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Population models reveal the importance of early life-stages for population stability of an imperiled turtle species

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Abstract

Demographic models are useful for projecting population trends, identifying life stages, most important to population dynamics, and investigating the demographic effects of potential management scenarios. We incorporated site-specific population parameters into stage-based matrix models to estimate population growth and to assess potential management scenarios for five intensively sampled (>15 years) populations of federally threatened bog turtles (*Glyptemys muhlenbergii*) in North Carolina, USA. Only two of the five populations modeled were stable or growing under estimated vital rates. Long-term sampling of bog turtle populations in NC suggests the declining populations in this study share several demographic characteristics with other populations in the region. Elasticity analysis revealed small changes in adult survival rates have the largest effect on population growth rate. These models also highlight that increased survival of egg and juvenile stages can sometimes buffer higher adult mortality and emigration, and reduced survival at multiple life stages can induce population-level decline. Our results indicate that management scenarios targeting increased recruitment (especially a head-start scenario) provide increased population growth among all populations, and allowed two of three declining populations to reach stability under current estimated vital rates. Population growth rates will be higher when population augmentation coincides with habitat restoration efforts that increase survival and site fidelity at all life stages. These models emphasize the importance of considering site-specific dynamics when evaluating conservation interventions for an imperiled long-lived species.

Introduction

Many conservation challenges are associated with small and declining populations of rare species. Such species are vulnerable because they are less resilient to disease (De Castro & Bolker, 2005), habitat degradation (Schleuning *et al.*, 2009) and genetic, demographic, and environmental stochasticity (Soule & Simberloff, 1986; Stacey & Taper, 1992; Lande, 1993; Hanski, 1998). Estimates of the number of individuals within populations offer snapshots that can guide conservation funding and additional research; however, demographic models add critical information for decision-making as they further elucidate the status and trajectory of a population through estimates of age structure and population growth rate. Such data are vital since policy decisions are often influenced by the availability of scientific information (Martín-López *et al.*, 2009). Therefore, a moderately abundant but severely declining population may not receive conservation resources if data are lacking to demonstrate its decline. Stage-based demographic modeling can provide insight into specific conservation actions that are likely to stabilize or increase abundance within populations of concern. For example, a stage-based model for Black Oystercatcher *Haematopus bachmani* populations revealed that pair productivity, which integrated hatching and fledging success, offered the most valuable metric for monitoring population growth potential of the species (Meehan *et al.*, 2018). A similar model was used to provide data to support a decision to implement artificial propagation and targeted translocation as a means of re-establishing bull trout *Salvelinus confluentus* in parts of northwestern, USA (Benjamin, Brignon & Dunham, 2019).

Long-term demographic data are especially important to understanding population trends of species with long generation times because such species are slow to recover from demographic perturbations (Crouse, Crowder & Caswell, 1987; Heppell, 1998; Wheeler *et al*., 2003; Enneson & Litzgus, 2008; Keevil, Brooks & Litzgus, 2018). In some cases, these species may even suffer from extinction debt, a conceptual framework in which a substantial lag time exists between the factors that initiate species decline and the ultimate loss of the species (Kuussaari *et al*., 2009; Lovich *et al*., 2018). Certain population characteristics, such as lack of recruitment or low survival at specific life stages, can reveal such debt and identify opportunities for targeted intervention. For example, much of the current management for the long-lived and federally threatened American crocodile *Crocodylus acutus* focuses on nest and hatchling survival, but a stage-based model indicated that extending protection to juveniles would bolster conservation benefits to the species (Briggs-Gonzalez *et al*., 2017). While populations of rare and long-lived turtle species often have similar markers of extinction debt, biologists are beginning to generate robust enough demographic data to quantitatively characterize population status and evaluate management actions best suited to improve declining turtle populations (Enneson & Litzgus, 2008; Spencer, Van Dyke & Thomson, 2017).

The bog turtle *Glyptemys muhlenbergii* is a highly cryptic, semi-aquatic species that occupies open-canopy freshwater wetlands (e.g., bogs, fens, and wet meadows) in the eastern United States. The bog turtle exhibits a suite of life-history traits characteristic of long-lived species that may increase its vulnerability to population declines: low fecundity, high nest mortality, and delayed sexual maturity (Ernst & Lovich, 2009). The species is recognized as one of the rarest and most imperiled turtle species in North America (Herman & Tryon, 1997; Ernst & Lovich, 2009). The species is described as critically endangered on the IUCN Red List (van Dijk, 2011) and is federally Threatened in the United States [turtles in the southern portion of its range are Threatened due to Similarity of Appearance, a designation that confers protection for the turtle but not the habitat they occupy (USFWS, 1997)]. Although quantitative range-wide estimates of abundance are not available, a 90% decline over the course of twentieth century is probable (van Dijk, 2011), likely resulting from combinations of habitat degradation and loss as well as poaching for the pet trade and increased rates of predation by human-subsidized mesopredators (USFWS, 2001).

Project Bog Turtle and The North Carolina Wildlife Resources Commission have performed long-term monitoring (>15 years) of many bog turtle populations in North Carolina, USA. A recent publication (Tutterow, Graeter & Pittman, 2017) analyzing these data suggests that the eight most intensively studied populations have generally low, but variable recruitment patterns as well as lower adult survival rates when compared to bog turtle populations elsewhere (Shoemaker *et al*., 2013). Adult survival rates for bog turtles in North Carolina were also lower than estimates for the closely related spotted turtle *Clemmys guttata* (Enneson & Litzgus, 2008). Minimum Viable Population (MVP) abundance thresholds generated for stable bog turtle populations in New York (Shoemaker *et al*., 2013) suggest that several of these populations in North Carolina are at risk of extirpation. Other populations in North Carolina have abundance estimates above this MVP threshold but have survival estimates and demographic characteristics indicative of decline. These data suggest more study of the populations in North Carolina is warranted.

Population models that incorporate survival estimates for each bog turtle life-stage would be useful to determine population status and to investigate where management efforts should be focused to stabilize or bolster bog turtle populations. We used stage-based population projection matrices to examine the effects of estimated annual survival on population growth rates (λ) for five bog turtle populations in North Carolina. Additionally, we examined the implications of altering vital rates within these stage-based models in a way that mimicked potential recruitment-focused management actions to understand the value of such efforts to the focal populations (Enneson & Litzgus, 2008).

Materials and methods

Study area

We built matrix models for five well-studied bog turtle populations located in western North Carolina, USA. Study sites vary in size but are generally thought to have limited connectivity to other wetlands due to intensive ditching, development, and other factors (Weakley & Schafale, 1994; Stratmann, Floyd & Barrett, 2019). While a loss of wetland habitat is commonplace across the region, some larger sites (≤1.25-ha) exist within mostly intact agrarian landscapes characterized by a mosaic of woodland and pasture, while others are wetland fragments (~0.3-ha) nestled within developed areas. All wetland sites maintain a strong groundwater connection and have a diverse open-canopy, floral community with patches of woody shrubs interspersed amongst emergent vegetation. Sites A & B remain under a continuous moderate grazing plan at ~1.8 cattle/hectare. Sites D has been actively managed via goat grazing or manual vegetation thinning every 3–4 years for the last 20 years. Cattle were excluded from Site H in 2006, which has resulted in approximately 40% of the wetland becoming overgrown with woody vegetation. Site E has a history of moderate grazing pressure (see Pittman *et al*., 2011) and was under active woody vegetation management since 2006. These properties are either owned privately or by land conservancy organizations.

The five focal sites are a subset of sites evaluated in Tutterow *et al*. (2017). We follow their naming convention to facilitate comparison and future study. Compared to other known bog turtle sites in North Carolina, Sites A and B possess two of the three most robust bog turtle populations known in the state (Tutterow *et al*., 2017). These populations exist off the Blue Ridge Escarpment approximately 4.3 km from each other at 416- to 547-m elevation. Data collected in 1996–2017 indicated that juveniles were highly represented in both populations (observed juvenile fractions > 0.4) and juvenile survival (0.81 and 0.77, respectively) was an average of 38% higher in these populations than in Sites D and E (values derived from Tutterow *et al.*, 2017 and more recently collected data; see ‘Materials and methods’ section). Sites A and B experienced successful recruitment in each of the last 10 years, determined by counting growth rings over the 2016–2017 field seasons, and egg survival rates were high in 2016 and 2017 (62 of 120 eggs survived to yield a 0.52 pooled average egg hatch rate; Knoerr, Graeter & Barrett (2021)).

Sites D and H exist at higher elevations (approximately 954 and 869 m, respectively). Site D houses one of the three largest populations known in the state. Both populations are dominated by older turtles (median estimated age >25 years) with an obvious recruitment event having also occurred 10–12 years ago at both sites. Juveniles represented 10%–20% of total encounters at Site D from 2003 to 2017, and at site H from 1992 to 2017. Similar to Daigle & Jutras (2005), we believe that the lower proportion of juveniles encountered likely reflects less recruitment in these populations. Juvenile survival is estimated to be 0.49 at site D and is not empirically available for Site H. Egg survival was <0.01 (1 of 106 eggs hatched) at Site D in 2016–2017 and 0.15 (4 of 26 eggs) at Site H in 2017, with losses primarily due to predation by skunks at Site D and small mammals at Site H (Knoerr *et al.*, 2021).

Site E harbors a highly isolated population of bog turtles in the North Carolina piedmont at 218 m elevation. The population declined from an estimated 36 turtles in 1994 to 11 turtles in 2007 (Pittman *et al.*, 2011). Based on exhaustive sampling from 2012 to 2015, this population appears to be primarily comprised of older adults (median estimated age > 25 years). This population has a lower proportion of juvenile captures and lower juvenile and adult survival rates relative to Sites A and B (Tutterow *et al.*, 2017). Fewer than 10 turtles were estimated to exist in site E as of 2019.

Collectively, these five sites represent the broadest range of demographic states for bog turtle populations in North Carolina, from highly abundant populations that display annual recruitment to a nearly extirpated population with limited recruitment observed in recent decades (Tutterow *et al.*, 2017). Long-term (>15+ years) monitoring data suggest that the demography and status of these populations (particularly Sites H and E) may be representative of many others in the region (Graeter, unpublished data).

Matrix model

We parameterized deterministic 3 × 3 stage-based population projection matrices to examine demographic effects of different management scenarios in each population (Caswell, 1989). We defined life stages as: (1) eggs/hatchlings, (2) juveniles (<80-mm carapace length; CL), and (3) adults (≥80-mm CL), according to a published age of sexual maturity for the species (Ernst, Barbour & Lovich, 1994; Whitlock, 2002). Although there appears to be some variation among sites in growth patterns that correlate with changes in elevation and temperature, our data suggest that many turtles reach 80-mm CL by approximately year seven. We define the egg/hatchling stage as beginning when eggs are laid (~June 15) and persisting until April 15 (10 months) of the next year. The stage-based matrix (A) contained the following parameter structure:

$$A = \begin{bmatrix} 0 & 0 & F_3 \\ P_{21} & P_{22} & 0 \\ 0 & P_{32} & P_{33} \end{bmatrix}.$$

F_3 is the fecundity of adult females and P_{ji} is the probability that individuals in class i survive and transition into stage j (Enneson & Litzgus, 2008). The projected population growth rate (lambda; λ) is the dominant eigenvalue, the stable stage distribution (i.e., the proportion of individuals in each stage class when λ stabilizes) is the right eigenvector, and the reproductive value (i.e., the relative contribution of individuals in each stage class to future population growth) is the left eigenvector of the matrix (Morris & Doak, 2002). The stage-based matrix was a females-only model, which is consistent with other demographic studies using matrix population models for species with polygamous mating (Enneson & Litzgus, 2008; Hyslop *et al.*, 2012).

To determine the life stage that contributed most to bog turtle population growth, we conducted elasticity analyses for each population. The elasticity matrix estimates the proportional sensitivity of each stage class, and accounts for differences in the scaling of sensitivity values among different vital rates (Morris & Doak, 2002). When a matrix element corresponds to a high elasticity value, small changes to the associated vital rate will result in larger changes to λ. We calculated all matrix parameters, including λ, stable stage distributions, reproductive values, and stage class sensitivities (effect of additive change in survival on population growth) and elasticities with the popbio package in R (Stubben & Milligan, 2007; R Core Team, 2017).

Parameter estimates

Four of the five sites from this study were monitored for egg survival. Eighty-three bog turtle nests were found in 2016–2017 through radio-telemetry, thread spooling, and nest searching (Knoerr *et al.*, 2021). The number of eggs in each nest was recorded at first discovery, generally (>80%) within 12 h of nesting, providing an estimation of clutch size. Site-specific and regional average egg survival was estimated by monitoring egg fate throughout each summer (2016–2017) with camera trap and visual inspection (Knoerr *et al.*, 2021). Site E was excluded from the nest study as adult female abundance was too low to develop meaningful egg survival estimates. Thus, we set Site E egg survival to the regional average.

We estimated fecundity using the following equation (Enneson & Litzgus, 2008):

$$F_3 = (\text{avg.clutch size}) \times (\text{avg.clutchfrequency}) \times (\text{adultsurvival}) \times 0.5.$$

We generated site-specific clutch sizes (2.96–3.77 eggs) for sites where we detected at least eight nests. Clutch frequency (0.85) was derived by palpating all captured adult female turtles in June 2016 and 2017 in the four intensively studied populations to determine if females were gravid (Knoerr *et al*., 2021). Because encounter data are slightly female-biased (Tutterow *et al*., 2017), we estimated annual adult survival for each NC bog turtle population individually and found no evidence of sex-specific differences in survival. Considering that bog turtle sex is genetically determined (Literman *et al*., 2017), sex-specific differences in survival may exist at the juvenile stage (Tutterow *et al*., 2017). For our model, we assumed a 1:1 sex ratio and halved the estimate of annual fertility to account for the use of a female-only model.

Bog turtle hatchling survival rates have not been estimated empirically, but it is well-documented that hatchling turtle survival overall is significantly lower than that of later life stages. Shoemaker *et al*. (2013) estimated egg and hatchling survival to be low (0.33) for stable New York bog turtle populations. Other studies estimated or documented low hatchling survival estimates (0.11–0.42) for other semi-aquatic turtle species (Congdon, Dunham & van Loben Sels, 1993; Paterson, Steinberg & Litzgus, 2012; Dragon, 2015). Because we hypothesized that there would be site-specific variation in survival at this life stage, we calculated hatchling survival as 0.40 times the site-specific juvenile survival estimate (0.2–0.33). Subsequent sensitivity analyses (Fig. 1) suggested that altering this estimate ±0.20 would have had limited influence on a populations capacity to reach $\lambda = 1$. We scaled this adjusted annual parameter to an 8-month period and multiplied it by egg survival to calculate an estimate for the egg/hatchling stage (P_{21}).

A previous study leveraged long-term recapture data to produce site-specific juvenile and/or adult apparent survival estimates for the populations presented here (Tutterow *et al*., 2017). We obtained annual estimates of adult survival within the five populations using open population Cormack-Jolly-Seber models (CJS; Lebreton & Cefe, 2002) in Mark, a program which can estimate year-specific apparent survival and recapture parameters using mark-recapture records (Version 6.2; White & Burnham, 1999), as described by Tutterow *et al*. (2017) in a size-based analysis (Supporting Information Appendix S1). We chose to leverage the CJS approach of Tutterow *et al*. (2017) since it was already established in the literature as a reasonable approach to estimating survival. P_{33} was set equal to the annual adult survival rate because we did not include a maximum age in the model. We used multistate capture–recapture analyses (Lebreton & Cefe, 2002) that allowed individuals to transition from juvenile (<80 mm CL, corresponding to approximately 1–6 years) to adult (≥80 mm CL, corresponding to approximately 7+ years) stages during each annual sampling period to estimate juvenile survival probabilities (σ_j) and juvenile transition probabilities (ψ) for Sites A, B, D, and E. We used the top-ranked CJS model to inform our multistate analyses (Tutterow *et al*., 2017). Because we had insufficient data to generate juvenile survival at Site H, we took an average of the four other empirically estimated juvenile survival estimates to derive this site-specific vital rate. The multistate transition probabilities had narrow confidence intervals for Sites A and B but wide confidence intervals around values not deemed biologically feasible for Sites D and E. Thus, for Sites D, E, and H, we generated transition probabilities by deriving the mean survival:transition ratio for Sites A and B, and then dividing site-specific survival at Sites D, E, and H by this ratio. To calculate the probability of juveniles surviving and persisting in the juvenile class (P_{22}), we used the following equation derived from (Enneson & Litzgus, 2008) where:

$$P_{22} = (1 - \psi) \times \sigma_j.$$

Next, we calculated the matrix element P_{32} as the product of ψ and σ_j, which represents the probability of transitioning from the juvenile to adult stage, conditional on survival (Morris & Doak, 2002).

$$P_{32} = \psi \times \sigma_j$$

Parameterizing the stage-based matrix

We generated three alternative stage-based matrix parametrizations to model three-egg survival scenarios for each of the populations. First, we generated site-specific lambda (λ) values by using site-specific parameters. We interpret values of $\lambda \geq 1$ as stable and <1 as declining but acknowledge that this method ignores sampling variance associated with all parameters that go into the matrix model, therefore, we cannot provide estimates of uncertainty around our point estimate of lambda. We then generated a second round of lambda (λ) values where we replaced the observed site-specific egg survival estimate, which may fluctuate in any given year, with the regional average egg survival estimate to assess the effects of this more moderate estimation on population growth. As juveniles are less frequently encountered than adults (Shoemaker *et al*., 2013), we aimed to generate stable stage distributions that equaled or exceeded the raw proportion of juveniles observed in our study sites. In the case of Sites A and B, the observed proportion of juveniles exceeded the proportion of juveniles estimated to exist under the regional average model. Thus, we generated a third model specifically for the eigenvalue analysis where we incorporated the pooled average egg survival at Sites A and B for those sites ('High') and the regional average egg survival for the remaining sites ('Average'). We refer to this as the 'High vs. Average' egg survival model (see Supporting Information Appendix S1).

Incorporating management scenarios

To evaluate the efficacy of potential management strategies to improve bog turtle population growth rates, we varied egg survival in the matrix models using the hatching success of eggs from three 'recruitment augmentation scenarios': (1) eggs protected with predator excluder cages in the field (protected eggs), (2) eggs incubated in the laboratory (lab-incubated eggs), and (3) a 1-year head-start scenario.

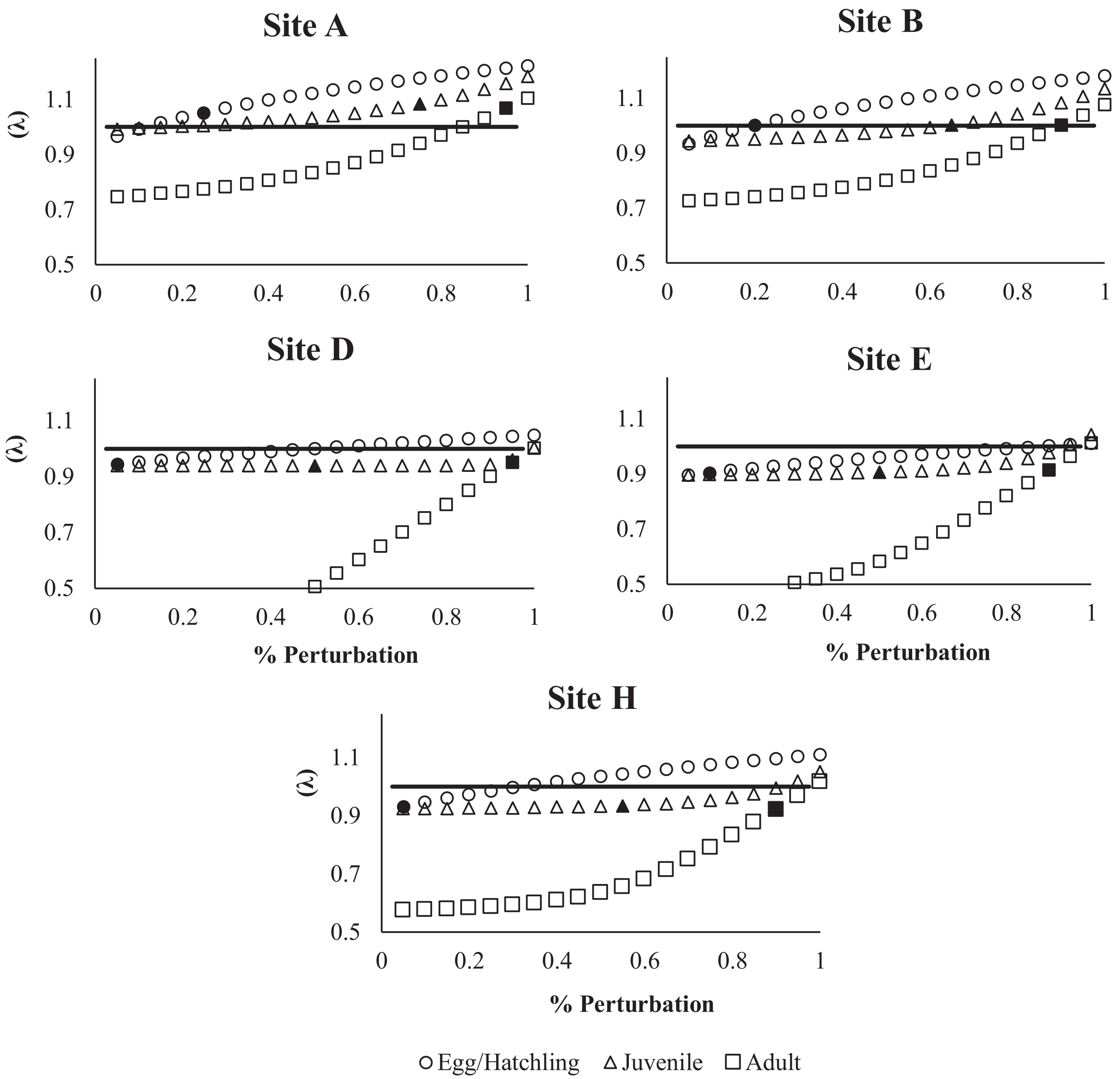

Figure 1 Sensitivity curves demonstrate incremental change (from 0% to 100%) to survival probability of each stage (egg/hatchling, juvenile, adult) and the effects on population growth rate (λ) in stage-based matrix models for five bog turtle populations in North Carolina. Solid horizontal line represents $\lambda = 1$. Solid symbols represent site-specific observed survivorship values. The vital rate estimates at other life-stages are held constant at these observed values when perturbations are made.

Each recruitment augmentation scenario assumed 0.70 of available nests are recovered for management intervention in each respective wetland (except Site A, where we modeled 0.40 nest recovery due to greater abundance), which translates to a maximum of 25 nests recovered when incorporating site-specific abundance estimates and clutch frequency (our field observations suggests that 0.7 recovery is feasible when intensively monitored). For protected eggs, we model 0.40 average egg survival, which is based on recent observations (Macey, 2015; Zappalorti *et al*., 2017). If observed unprotected egg hatch success was above the 0.40 estimate (as occurred at Sites A and B), the protected egg survival estimate was conservatively set 10% above the site-specific one. Similarly, data averaged from Macey (2015) and Zappalorti *et al*. (2017) derived a lab-incubated egg survival estimation of 0.81. The head-start scenario also assumed 0.81 average egg survival and 0.95 hatchling survival during captivity (Ogle, unpublished data). Because released 1-year head-started turtles would be approximately equal in size to wild 3-year old bog turtles (M. Ogle, unpublished data), we set released head-start survival probabilities equal to the site-specific juvenile survival estimate. We also increased head-start model transition probabilities by 1.17 times the site-specific estimate because we predict these turtles will spend 2–3 fewer years in the juvenile stage. Finally, survival of eggs not recovered for management efforts and left in situ in the wild (0.60 for Site A and 0.30 for remainder) was set equal to the ‘High vs. Average’ egg survival parameterization.

The resulting egg/hatchling survival equation for a recruitment augmentation scenario involving all sites except Site A (where proportion of eggs recovered = 0.40 and eggs remaining in their wild state = 0.60):

$$\begin{aligned} P_{21} &= \left(\left(\sigma_{\text{art.incubation}} \times \sigma_{\text{captive hatchling}} \times 0.7\right)\right) \\ &\quad + \left(\left(\sigma_{\text{high/avgegg}} \times \sigma_{\text{8monthhatchling}}\right) \times 0.3\right). \end{aligned}$$

We calculated site-specific λ values for each recruitment augmentation scenario. In addition to examining the success of potential conservation measures, we generated sensitivity curves to evaluate the effects of incremental changes to vital rates (i.e., egg, juvenile, and adult survival) on λ. To create the sensitivity curves for each site, we perturbed each vital rate individually while other vital rates retained original values. We considered the matrix model with the hatching success of unprotected eggs as the ‘original’ matrix that we altered by perturbing vital rates in increments of 5% (from 0% to 100%). We recalculated λ after each perturbation trial.

Results

Average clutch size for the 83 nests recorded across the region was 3.28 eggs/nest. The regional average egg survival was approximately 0.28. Site-specific stage-based parameters for various conservation scenarios related to egg survival as well as juvenile survival, adult survival, and transition probabilities are provided in the Supporting Information Appendix S1.

The stable-stage distribution results estimated with the ‘High vs. Average’ egg survival model suggested that Sites A and B should have the largest proportion of individuals in the juvenile stage (0.24 and 0.28, respectively), while Site D is estimated to have the lowest (0.09). Excluding eggs and hatchlings, these estimates translated to approximately 48% juveniles at Site B and 20% at Site D, a slightly higher proportion than what we have observed in field encounters at these sites.

The reproductive values of adults were similar for Sites A and B, with adults contributing 10–13 times more to future population growth than eggs and hatchlings. The reproductive value of the adult class for Sites D, E, and H was greater, with adults contributing 36–96 times more to future generations than eggs and hatchlings (Table 1).

Elasticity analyses indicated that survival of the adult class (P_{33}) proportionally contributed the most to population growth rate (Table 1) with adult survival elasticities above 0.7 for all sites. Juvenile survival (P_{22}) contributed at least twice as much to population growth at Sites A and B than the other three sites. Juvenile survival elasticities ranged from 0.025 at Site D to 0.22 at Site B.

Table 1 Stable stage distributions (the right eigenvector), reproductive values (the left eigenvector), and elasticity values from stage-based population projection models for five bog turtle populations in North Carolina using the ‘High vs. Average’ egg survival model, where we pooled average egg survival at Sites A and B for those sites (‘High’) and the regional average egg survival for the remaining sites (‘Average’)

Site	Egg/hatchling	Juvenile	Adult
Stable stage distribution			
A	0.402	0.240	0.358
B	0.424	0.279	0.297
D	0.521	0.094	0.386
E	0.517	0.106	0.377
H	0.494	0.138	0.368
Reproductive values			
A	1	4.29	10.15
B	1	4.28	12.87
D	1	10.22	95.76
E	1	9.61	77.52
H	1	8.47	35.65
Elasticity values			
A	0.079	0.159	0.717
B	0.078	0.219	0.703
D	0.014	0.025	0.961
E	0.017	0.033	0.950
H	0.033	0.079	0.887

The stable stage distribution depicts a constant proportion of individuals in each stage class through time. The reproductive value is the relative contribution to future population growth an individual in a particular class is expected to make. Elasticities of vital rates show the proportional contribution of each stage class to overall population growth rate (λ).

The sensitivity curves demonstrated the proportional effects of vital rate perturbations on λ and corroborated that a small change to adult survival resulted in the greatest change to λ (Fig. 1). Effects of adult survival increased as a population experienced greater decline. At Site D for example, a 10% decline in adult survival reduced λ by approximately 10%, while a 10% decline in egg and hatchling survival reduced λ by approximately 1%. However, except at Site E, high survival of egg and hatchlings resulted in the greatest population growth rate under no improvement to adult or juvenile survival. For example, under a best-case scenario of 100% egg and hatchling survival, Site A experienced 22% in population growth rate compared to 18% or 11% growth under scenarios of 100% juvenile or adult survival, respectively. For Site E, egg and hatchling survival had a limited effect on population growth rate, and population stability only occurred when juvenile or adult survival approached 100% (Fig. 1).

For sites A and B, sensitivity curves demonstrated that if other vital rates remain constant, Site A could absorb an 8% decrease in adult survival, while nearly any decrease in adult survival at Site B was projected to lead to population decline

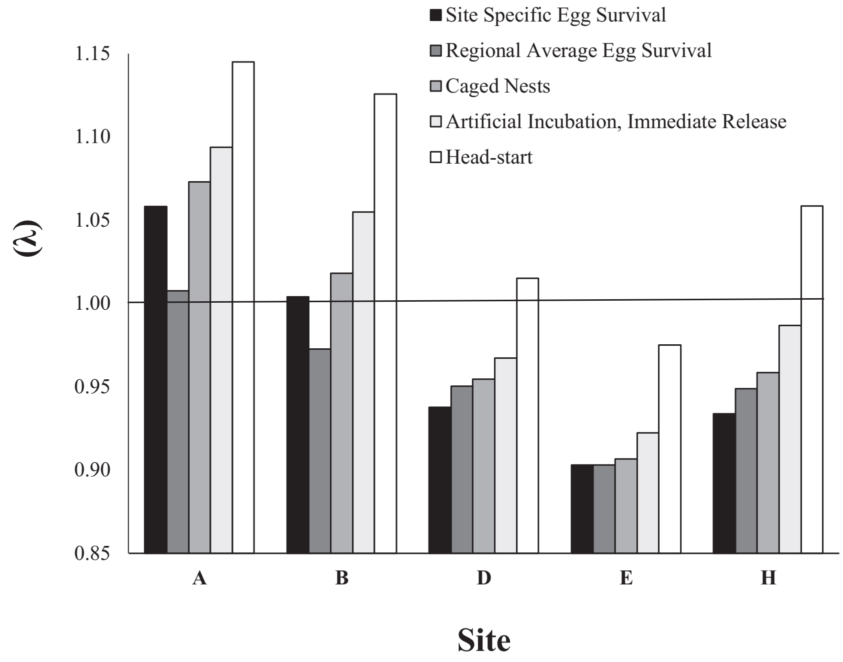

Figure 2 The effect of potential management scenarios targeting bog turtle recruitment (unprotected nests at site-specific and average egg survivorship, nests protected with predator excluder cages, lab-incubated eggs, and lab-incubated/head-started turtles) on population growth rate (λ) in stage-based matrix models for five bog turtle populations in North Carolina.

(Fig. 1). Population growth rates for all remaining sites were estimated to be <1 (Fig. 2). For each of these sites, substantial increases would be required in any one stage to yield a positive λ, and in some cases, no amount of increase at one life stage resulted in $\lambda > 1$. Site E would require particularly significant intervention, with a 10% increase in adult survival or a 90% increase in egg and hatchling survival needed to result in a $\lambda > 1$.

Under site-specific hatching conditions, both Sites A and B were the only populations estimated to be stable or experiencing population growth ($\lambda = 1.06$ and 1.00 respectively) (Fig. 2). Sites D, E, and H appear to be experiencing 6%–10% annual decline ($\lambda = 0.94$, 0.90, and 0.93, respectively). Protection of eggs with predator excluder cages resulted in marginal increases in λ but did not stabilize any of the declining populations. For sites experiencing extensive nest predation (D and H), caging nests increased population growth rates by approximately 2%. Lab-incubating eggs substantially improved λ for Sites A, B, D, and H, which exhibited 3–5% increases in population growth (Fig. 2). The head-start scenario resulted in the largest increases to population growth rate (6.4%–14.4%), and was the only potential management strategy modeled that stabilized or grew all populations except Site E (Fig. 2).

Discussion

Of the five bog turtle populations modeled, we found only two that exhibited stability or growth when incorporating site-specific vital rates (Sites A and B). As evidenced by capture data, recruitment has been continuous for at least a decade at sites A and B, and successful recruitment likely results from lower nest predation, moderate incubation temperatures (Knoerr *et al.*, 2021), and high juvenile survival (Tutterow *et al.*, 2017). Our results for Sites A and B demonstrate how population stability can be maintained even when adult survival declines (Fig. 1). For both of these populations, survival estimates for the egg and juvenile life stages are high, as are transition probabilities, effectively compensating for low to moderate adult survival (0.902–0.935). Site B appears to be in a more precarious state because nearly any decreased survival at any stage is projected to lead to population decline. As stochasticity was not incorporated into these models (beyond what the long-term nature of the data partially accounts for), it is probable that catastrophic events could lead to decline of these populations, particularly Site B. Because we did not model variance around matrix parameters, in any given year a population we estimated as $\lambda \geq 1$ has some probability of being in decline, and populations with lambda <1 have some probability of being stable, particularly when estimates of lambda are close to 1.

Longevity and iteroparity are thought to have historically buffered turtle populations against high mortality at the vulnerable egg and hatchling stages (Congdon *et al.*, 1983). These life-history traits allow turtles to persist through harsh years and compensate with higher fecundity during favorable years (Litzgus, 2006), effectively smoothing inter-annual changes in population growth rate. This evolutionary strategy is theoretically dependent upon extremely high adult survival

(Congdon & Gibbons, 1990; Heppell, 1998, Crowder & Crouse, 1996, Roff, 2002). Shoemaker *et al.* (2013) concluded that stable New York bog turtle populations had annual adult survival estimates of about 96%. It was estimated that adult survivorship needed to be ≥ 96% for wood turtle *Glyptemys insculpta* populations to remain stable or grow (Jones *et al.*, 2015). Enneson & Litzgus (2008) predicted population decline for a stable Ontario spotted turtle population if adult survival fell below 93%. The adult survival and associated λ values estimated for some bog turtle populations in North Carolina are estimated to be lower than these representative benchmarks (Tutterow *et al.*, 2017; Fig. 2). In some populations, the factors that reduce survival at the adult stage, such as poor habitat conditions, may simultaneously impact other stages. Thus, adult and juvenile survival can be highly correlated (Pike *et al.*, 2008). Nevertheless, some level of lower adult survival can be tolerated when survival is inflated at other life stages (Fig. 1), as is the case of the stable populations modeled in this study.

Several population modeling studies of turtles have shown that small increases in adult mortality may destabilize populations (Crouse *et al.*, 1987; Heppell, 1998; Enneson & Litzgus, 2008; Keevil *et al.*, 2018; Howell *et al.*, 2019). High elasticity values (0.70–0.96) across all sites, but particularly at Sites D, E, and H clearly support the relative importance of adult survival to population stability for bog turtles (Table 1). Estimated population growth rates varied greatly among sites, with some estimates low enough to suggest dramatic management intervention will be necessary to stabilize populations. Targeted efforts to increase recruitment at Sites D and H may increase population growth rate or stabilize these populations (Figs 1 and 2). Site E had such low underlying vital rates that it is likely to continue precipitous declines under the management scenarios presented here unless increases in survival occur at multiple life stages (Fig. 1).

Estimating reasonable survival probabilities for head-started turtles compared to their wild counterparts was critical to assessing the effect of a head-start initiative on population growth rates. Several sources have recorded comparatively high survival for head-started turtles (Kuhns, 2010; Michell & Michell, 2015; Dresser, Ogle & Fitzpatrick, 2017). Head-started 9-month-old turtles in Tennessee are thought to be similar in size to their 3-year-old wild counterparts (M. Ogle, unpublished data); thus, we adjusted the estimate of transition probability to reflect the reduced time in the juvenile life stage. It should also be noted that as low abundance populations can be disproportionately influenced by Allee effects (Berec, Boukal & Berec, 2001), and the juvenile survival estimate for Site H was an average of the other four sites, the population growth rate estimated under current and management conditions may be lower than what was modeled. We also chose to model these populations without estimates of immigration (Tutterow *et al.*, 2017) since we believe such events have a very low probability of occurrence (Shoemaker & Gibbs, 2013; Smith & Cherry, 2016). The distances between these populations and their nearest known neighboring populations (>4.3 km straight-line distance, with the exception of Site B) exceed the average home ranges and most successful immigration distances recorded for bog turtles (Carter, Hass & Mitchell, 2000; Morrow *et al.*, 2001). If immigration is a factor, it is most likely to occur in the populations modeled to be stable, particularly site B (nearest population 0.93 km straight-line distance). Immigration is least probable in the populations where intervention has most utility. In addition, the multistate capture-recapture analysis did not provide reasonable transition probability estimates for Sites D or E. We derived a method of adjusting the estimates (see 'Materials and methods') that we deemed preferable to other methods (Crouse *et al.*, 1987; Caswell, 1989), which estimated the transition probability as a function of the stage-specific survival probability and the duration of the life stage. The approach of Crouse *et al.* (1987) and Caswell (1989) would have resulted in more conservative transition probabilities than we derived with our analysis. The early methods (Crouse *et al.*, 1987; Caswell, 1989) may have contributed to the historical perspective that head-start programs have limited conservation utility for turtle species (Heppell, Crowder & Crouse, 1996).

Increased recruitment may substantially contribute to some populations improving population growth rate or reaching stability in a given year. Of the management tools evaluated, head-starting was the most effective for improving population growth rate. The historical perspective on the utility of turtle head-start programs to stabilize populations was generally critical (Mrosovsky, 1983; Woody, 1990; Frazer, 1992; Heppell *et al.*, 1996), in part because the approach does not ameliorate the actual threats driving population decline (i.e., it is a 'halfway technology'; Frazer, 1992). Some critiques of recruitment augmentation appear to be based on strict assumptions, such as Shoemaker (2011), where head-started bog turtles were assumed to have survival rates and juvenile periods equal to their same-aged (not same-size) *in situ* cohort. Our modeling approach posited higher juvenile survival rates and subsequent results highlight the need to strongly consider the value of head-start programs.

Recent studies of freshwater turtles have concluded that caged nest and head-start initiatives may be valuable tools to address recruitment problems, increase turtle numbers, and stave off extinction threats (Spinks *et al.*, 2003; Kuhns, 2010; Riley & Litzgus, 2013; Buhlmann *et al.*, 2015; Spencer *et al.*, 2017). Enneson & Litzgus (2008) conducted a stage-based matrix analysis on a stable spotted turtle population in Ontario, Canada and found that protection of eggs may be an efficient conservation strategy when egg or juvenile survivorship was below 0.29 and 0.69, respectively. Models developed by Spencer *et al.* (2017) provided support for head-starting eastern long-necked turtles *Chelodina longicollis* and they suggested that it could be an effective primary management tool in a broad-scale, integrated plan. Importantly, this analysis and others (Kuhns, 2010) suggest that when survival is not increased elsewhere, turtle populations will begin to decline immediately after head-starting initiatives cease. An effective conservation solution will be implemented when the multiple threats facing different life stages are concurrently addressed (Crawford *et al.*, 2014).

Conclusions

Our results suggest that management plans targeting an endangered freshwater turtle will be improved when tailored to site-specific dynamics. For some sites, recruitment augmentation (especially a head-start scenario) may help declining populations reach stability or grow (Figs 1 and 2). Population growth rates will likely be higher when recruitment efforts coincide with management (such as vegetative and hydrological restoration; Stratmann *et al.*, 2019) that increases survival and site fidelity at other life stages. Some of our study sites have a high probability of extinction and are unlikely to stabilize via any in-site recruitment augmentation efforts alone (Fig. 2; Shoemaker *et al.*, 2013). Deciding whether captive breeding and/or translocation are viable tools for such populations is an open question because regional and local habitat issues may have created a population sink (Schwartz *et al.*, 2012). As financial resources are limited, choosing conservation actions at one site may preclude action at others (Wilson & Law, 2016). The analyses performed help managers make informed decisions as to where and how they might maximize available resources within region-scale conservation plans for at-risk species.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Vital rates used in the stage-based matrix population models for five well-studied bog turtle populations in North Carolina.