle captures per year from 2008–2014, the time period when sampling was most consistent from one year to the next; at Site B there was an average of $2.1 \pm 1.7$ new turtle captures per year from 2008–2014. In addition to the adult survival analyses (described above) that were run individually for each site, we pooled adult capture histories for sites A, B, and E from 1996–2014 (the period during which 12 sampling years from each site overlapped) to test for the effect of site on adult survival. We considered eight models, including the global model $\Phi_{(site(t))}p_{(site(t))}$, representing time-varying differences in survival and recapture probabilities among the sites A, B, and E. We made the assumption that recapture probability varied over time as a result of variation in sampling effort among years. Subsequent nested models differed in time and site effects in the survival parameter.

To estimate juvenile survival for sites A, B, and E, we used multistate capture-recapture models (Lebreton and Pradel, 2002) that allowed individuals to transition from the juvenile (1–6 years) to the adult (7+ years) stage during each annual sampling period. Multistate models have been used in multiple contexts (White et al., 2006), including metapopulation dynamics (Roe et al., 2009; Spendelow et al., 2016), but we applied the multistate model to account for stage class transitions over time. Our models included three fundamental parameters: annual survival probabilities ($\Phi$), recapture probabilities (p), and transition probabilities ($\psi$) for each state. We used our results from the adult survival analyses to inform our selection of candidate models for juvenile survival. We considered the models $\Phi_{(stage(.))}p_{(t)}\psi_{(ja(.))}$ and $\Phi_{(stage(.))}p_{(stage(t))}\psi_{(ja(.))}$, both specifying constant survival for juveniles and adults over time ($\Phi_{(stage(.))}$), time-varying recapture probabilities (set equal [$p_{(t)}$] or unequal [$p_{(stage(t))}$] for the age classes depending on the model), a constant transition probability from the juvenile to adult stage ($\psi_{(ja(.))}$), and a fixed transition probability of 0 from the adult to juvenile stage ($\psi_{(aj)}$). We tested for differential detectability of juveniles with the model $\Phi_{(stage(.))}p_{(stage(t))}\psi_{(ja(.))}$. Mark-recapture data were analyzed separately by site.

We included entire capture histories (1996–2014) for sites A and B in the juvenile survival analyses, but excluded years with low sampling effort (i.e., a single occasion in a given year). To allow us to compare juvenile survival of these more robust populations to a small, intensively sampled population with few recaptured juveniles, we estimated juvenile survival at Site E over the time period corresponding to when juveniles were most frequently captured at that site (1992–1998). We could not fit fully parameterized multistate models for Site E across all sampled years because of the precipitous decline in juvenile captures over time. For example, the number of turtles initially captured as juveniles and recaptured in subsequent years declined from eight juveniles (of 17 total juveniles) from 1992–1998 to one juvenile (of three total juveniles) from 2001–2014. Thus, we considered the same model set described for sites A and B, but restricted our analysis to mark-recapture data from 1992–1998 for Site E. Too few and infrequent captures of juveniles prevented us from estimating juvenile survival at other sites.

***Goodness of fit.***—We used the bootstrap goodness of fit test to evaluate the fit of the global, most parameterized model [$\Phi_{(t)}p_{(t)}$; $\Phi_{(site(t))}p_{(site(t))}$; $\Phi_{(sex(t))}p_{(sex(t))}$; $\Phi_{(stage(.))}p_{(stage(t))}\psi_{(ja(.))}$] for all demographic factors (Burnham and Anderson, 2002). We ran 1,000 simulations and noted the placement of the observed deviance of the global model compared to the simulated deviances; we expected the observed deviance to fall approximately at the halfway point among the simulated deviances ranked in increasing order. We calculated a c-hat value for each global model by dividing the observed deviance by the mean of the simulated deviances. We used Akaike's Information Criterion adjusted for small sample sizes (AICc) and corrected for overdispersion when the c-hat value was greater than 1, resulting in $\Delta$QAICc values (Burnham and Anderson, 2002). We selected the model with the lowest $\Delta$QAICc value as the most parsimonious model. When more than one model was supported for the sex-specific model set (with an Akaike weight of at least 0.2), we used model averaging, which considered the weight of evidence for each model when calculating survival estimates, taking model uncertainty into account (Burnham and Anderson, 2002).

## RESULTS

***Sex and age structures.***—The sex structure revealed that for ten of the 11 sites, more females were captured than males (Fig. 2A). Accordingly, there was no relationship between the proportion of female captures and adult survival estimates ($r^2 = 0.08$, $P = 0.50$). Age-class structure, or the proportion of each population first captured as juveniles (age 1–6) or adults (age 7+), varied among populations (Fig. 2B). There was a positive relationship between the proportion of juvenile captures and adult survival estimates, but the trend was not significant ($r^2 = 0.33$, $P = 0.14$). Sites with more marked turtles also had a greater proportion of turtles first marked as juveniles than other sites ($r^2 = 0.64$, $P = 0.02$). Sites A and B had the greatest proportion of initial juvenile captures, with 42.5% juvenile captures from Site A and 54.0% juvenile captures from Site B. Other sites had proportionately fewer juveniles represented in their populations, and no juveniles were captured at Site G.

***Adult survival.***—The results from the CJS models are estimates of apparent survival because the loss of marked individuals from each population could potentially be attributed to either mortality or emigration; however, these survival estimates may be representative of the true survival of the populations as Bog Turtles infrequently move among discrete wetlands (Morrow et al., 2001; Pittman and Dorcas, 2009). The best supported model of adult survival for five of eight sites indicated a constant survival probability and a recapture probability that varied with time, and no effect of sex for either parameter ($\Phi_{(.)}p_{(t)}$; refer to Supplements 7–14 for descriptions of the model of best fit for each site; see Data Accessibility). Estimates of annual adult survival for these eight North Carolina Bog Turtle populations ranged from 0.86 (95% CI = 0.74–0.93) at Site H to 0.94 (95% CI = 0.90–0.97) at Site A (Fig. 3). Generally, sites with more marked turtles had higher annual adult survival ($r^2 = 0.79$, $P = 0.01$). Models showed more variation in the survival estimates calculated for sites F, H, I, and J because of their small population sizes. For example, Site J—one of the smallest populations—had a relatively high annual adult survival estimate (0.92) with respect to the other sites, but also had a

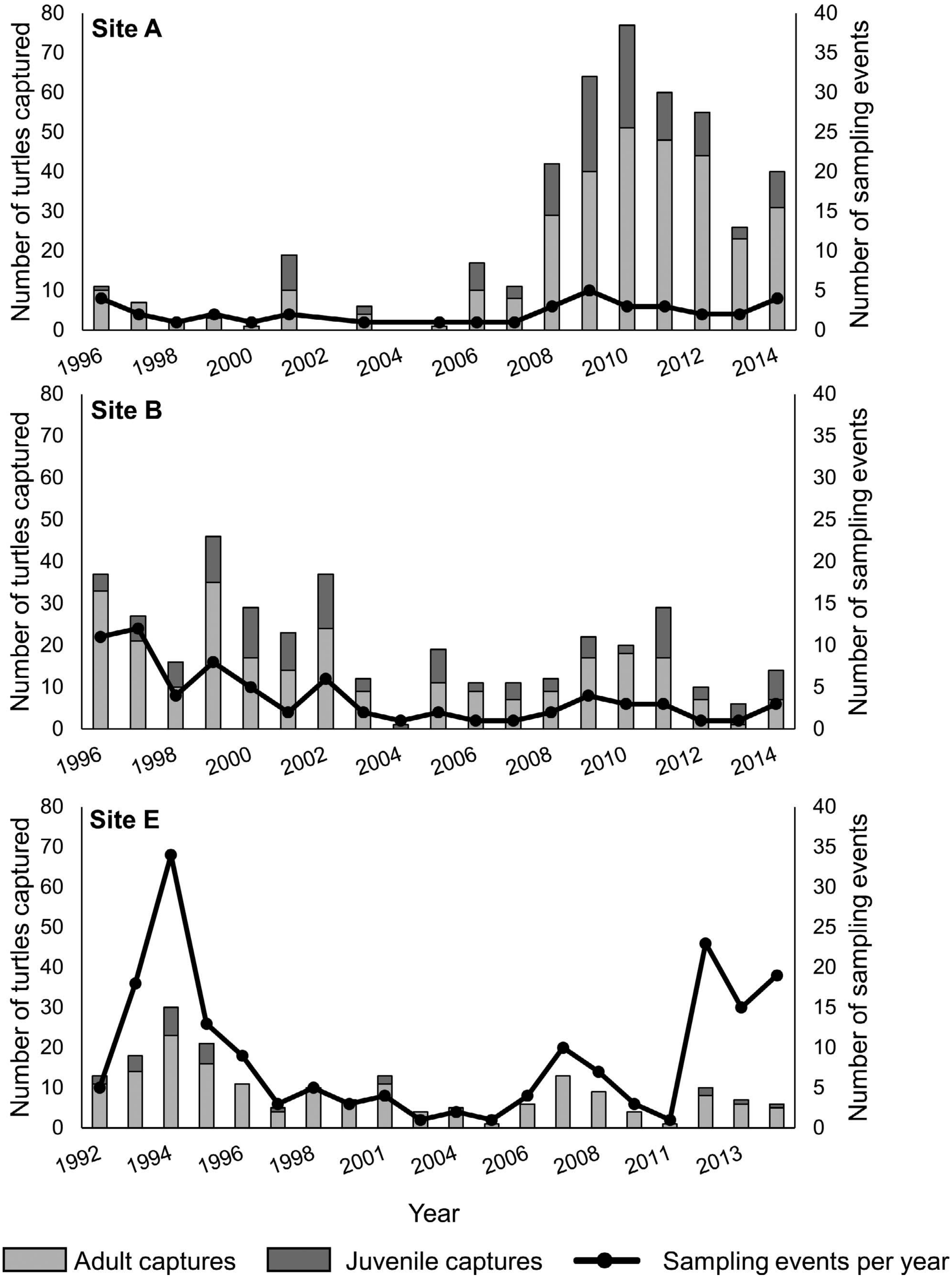


**Fig. 1.** The number of Bog Turtles captured each year, both adults (light gray) and juveniles (dark gray), as well as the number of sampling events per year (solid line with filled circles) at sites A, B, and E in North Carolina, USA.

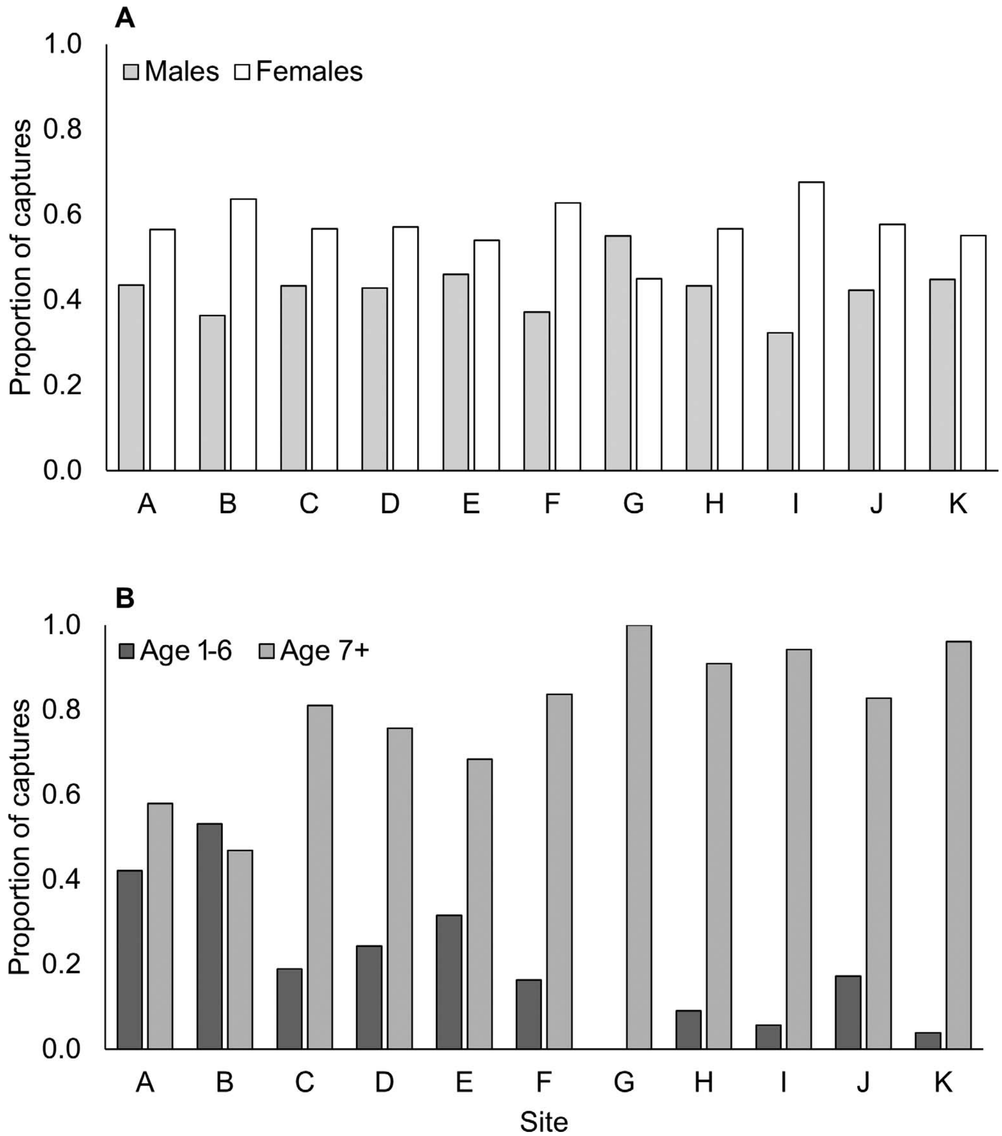


**Fig. 2.** (A) The sex ratio, the proportion of male and female Bog Turtles represented in each population A–K in North Carolina, USA. (B) Age structure and proportion of Bog Turtles first captured as juveniles (age 1–6) or adults (age 7+) at sites A–K in North Carolina, USA. The sites are ordered by number of marked turtles, from greatest to least. All captures were used and thus the sex and age structures may not reflect the current population.

wide 95% confidence interval (0.78–0.98). Of the five sites that supported a model with a sex-specific difference in survival (QAICc weight $\geq$ 0.2), the sex-specific model had a lower QAICc weight than the best supported model, one with survival unaffected by sex (refer to Supplements 1–6 for descriptions of each sex-specific model; see Data Accessibility). After model averaging, we found marginal differences in survival point estimates between males and females, but with overlapping confidence intervals. Thus, there was no detectable difference in survival between males and females across all sites. Only Site A supported a model (QAICc weight 0.33) specifying a sex-specific difference in the recapture probability, but with overlapping confidence intervals among all sampling intervals.

The pooled capture histories from sites A, B, and E supported (AICc weight 0.77) site-specific variation in adult survival (Supplement 15; see Data Accessibility). The most parsimonious model $\Phi_{(site(.))}p_{(site(t))}$ indicated a constant difference in survival and a time-varying difference in recapture probability among the sites. Adult survival was highest at Site A (0.94; 95% CI = 0.90–0.96), with lower point estimates calculated for sites B (0.88; 95% CI = 0.83–0.91) and E (0.87; 95% CI = 0.80–0.91).

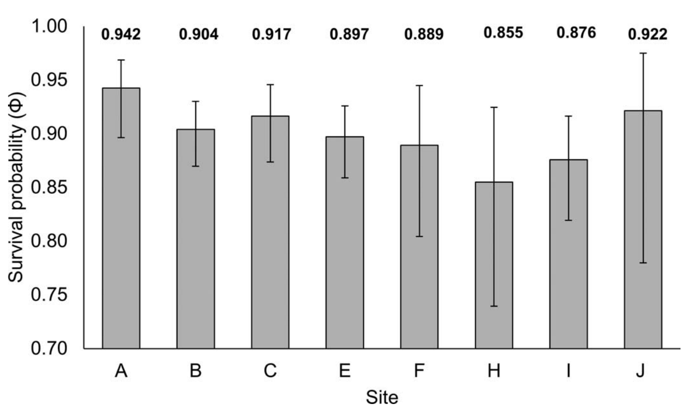


**Fig. 3.** Adult survival (age 7+) of eight Bog Turtle populations in North Carolina, USA. The sites are ordered by number of marked turtles, from greatest to least. The height of the bars indicates the estimated annual survival probability ($\Phi$), the data labels are the adult survival point estimates, and error bars are 95% confidence intervals.

***Juvenile survival.***—A total of 80 juveniles were captured at Site A from 1996–2014, 72 juveniles at Site B from 1996–2014, and 17 juveniles at Site E from 1992–1998. Sites A, B, and E supported the model $\Phi_{(stage(.))}p_{(t)}\psi_{(ja(.))}$, indicating a constant difference in the survival probability between juveniles and adults, but no difference in the time-varying recapture probability between the age classes (Supplements 16–18; see Data Accessibility). Point estimates of apparent juvenile survival were high for Site A (0.68; 95% CI = 0.54–0.79) and Site B (0.67; 95% CI = 0.54–0.78), but considerably lower (0.50; 95% CI = 0.24–0.76) at Site E (Fig. 4). Because of the variability in juvenile captures, 95% confidence intervals were wide.

## DISCUSSION

In this study we estimated Bog Turtle survival rates—adult, sex-specific, and juvenile survival—and determined that adult survival varied among the most intensively studied sites. We observed that sites with a greater number of turtles generally had higher adult survival than smaller populations, had a greater proportion of individuals first captured as juveniles, and had higher juvenile survival than a declining population (i.e., Site E). Species with long generation times typically have high adult survival, but adult survival estimates for sites B–K were relatively low for maintaining stable turtle populations. For example, Enneson and Litzgus (2008) used a stage-classified projection matrix for Spotted Turtles (*Clemmys guttata*) and determined that annual adult survival below 0.93 resulted in population declines. Because Spotted Turtles are closely related to Bog Turtles and share similar life-history characteristics, we used 0.93 as the adult survival threshold for stable Bog Turtle populations. In this context, only Site A is above the 0.93 potential marker of a stable population.

Estimates of Bog Turtle survival have been reported for adults from an isolated population in North Carolina (the same population referred to as Site E in this study), for adults from two sites in Massachusetts that differed in habitat quality, and adults and juveniles from populations in New York and Massachusetts (Pittman et al., 2011; Shoemaker et al., 2013; Sirois et al., 2014). Sirois et al. (2014) estimated adult survival at 0.99 for a site in Massachusetts with high quality habitat, and Shoemaker et al. (2013) estimated adult survival at 0.96 for a complex of populations along the border of New York and Massachusetts. Both studies from the northern population network reported adult survival estimates higher than any estimates from the North Carolina populations in this study (0.86–0.94).

Elasticity analyses examining the proportional contribution of a life stage to the population growth rate revealed that small changes in adult survival can greatly impact population growth for freshwater turtles (Congdon et al., 1993; Heppell, 1998; Bowen et al., 2004). Although we did not observe a clear difference in adult survival among the more robust and smaller populations when we analyzed sites separately, when we modeled adult survival for the intensively sampled sites A, B, and E collectively, the best supported model indicated differences in survival among the sites. Therefore, variation in adult survival could potentially account for the observed differences in age structure among Bog Turtle populations.

The sex structure of the populations revealed a female bias, a pattern also described by Shoemaker et al. (2013). However, we did not find a sex-specific difference in the survival or recapture probability. One biological explanation for the female bias is temperature-dependent sex determination (TSD). Although the pattern of sex determination has not been described for Bog Turtles, the Bog Turtle's congener Wood Turtle (*Glyptemys insculpta*) has genetic sex determination (Ernst and Lovich, 2009). Thus, it is unclear why females are more frequently captured, but we suggest an alternative

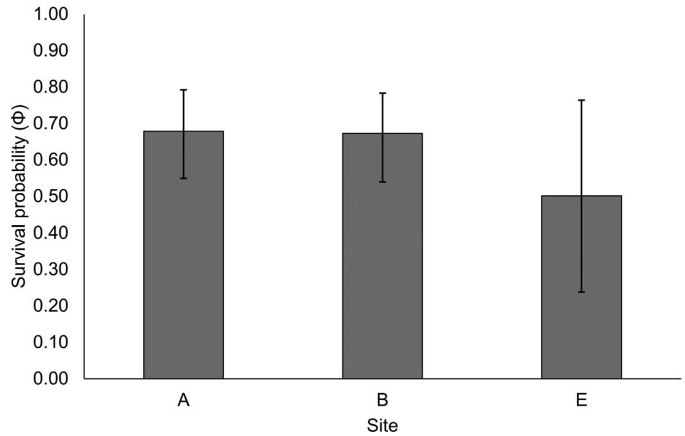


**Fig. 4.** Juvenile survival (age 1–6) of three Bog Turtle populations in North Carolina, USA. The height of the bars indicates the estimated annual survival probability (Φ), and the error bars are 95% confidence intervals. Note that juvenile survival was estimated from multistate models for each site. Additionally, juvenile survival for Site E was estimated over the time period corresponding to the greatest number of juvenile captures (1992–1998).

hypothesis that supports our observations. Male-biased dispersal has been documented for Bog Turtles (Lovich et al., 1992) and other turtle species (Tuberville et al., 1996; Sheridan et al., 2010). If male juvenile Bog Turtles are dispersing and are consequently at a higher risk of mortality, we would expect to observe female-biased sex ratios, but not document differences in adult survival between the sexes.

Low fecundity (i.e., females lay 1–6 eggs) and relatively low adult survival in comparison to other turtle species may make Bog Turtle populations more sensitive to changes in juvenile survival (Ernst and Lovich, 2009). The only other source for Bog Turtle juvenile survival rates calculated age-specific estimates, making direct comparisons to our results difficult. For turtles aged 1–6, survival estimates ranged from 0.48 for yearling turtles to approximately 0.85 for six-year old turtles (Shoemaker et al., 2013). Juvenile Bog Turtles are not as well understood as adults, and thus we primarily rely on juvenile data from other species to discuss Bog Turtle juvenile survival estimates. Juvenile survival for freshwater turtles ranges from 0.72 for Mud Turtles (*Kinosternon subrubrum*) to 0.78 for Blanding's Turtles (*Emydoidea blandingii*) and to 0.82 for Spotted Turtles (Frazer et al., 1991; Congdon et al., 1993; Enneson and Litzgus, 2008). Apparent juvenile survival for Site A (0.68; 95% CI = 0.54–0.79) and Site B (0.67; 95% CI = 0.54–0.78) was consistent with estimates reported for the other freshwater turtle species, but Site E was much lower (0.50; 95% CI = 0.24–0.76).

Additionally, adults were disproportionately represented in the populations of all sites except for Site B (46.0% adults). However, the adult bias we observed could be partly explained by lower detectability of juvenile Bog Turtles compared to adults because of their small size and poorly understood behavior patterns. In comparison to a juvenile fraction of 0.58 reported for a complex of northern Bog Turtle sites, the juvenile fraction for Site B (0.54) was most similar (Shoemaker et al., 2013). Most importantly, the disparity in the juvenile fraction between more robust (A and B) and smaller (C–K) populations suggests that low nest success, juvenile survival, and/or low reproductive rates could be limiting factors for many Bog Turtle populations in North Carolina.

Demographic information is most complete for Site E and thus it serves as an important case study. Site E declined from an estimated 36 turtles in 1994 to an estimated 11 turtles in 2007 (Pittman et al., 2011). No new adults have been captured since 2006, and only two new juveniles have been captured since 2002, despite substantial increases in sampling effort in recent years. Untangling the cause/effect relationship of external threats (i.e., habitat degradation or isolation from other Bog Turtle populations) and declines in vital rates is difficult for a population like Site E that is likely affected by multiple stressors. Site E is a well-studied site that may be similar to most of the Bog Turtle sites in this study: populations composed primarily of adults with relatively low adult survival. In contrast, sites A and B may be representative of the most robust populations in the state. Adult survival at all sites may be relatively low for Bog Turtle populations (Shoemaker et al., 2013), making high juvenile survival especially important for population stability.

When the Bog Turtle was federally listed in 1997, there were insufficient data and survey coverage in both the northern and southern population networks. Although the turtle itself was protected, habitat in the southern population network did not receive protection under the Endangered Species Act (USFWS, 1997). Available information suggested that the southern population network did not face the same extent of threats as the northern network, particularly in North Carolina. Even if this was once true, it is not likely the case now, considering the rapid growth of North Carolina's human population (US Census Bureau, 2011) and the associated habitat loss, degradation, and fragmentation. The lower adult survival of the North Carolina Bog Turtle populations in this study could indicate that the southern population network is in decline. Because North Carolina represents the majority (63.9%) of the southern network, our findings fill in crucial knowledge gaps regarding Bog Turtle population demography in the southern U.S. Our study is the first to describe Bog Turtle vital rates on a statewide scale, and thus the broad patterns of survival we observed for adults and juveniles in North Carolina are likely indicative of the state of other Bog Turtle populations in the southern network. Our results suggest that North Carolina Bog Turtle populations, previously considered a stronghold of the southern population network, are in decline. Population monitoring should continue to allow for future assessment of the species' status. More effective habitat and population conservation actions should occur to preclude federal listing of the southern population as Threatened or Endangered under the Endangered Species Act.

***Management implications.***—If conservation efforts do not yield improvement, the relatively low adult and juvenile survival of North Carolina Bog Turtle populations may result in local and regional extirpations of the species. In addition to immediate on-the-ground actions, such as continued habitat protection, management, and restoration, we propose a reworking of conservation strategies for the Bog Turtle using a more integrated approach that considers the apparent threats to Bog Turtle survival in the context of the fundamental life-history traits and the demographic characteristics that make Bog Turtles vulnerable. In other words, to manage threats associated with anthropogenic causes, it is important to consider the life-history traits (e.g., low fecundity), vital rates (e.g., nest success, adult and juvenile survival), and ecology (e.g., naturally occur in small, but connected populations) of Bog Turtles. In this case, population growth and stability depends on the survival and fecundity of a few reproductive females. Additionally, if hatchlings and juveniles have a low probability of surviving to maturity, then a population becomes dominated by older turtles. Consequently, an "older" population could be susceptible to declines from anthropogenic causes because of low recruitment. Thus, it is essential that future research focus on increasing our knowledge of fecundity, nest success, and juvenile survival so that conservation efforts can promote population stability and increase population viability in North Carolina and across the species' range.

## DATA ACCESSIBILITY

The supplemental materials referenced in this manuscript are available from the Figshare Digital Repository: https://dx.doi.org/10.6084/m9.figshare.3492878.

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