8-2018

Hatch Success and Population Modeling for the Critically Endangered Bog Turtle in North Carolina

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Recommended Citation

Knoerr, Michael Donald, "Hatch Success and Population Modeling for the Critically Endangered Bog Turtle in North Carolina" (2018). *All Theses*. 2930.
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HATCH SUCCESS AND POPULATION MODELING FOR THE CRITICALLY ENDANGERED BOG TURTLE IN NORTH CAROLINA

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Wildlife and Fisheries Biology

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by
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August 2018

Accepted by:
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ABSTRACT

Recent literature suggests that several North Carolina bog turtle (*Glyptemys muhlenbergii*) populations are in decline, and many of these populations have few remaining individuals with low annual survival probability. Most populations appear dominated by older adults with few juveniles encountered; however, the proportion of juveniles encountered at two populations is dramatically higher. The reason for this variability is unknown. We conducted a nest monitoring study in 2016 and 2017 to test the hypothesis that nest survival patterns explain the observed population age structure. We collected the largest dataset yet compiled on the fate of naturally-incubated bog turtle eggs as well as the first study of its kind in North Carolina. Predation was the primary driver of nest failure across all sites. Populations with more juvenile encounters had substantially higher egg survival. These observations support the hypothesis that variation in egg survival may be linked to observed variation in recruitment patterns. We subsequently incorporated site-specific population parameters, including site-specific egg survival, into a stage-based matrix model to estimate population growth rates and to assess potential management scenarios for five bog turtle populations. Only two of the five populations modeled were stable or growing under current vital rates. Our results demonstrated that management scenarios targeting increased recruitment (especially a head-start scenario) may substantially contribute to some populations reaching stability. Population growth rates will likely be higher when recruitment augmentation coincides with wetland restoration efforts that increase survival and site fidelity at other life stages.

DEDICATION

I dedicate this thesis to my mother Nancy. You supported my love for turtles and nature early on. You gave me opportunities to pursue my passion, even when you didn't fully understand it. You brought me camping in Michigan when I was 13 in search of beautiful rivers and the mythical wood turtle (the other *Glyptemys*). I promise that you will have a waterproof tent the next time we camp in the north woods.

ACKNOWLEDGEMENTS

This project stems from decades of field labor-a labor of love- by over a dozen individuals who are passionate about bog turtle conservation. It was these efforts that made my research a reality, as recapture data suggests several populations are in decline. I am indebted to the people that make up Project Bog Turtle, to Dennis Herman for his guidance, and to Annalee Tutterow and Dr. Shannon Pittman for their excellent work proceeding my own. My particular project gained traction via two key people, Gabrielle Graeter and Dr. Kyle Barrett. I am thankful to Gabrielle and the North Carolina Wildlife Resources Commission for supporting this project and trusting me to perform good science while working in North Carolina’s most important bog turtle populations. Dr. Kyle Barrett gave me the opportunity of a lifetime, and offered unwavering support. He also made me a substantially better scientist along the way.

A special thanks to Adam Warwick and The Nature Conservancy for supporting this project and giving me access to their properties. Thank you to Michael Ogle and Zoo Knoxville for providing funding via the Bern Tryon Grant. Thank you to Sue Cameron and Mark Endries of the United States Fish & Wildlife Service for supporting our ongoing research. Thank you to Dr. JJ Apodaca for the guidance and for providing field equipment and technicians. Thank you to Rob Carmichael of the Wildlife Discovery Center for providing radio-telemetry gear. Thank you to Dr. Jeff Wilcox for helping us install hydrological wells in the heat of summer. Thank you to my committee members Dr. Beth Ross and Dr. Cathy Jachowski for your technical support.

An enthusiastic thank you to my field technicians, lab-mates and volunteers. We are able to say something meaningful because of your efforts to collect a robust dataset. Your efforts, day and night, made all the difference. Thank you to: Michael Holden, Cody Davis, Kirsten Brown, Maria Alvarez, Amy Almond, Alison Cercy, Michael Frazier, Sam McCoy, Morgan Harris, Worth Pugh, Dr. Mike Osbourne, Katelyn Pollock, Jill Newman, Joel Mota, David Hutto, Ryan Lubbers, Bryan Suson, and Sam Silknetter. A special thank you to my wonderful fiancé Micaela Scobie who became an expert at finding bog turtles who tolerated my extended absences in the name of turtle conservation.

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CHAPTER 1

HATCH SUCCESS OF THE BOG TURTLE, *GLYPTEMYS MUHLENBERGII*, IN NORTH CAROLINA

Abstract. — Recent literature suggests that several North Carolina bog turtle populations are in decline, and many of these populations have few remaining individuals with low annual survival probability. Most populations appear dominated by older adults with few juveniles encountered; however, the proportion of juveniles encountered at two populations is dramatically higher. The reason for this variability is unknown. We conducted a nest monitoring study in 2016 and 2017 to test the hypothesis that nest survival patterns explain the observed population age structure. We documented the fate of 272 eggs from 83 nests encountered across seven sites. This represents the largest dataset yet compiled on the fate of naturally incubated bog turtle eggs as well as the first study of its kind in North Carolina. Approximately 28% of eggs hatched across all sites over both years. Predation was the primary driver of nest failure across all sites. Both mesopredators and smaller mammals substantially contributed to nest failure. Cooler temperatures, which prolong incubation and thus predation risk, may also hinder recruitment at higher elevation sites. Populations with more juvenile encounters had substantially higher egg survival. Although our dataset is limited, these observations support the hypothesis that variation in egg survival may be linked to observed variation in recruitment in these populations. Reduced vital rates at other life stages may inflate the importance of successful recruitment events in order to maintain population stability.

Introduction

Habitat loss and degradation is the leading cause of species extinction in North America (Diamond 1984; Noss et al. 1995) and among the leading causes of global declines of turtle populations (Gibbon et al. 2000). Land conversion and landscape fragmentation can also increase secondary threats such as genetic isolation, road mortality, and predation by human-commensal mammals on turtles and their nests (Mitchell & Klemens 2000; Gibbs & Shriver 2002; Fahrig 2003; Macey 2015). Semi-aquatic turtle species are particularly susceptible to decline because they have very specific habitat requirements, making their populations vulnerable to habitat alteration (Litzgus & Brooks 2000; Litzgus & Mousseau 2004; Pittman & Dorcas 2009).

Bog turtles (*Glyptemys muhlenbergii*) are a semi-aquatic species found in bogs, wet meadows, and fens (Ernst et al. 1994; Buhlmann et al. 2009; Pittman & Dorcas 2009). In the southern portion of their range, bog turtles are found primarily in fens, referred to as mountain bogs by land managers. These wetlands are among the most imperiled wetland types found in the United States today. Residential development, road construction, and the drainage of these wetlands for agricultural use have resulted in a 90% decline in mountain bog habitat throughout the region such that less than 500 ha remain (Weakley & Schafale 1994; Noss et al. 1995; Herman & Tryon 1997). Many remnant bogs are moderately to highly degraded as a result of nutrient enrichment (Drexler & Bedford 2002; Bedford & Godwin 2003), which promotes the growth of woody vegetation (Kiviat 1978; Lee & Norden 1996; Tesauro & Ehrenfeld 2007) and invasive plant species (Dick 2013). Other forms of degradation include drain tile installation and ditching, extensive beaver activity, overgrazing of cattle, and mining activities (Bedford & Godwin 2003). Together, these events create a continuum of wetlands in different stages of degradation (Stratmann 2015).

Bog turtles are considered to be one of the most imperiled chelonians in North America (Seigel & Dodd Jr 2000; Rosenbaum et al. 2007). Although quantitative range-wide estimates are not available, a 90% decline in bog turtle populations over the course of the 20th century is likely (van Dijk 2011). The bog turtle's geographic range is discontinuous, split into a northern population network (extending from Massachusetts to Maryland) and a southern population network (extending from southern Virginia to northern Georgia (Ernst & Lovich 2009). The northern population network was listed as federally threatened under the Endangered Species Act (ESA) in 1997. While bog turtle habitat in the southern population network does not receive protection under the ESA, southern bog turtles are protected from collection due to a "similarity of appearance" to those in the northern population (Somers 2000; USFWS 2001). Bog turtles are state listed in every state in which they occur and are ranked Critically Endangered by the IUCN Red List of Threatened Species (van Dijk 2011).

A recent study across several North Carolina bog turtle populations (Tutterow et al. 2017) indicated adult survival probabilities were dramatically lower compared to some northern populations of bog turtles (Shoemaker et al. 2013) and closely related species such as the spotted turtle (*Clemmys guttata*; Enneson & Litzgus 2008). These low estimates of apparent adult survival indicate that certain bog turtle populations in NC may be in decline, as small changes in adult survival are known to have the greatest impact on population growth rate for turtles (Congdon et al. 1993; Heppell 2000). Records of juveniles are also absent or rare in most of these sites with the exception of two populations, where > 40% of encounters over more than two decades have been juveniles (Tutterow et al. 2017). The mechanism(s) driving this disparity in proportion of juveniles encountered is not well understood but may be linked to variation in fecundity, nest success, hatchling or juvenile survival (Tutterow et al. 2017). Extended recruitment (defined as turtles transitioning from eggs to hatchlings, hatchlings to juveniles, or juveniles to adults) failures compounded with deflated survival at other life stages may destabilize populations (Congdon et al. 1983; Daigle & Jutras 2005; Chapter 2). Thus, early life-stages may have become an increasingly important limiting factor for many bog turtle populations (Tutterow et al. 2017).

It is widely reported that nest and hatchling survival are dramatically low for most turtle species (Mitchell 1988; Frazer et al. 1990, 1991; Iverson 1991b; Congdon et al. 1993; Paterson et al. 2012; Dragon 2015; Spencer et al. 2017). Predation is recognized as a major source of freshwater turtle nest failure (Congdon et al. 1983; Marchand & Litvaitis 2004). Although multiple taxa have been identified as predating turtle nests (Buhlmann & Coffman 2001; Butler et al. 2004; Draud et al. 2004), mesopredators appear to be the greatest source of nest predation in many systems (Snow 1982; Congdon et al. 1983; Christens & Bider 1987; Temple 1987; Robinson & Bider 1988; Feinberg & Burke 2003). Changes in vegetation and hydrology decrease available nesting area and likely elevate mesopredator densities, both of which may further increase probability of nest predation beyond the historical norm (Temple 1987; Kolbe & Janzen 2002b; Marchand & Litvaitis 2004). Infertility, flooding, heat stress, and an inadequate thermal environment are additional sources of nest failure (Christens & Bider 1987) and are likely linked to both landscape and in-site characteristics.

We hypothesize that reduced egg survival is primarily driven by mesopredators and that these predation events may dampen bog turtle recruitment rates. We also hypothesize that some wetland-scale habitat characteristics may increase predator access to and detection of bog turtle nests. In addition, as these focal populations represent a wide elevation gradient, we hypothesize that a colder thermal nest environment will result in longer incubation periods that reduce probability of egg survival. The purpose of this research was to evaluate the above hypotheses via intensive nest monitoring over a two-season period.

Study Area

The wetlands studied here are located in western North Carolina, USA. The exact locations of these populations (defined as a group of turtles living in a particular wetland) have been withheld due to poaching concerns. Although we monitored nests across seven sites during the 2016 and 2017 field seasons, most nest observations came from four locations, sites identified as A, B, D, and H in Tutterow et al. (2017). These sites range from high elevation populations in the Blue Ridge Mountains, to lower populations off the Blue Ridge Escarpment. These wetlands are owned privately or by land conservancy organizations.

Sites A and B are lower elevation populations that exist off the Blue Ridge Escarpment at 416 – 547 m in elevation. Encounter data suggest that these sites are likely two of the most robust bog turtle populations in the state. Age estimated by counting scute annuli over the 2016 and 2017 field seasons indicate successful recruitment in each of the last 10 years. Juveniles were highly represented in both populations over the course of this study (observed juvenile fractions > 0.4).

Sites D & H are high elevation populations (approximately 869 and 954 m, respectively). As evidenced by encounters over the 2016 and 2017 field seasons, both populations are dominated by older turtles (median age >25 years) with an obvious recruitment event having also occurred 12 – 14 years ago at both sites as estimated by counting scute annuli. Juveniles represent 0.1 – 0.2 of total encounters at Site D from 2003 – 2017 and Site H from 1992 – 2017.

Collectively, these sites represent a range of bog turtle population demography. The demography and status of our aging populations, particularly Site H, appear representative of many other populations in the region. Although other populations in NC are likely in greater risk of extirpation, the underlying abundance in those populations is so low as to limit our ability to draw inference as it relates to egg survival. For this reason, only populations where encounter data over the past 10 – 15 years suggests an abundance of at least 15 adult turtles (North Carolina Wildlife Resources Commission, unpublished data) were included for intensive nest monitoring.

Methods

Field methods

We primarily found bog turtles by probing (Carter et al. 1999) and visual encounters. Trapping was also employed at lower abundance sites. Traps consisted of non-baited wire mesh devices that were placed in rivulets and other wet areas (Somers 2008). The bottom of the traps were partially submerged (1 – 2 cm) in water and were covered with vegetation to prevent overheating of trapped turtles. The traps were checked daily. We searched each wetland an average of 30 hours per week from May 15 – June 15 in both years. All females were palpated in May, June, and July to determine whether they were gravid. Most female turtles that were of adequate size or had signs of gravidity were monitored via radio-telemetry with a 3.6 gram R1680 model Advanced Telemetry System unit, attached with epoxy putty (J-B Weld-WaterWeld) to the mid/posterior pleural scutes. We tracked these turtles every 2 – 3 days until the first nesting event of the season and then twice a day until they nested. Once the nesting season began, we also employed the use of thread-bobbins to aid in nest recovery. These bobbins were wrapped in cellophane and PlastiDip® (Wilson 1994) and placed on the posterior marginal and pleural scutes utilizing a 5-minute two-part epoxy (Devcon home 5-Minute Two-Part Epoxy). These 150 m thread-bobbins weighed approximately 3 g (3.5 g attached). In order to limit weight related stress, we made sure to keep these devices ≤ 7% of the turtle’s weight, thus we only used this combination on turtles that weighed ≥ 115 g. As the gravid turtles frequently made substantial within-wetland movements through the nesting period, it was important to replace the thread-spool every 1 – 3 days.

We primarily located nests by radio-tracking gravid female turtles in the evenings to their respective nesting areas. Red headlamps were employed after dusk to limit disturbance to nesting turtles. An active turtle at or after dusk suggests nest searching and/or laying behavior. Thus, once the active turtle was observed, we would place flagging on vegetation 1 – 2 m away from the turtle to aid in nest recovery the next morning. Upon return, we would track the turtle and determine if she was still gravid via palpation. If she was no longer gravid, we would carefully check the tussock area where she had been observed the night prior wearing nitrile gloves. If the nest was not found this way, we would backtrack along the thread from her encounter location that day to the previous one approximately 12 hours earlier, carefully searching for disturbed areas along the thread. Twenty nests were also found opportunistically, either by observing females without transmitters laying eggs or by carefully searching in nesting areas.

Once the nest was found (generally within 12 hours of laying), we recorded nest characteristics and counted the number of eggs. At each nest site, we estimated the % standing water within 2 m of the nest and the % scrub or shrub habitat within 0.5 m of the nest. We assigned a value from 0 – 4 (none to maximum density) to represent the density of emergent vegetation and the density of woody stems. Finally, we measured the distance from the nest to the edge of the wetland and to the nearest forest edge. In addition, to record variation in thermal nest conditions across sites and nest inundation, we placed a sealed (PlastiDip®) thermochron iButton (stream-rinsed to remove odor) in the nest tussock or hummock approximately 100 – 150 mm away from the eggs at a comparable depth. We recorded temperature at hourly intervals from first placement until signs of hatching. If the nest was predated, the iButton was left in place until other nests within the wetland hatched. A trail camera (Bushnell Trophy® Cam HD Essential E2) was placed on a stake approximately 1 – 3 m from the nest to record nest predation events. The trail cameras and surface of the nests were periodically checked for evidence of predation through the incubation period. Through the hatching window (August – October), the eggs were periodically exposed to document their hatching status. In order to better assess fertility, eggs that had failed and begun decomposition were opened to determine whether an embryo was present.

Analysis Methods

We categorized the fate of all nests throughout the incubation period. As predation was the dominate source of all failed eggs, we used binary logistic regression (GLM function) to test hypotheses about the relationship between nest predation (a nest was defined as having been predated if ≥ 1 egg was eaten) and environmental conditions within and among sites. Before analyzing the data, we evaluated all bivariate correlations among variables, and eliminated one variable from any pair with a correlation coefficient > 0.70. We also converted all covariate measurements to z-scores prior to analysis. We evaluated six models that represented various hypotheses about the environmental drivers of nest predation (Table 1). In order to generate an overdispersion parameter, we evaluated the global model using a quasibinomial distribution. Because the estimate of the overdispersion parameter was ~1 in that model, all subsequent models used a binomial distribution. We compared the relative support for all models using Akaike information criterion corrected for small sample size (AICtab function, AICcmodavg package in R (Mazerolle 2017). We subsequently created an AICc table for the two best supported models and utilized the modavg function to average the parameter estimates appearing in these models, because the modes had similar AIC support and model weights.

To evaluate hypotheses related to thermal environments of bog turtle nests, we used general linear models (GLM). We considered seven different measures of the thermal environment; however, after eliminating correlated variables ($R > 0.7$) we used only three in our analyses: mean daily nest temperature, mean minimum nest temperature, and mean maximum daily range of nest temperature. We first used a GLM to assess the effect of site and year on temperature variables (glm function, Gaussian family; Car package in R; (Fox 2011) for 55 nests. We compared candidate models using Akaike information criterion (AIC). If we established that a difference existed amongst the means, we utilized the Tukey test (post hoc) for pairwise comparisons. To test for a relationship between thermal environment and incubation period, we applied a GLM to 18 of the 55 available thermal datasets where incubation period was known.

Results

Over 300 individual bog turtles and 83 bog turtle nests (272 eggs) were found across both field seasons. This nest dataset represents the largest yet compiled on the fate of naturally incubated bog turtle nests. Seventy-eight of those nests (252 eggs) came from four sites (Table 2). Approximately 28% of eggs (75 eggs) hatched across all sites over both years. Average egg survival by site ranged from <1 – 56% over both years. The highest egg survival observed at one site (Site A) in a given year was 60%.

Predation accounted for the greatest source of nest failure (Table 2). The two sites with robust data (≥25 eggs per season) over both field seasons showed limited inter-annual change in egg predation, with Site A experiencing 12 and 22% predation and Site D experienced 96 and 84% predation in 2016 and 2017, respectively. As evidenced by both trail camera images of the predators digging up nests and eggshell fragments (Fig. 1), mesopredators accounted for 98 of 144 (68%) predated eggs over both seasons across all sites. Striped skunks (*Mephititis mephitis*) accounted for 92% (48/50) of predated eggs and 84% (47/56) of total egg failure at Site D over both field seasons. Raccoons (*Procyon lotor*) and Virginia opossums (*Didelphis virginiana*) predated nests as well. Collectively, these two species depredated 10 eggs across 4 events (defined as all nests predated by the same predator in a single night) across sites. Of nests with known lay dates, mesopredator events took place 3 – 59 days after laying (mean= 18.6 days).

Small mammals accounted for ~31% of all predated eggs but as much as 100% of predated eggs at Site H in 2017 (85% of the total eggs documented at that site). Multiple small mammal species may have been responsible since there were a wide range of predation signs observed: all eggs missing with no obvious disturbance, single eggs missing, or egg(s) partially chewed on (Fig. 1). Although we do not have photos of these small mammals actively predating nests (small mammal predators either emerge from below the nests or are too small to trigger cameras), we do have photos of them in the wetlands and other physical evidence of their presence (burrows, tracks, scat) around the nests. Of nests with known lay dates, small mammal predation events (as defined above; n=15) took place from the night of laying through egg piping (1 – 94 days, mean= 54 days). Other animal sources of nest destruction include trampling by cows (n = 5) and one case where a nest was exposed and partially predated by a crayfish (*Cambarus sp*.) while excavating its burrow. Other apparent sources of egg failure included flooding, overheating, infertility, and developmental problems (Table 2).

Among nests lost to predation, two models (Predator Access and Predator Access + Site) received substantial support. These models collectively represented 74% of the Akaike weight of all models (Table 1). For the shared variables, parameter estimates were not substantially different; nevertheless, we used model averaging to generate final parameter estimates for variables hypothesized to influence predator access to nests. Of the four variables included in the top model, only emergent density and distance to wetland boundary had a significant effect size (Fig. 2). The probability of nest predation decreased with higher emergent density and increased with greater distance to the edge of the wetland.

Mean incubation temperature ranged from 20.45 – 23.21 °C and was significantly different both across our four sites and years for the 55 nests with thermal data (GLM, Table 3). All sites possessed significantly different mean daily nest temperatures, mean minimum temperatures and mean maximum daily range except sites D & H (Tukey HSD; Fig 3, Table 3). Of 18 nests with known incubation periods and thermal data, incubation periods ranged from 60 – 95 days (mean = 75 days). Among the four nests in sites with elevations > 869 m, incubation periods were approximately 21 days longer than nests (n = 14) at lower elevations (< 548 m). Mean nest temperature was the only significant predictor of incubation period (GLM, $p = < 0.0001$, $df = 14$, parameter estimate = -7.23). Nests with lower mean temperatures during their incubation had longer incubation periods (Fig. 4).

Discussion

A limited but growing body of research has been conducted on bog turtle nest survival across its range (Whitlock 2002; Byer 2015; Macey 2015; Zappalorti et al. 2017). Our research represents the first large-scale study of bog turtle nest survivorship in the southern population. No other study is yet available that has specifically targeted nest survival in populations representing a wide latitudinal or elevation gradient, or that possess dramatically different estimated vital rates and demographic characteristics. Bog turtle nest success varied dramatically among the four wetlands we surveyed; however, it was relatively consistent within sites across the two years of the study. Nest predation was the most prevalent driver of nest failure and among those nests predated most were consumed by mesopredators. Although it has been assumed that human-commensal predators such as northern raccoon, striped skunk, and red fox (*Vulpes vulpes*) are likely to represent the largest sources of increased bog turtle predation in altered habitats (USFWS 2001), our study is the first to positively identify mesopredators as bog turtle nest predators. In the case of Site D, a striped skunk or skunks systematically predated 27 of 33 known nests across multiple nights and over both years. Interestingly, the skunk(s) predated the nests nearly exactly one year apart, with the 2016 episode occurring 7/2–7/3 and the 2017 episode occurring 6/31 – 7/1, suggesting that this may be a learned behavior.

Several studies have demonstrated that mammalian predation is higher along ecological edges (Wilcove 1985; Temple 1987; Paton 1994; Kolbe & Janzen 2002a, b). Similar to Byer (2015), our data showed nest predation may be reduced along wetland boundaries for the bog turtle. We also observed higher probability of predation for nests surrounded by lower densities of emergent vegetation. Many turtle species have a known preference for nesting in open patches where higher nest temperatures accelerate embryonic development (Janzen 1994; Wilson 1998; Janzen & Morjan 2001; Kolbe & Janzen 2002a; Spencer & Thompson 2003; Micheli-Campbell et al. 2013; Petrov et al. 2018). The risk of large predation events is likely high if nests are clustered in these open areas in wetlands with abundant mesopredator activity. Site D, which had particularly high predation rates, may illustrate this phenomenon. A large proportion of nests at Site D were found within two meters of a rivulet that represents an edge between an open area and emergent vegetation. Further, mesopredators are known to use linear search patterns

(Congdon et al. 1993), so in some cases turtles may be selecting to nest in the very same areas that are preferred predator corridors.

Similar to other authors, we have evidence of substantial nest predation events via small mammals (Whitlock 2002; Byer 2015; Macey 2015; Zappalorti et al. 2017). Small predator species may include short-tailed shrew (*Blarina brevicauda*), mice (*Peromyscus sp.)*, and American mink (*Neovison vison)*. Black racers (*Coluber constrictor*) were also observed within Sites A and B and may account for some of the missing eggs. These predation events occurred from the night of laying through piping, but were a more likely source of nest failure later in the incubation period relative to predation via mesopredators. Collectively, the bog turtle nest predation events we recorded were later in the incubation period in comparison with other aquatic turtle species (Tinkle et al. 1981; Congdon et al. 1983; Congdon et al. 1987; Marchand et al. 2002; Spencer 2002; Butler et al. 2004). Most research has documented turtle nest predation primarily within the first week of laying (Riley & Litzgus 2014). Similar to observations by Byer (2015), it appears that nest predation remains a threat for bog turtles across the entire incubation period, which may be linked to the combination of predation tactics employed by both mesopredators and smaller mammals.

Of the four studies known to the author involving bog turtle nest fate in the northern population, average egg survival was low, ranging from 13 – 33% (Whitlock 2002; Byer 2015; Macey 2015; Zappalorti et al. 2017). Predation was the primary driver of egg failure across all studies and ranged from 51 – 73% (Table 4). Bog turtle egg predation and survival rates varied considerably by study, site, and year in these northern populations. Whitlock (2002) observed egg predation rates from 0.05 – 100% (18 eggs at Site 1 in 1995 and 46 eggs at Site 2 in 1997), while Zappalorti et al. (2017) recorded hatch success as high as 83% (18 eggs) in a given season. Similar to these studies, we found egg predation was the most substantial driver of egg failure across sites and years. Although substantial nest predation events were documented by (Whitlock 2002) and (Byer 2015), the predator was not identified. It is possible that mesopredators were responsible for some of these events.

Although egg failure was primarily driven by predation, other sources of failure were identified as well. The true proportion of eggs potentially affected by other variables (destroyed, infertility, developmental problems, flooding and heat stress) would likely be higher had nest predation rates been lower. Of those eggs that were not predated, ~10% did not develop across all sites; a state we attributed to infertility. In some cases, what was identified as infertility may have been failed embryonic development related to the thermal environment or other factors. The developmental problems observed (embryonic death or death at emergence and/or malformed hatchlings) may also be linked to genetic, epigenetic, and/or thermal characteristics as well. For example, only 11 of 106 known eggs were not predated at the high elevation Site D. Only two embryos clearly developed of those 11. In both cases, the eggs that developed were positioned at the top of each respective nest. Only one of those two survived the hatching process. As flooding was not an issue at this site, it is possible that thermal limitations prohibited development of the deeper eggs. Two nests were laid in areas of high emergent density and subsequently were buried atypically in the thatch of dead rush (*Juncus sp*.). Both of these nests experienced extreme and extended thermal variability as evidenced by iButton data and likely failed due to heat stress. Similar to Zappalorti et al. (2015), we also documented bog turtle egg mortality associated with inundation. Four eggs from two nests at Site A failed after the nearly fully formed embryos drowned. The highest egg in one of these nests was found partially inundated but successfully hatched. The hatchling had signs of extreme hypoxia (limb swelling, lethargy), but recovered over several hours. Four other eggs would likely have succumbed to drowning at Site A as well had we not elevated them 50 mm with additional sphagnum moss. Although it appears to play a minor role in comparison with nest predation, the effects of landscape and in-site characteristics on hydrological stability and limiting total viable nesting area may be an important consideration at some sites.

As these sites represent a wide elevation gradient (416 – 954 m), it appears that the thermal environment experienced by bog turtle eggs is dramatically different across sites and is primarily elevation dependent. It is possible that high elevation sites that also have high densities of emergent vegetation may thermally limit the size of viable nesting areas and force atypical nesting placement that increases risk of failure. It is clear that incubation temperature has a strong influence on incubation period and that nests with lower mean temperatures during their incubation had longer incubation periods (Fig. 4). As catastrophic predation was recorded at our high elevation sites, we were unable to observe egg survival trends as it relates to the thermal environment in a statistically significant way. Several literature sources have demonstrated that colder incubation temperature reduces embryonic survival, body size and performance, and increases time to maturity in turtles (Ewert & Legler 1978; Yntema 1978; Ewert 1979; Bobyn & Brooks 1994; Wilson 1998; Wood & Bjorndal 2000; Kolbe & Janzen 2002a; Spencer 2002; Du 2003; Schwanz et al. 2010; Dormer et al. 2016; Petrov et al. 2018).

It appears that a cooler climate and shorter breeding season may place additional constraints on our higher elevation populations analogous to bog turtles existing at the northern limits of the species geographic range (Whitlock 2002). Lower mean temperatures may result in insufficient windows for development, resulting in fewer eggs taking longer to hatch. Longer incubation periods may result in greater opportunity for nest predation events (Whitlock 2002), thermal extremes, and flooding. The hatchlings that emerge at the end of the growing season have a shorter window to find a suitable overwintering location to survive a harsher winter. Conversely, the low elevation populations appear to have been released from the ecological constraints that limit the scale and frequency of successful recruitment episodes in the montane populations.

Management implications

The lower proportion of juveniles encountered at sites D & H appears to be a genuine reflection of poorer recruitment in these populations. Limited and greatly punctuated successful recruitment episodes appear to be the norm for many sites in the region, with a few notable exceptions such as Sites A and B. Observed age structure in these populations mirrors our observations in nest survival, suggesting that these trends have continued for well over a decade. It should be noted that juvenile detection probabilities may vary by site, thus it is possible that differences in relative abundance may not be as dramatic as raw encounter data suggests. Annual survival probabilities of hatchlings and/or juveniles may also be different enough across sites to influence recruitment success. Future research that attempts to better understand differences in hatchling and juvenile survival as well as the linkages between nest predation rates and the surrounding land use would likely benefit conservation efforts for bog turtles.

High nest predation rates may not only reduce recruitment but may eventually impact the size and viability of these bog turtle populations and other threatened turtle species (Crouse et al. 1987; Marchand & Litvaitis 2004; Tutterow et al. 2017; Chapter 2). This is particularly amplified when multiple life-stages have deflated survival estimates, which appears characteristic of many North Carolina bog turtle populations. As our data suggest nest predation may pose serious threats to population persistence, we suggest potential solutions that include: vegetative and hydrological management that increase total viable nesting area and site fidelity, predator removal, protection of nests, and head-start programs at spatially and temporally explicit scales. As adult abundance is so low at some sites to severely limit the potential output of hatchling turtles regardless of time and financial investment, we would also suggest focusing efforts to create a surplus of turtles at pre-existing highly abundant populations from which to periodically seed small and declining populations (Spencer et al. 2017). An important next step is to assess site-specific population growth rates and the relative benefits of these management options to stabilizing and grow these bog turtle populations. This will be of critical value to aid in strategic conservation plans.

Table 1. AICc table ranking five hypotheses on the drivers of bog turtle nest predation across four wetlands and two years in western North Carolina, USA (data were pooled between sites and years). The Access Model included all factors hypothesized to influence mesopredator access to a nest (% standing water, distance to edge of the wetland, emergent density and the distance to the forest edge). The Detection Model included factors hypothesized to influence mesopredator nest detection (woody stem density, % scrub shrub, and emergent density). The site model represents the fact that each of these wetlands occurs in a different landscape context and there may be many drivers at that scale influencing nest vulnerability to mesopredators.

Model	K	AICc	ΔAICc	AICcWt	Cum. Wt	LL
Predator Access + Site	8	86.12	0	0.42	0.42	-34.01
Predator Access	5	86.64	0.52	0.32	0.74	-37.9
Site (Latent)	4	88.22	2.10	0.15	0.89	-39.84
Predator Detection + Site	7	89.18	3.06	0.09	0.98	-36.79
Predator Detection	4	92.17	6.05	0.02	1	-41.81

Table 2. Bog turtle egg fate (%) across four wetlands in western North Carolina, USA. Only sites with known fate of at least eight nests were included in the summary. Destroyed eggs were defined as non-predated eggs smashed or broken by animals; infertility was defined as eggs with no evidence of embryonic development (from visual inspection); developmental problems were those eggs that died after some period of development or while hatching without signs of inundation or heat stress; drowned was defined as eggs that became submerged during observed inundation events; heat stress was defined by desiccated failed eggs having undergone multiple days of temperatures <32 °C as evidenced by iButton data.

Site	# Eggs	Hatched	Predated	Destroyed	Infertile	Dev. Prob.	Drowned	Heat Stress
A	71	0.56	0.18	0.03	0.13	0.04	0.06	-
B	49	0.45	0.23	0.41	0.08	0.10	-	0.10
D	106	0.01	0.90	-	0.09	0.09	-	-
H	26	0.15	0.81	-	-	0.39	-	-

Table 3. Bog turtle nest temperature comparisons across sites and years (n = 55 nests across four sites) with either known or hypothesized incubation periods. All sites were located in western North Carolina, USA. Site A is represented by the intercept. Temperature variables were calculated from the duration of the incubation period; however, for failed nests (n = 37) we estimated duration based on hatch dates of other nests within the wetland.

	Parameter estimate	*t*-value	*p* Value	df
Response: mean daily temperature				
Intercept	23.21	110.86	< 0.0005	51
Site B	-0.97	-2.87	0.006	51
Site D	-2.63	-9.43	< 0.0005	51
Site H	-2.76	-7.11	< 0.0005	51
Year	1.17	4.39	< 0.0005	51
Response: mean minimum temperature				
Intercept	14.20	28.70	< 0.0005	51
Site B	0.75	0.944	0.35	51
Site D	-2.33	-3.54	0.0009	51
Site H	-4.27	-4.66	< 0.0005	51
Year	0.75	1.18	0.24	51
Response: mean maximum daily temperature range				
Intercept	7.65	15.46	< 0.0005	51
Site B	-1.11	-1.40	0.167	51
Site D	0.14	0.21	0.84	51
Site H	0.80	0.87	0.39	51
Year	2.08	3.29	0.002	51

Table 4. A literature review of the fate of wild, non-protected bog turtle eggs summarized by study, research years, and state(s). Data from all sites involved in each study were combined for one estimate per study and are represented as a percent of each total.

Author Survey years State	Byer (2015) (2013-2014) MD	Knoerr et al. (2016-2017) NC	Macey (2015) (2008-2012) NY	Whitlock (2002) (1994-1997) MA	Zappalorti et al. (2017) (1974-2012) NJ and PA
# Eggs	135	272	80	150	161
% Eggs predated	0.71	0.53	0.60	0.73	0.51
% Other Sources of Failure	0.16	0.19	0.10	0.07	0.16
% Eggs Hatched	0.13	0.28	0.30	0.19	0.33

Figure 1. Sample camera trap photos depicting bog turtle nest predation events of (A and B) striped skunks (*Mephititis mephitis*) and (C) Virginia opossum (*Didelphis virginiana*). Predation events of (D) small mammals were evident from the damage pattern on eggshells.

Figure 2. The effect size estimate and associated 95% confidence intervals for a model of environmental covariates and bog turtle nest predation. The "Predator Access Model" included four variables; however only emergent density and distance to edge had a significant effect. The probability of predation increased with lower emergent density and greater distance to wetland edge.

Figure 3. Mean daily nest temperature (°C) for 55 bog turtle nests across four sites in North Carolina, USA with either known or hypothesized incubation periods. Hypothesized incubation periods were generated for failed nests where iButtons were left in place until other nests within the wetland hatched (n = 37).

Figure 4. The effect of mean nest temperature on incubation period for 18 bog turtle nests at four sites in North Carolina, USA with known lay and hatch dates.

Figure 1.

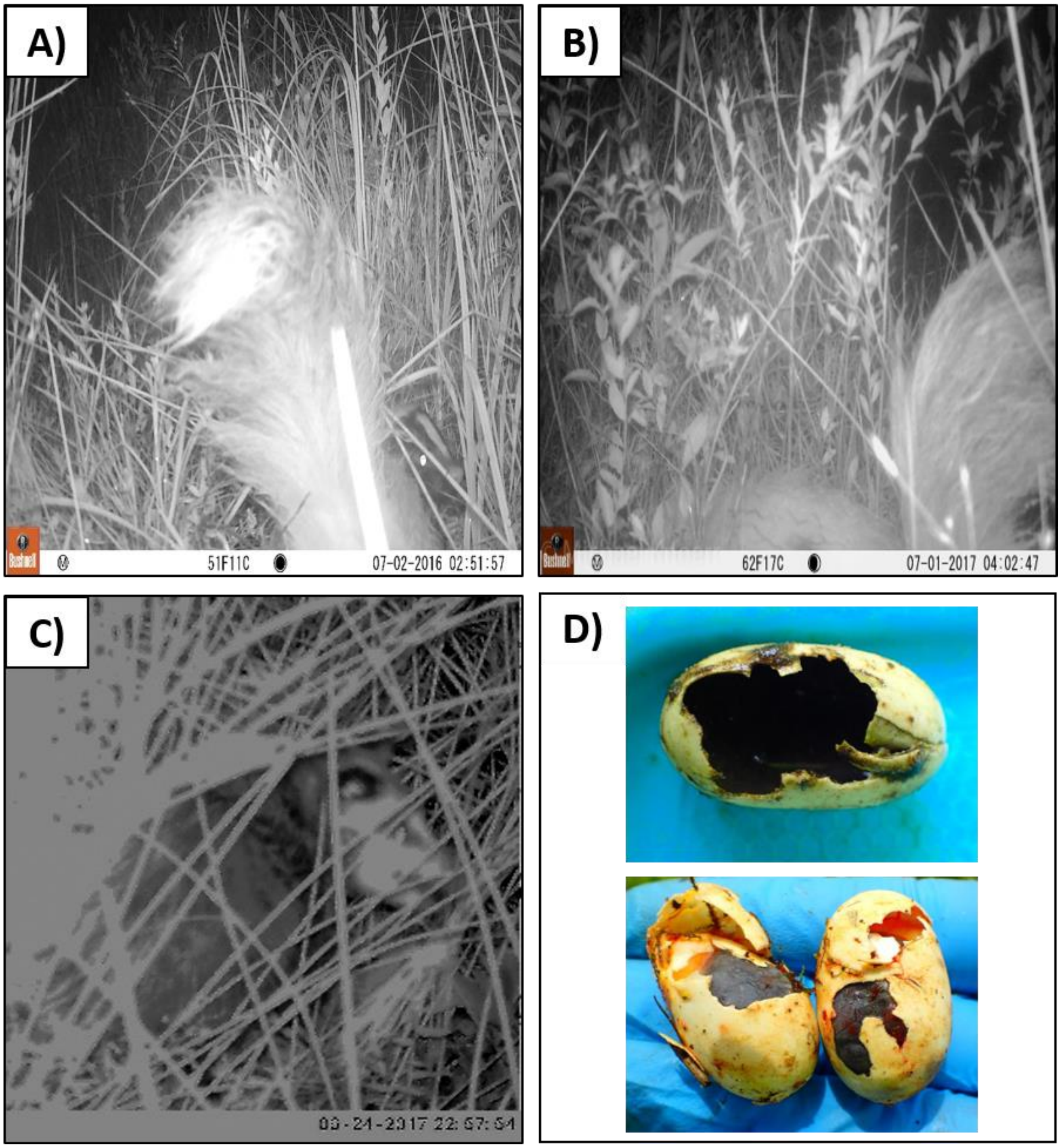

A)
51F11C
07-02-2016 02:51:57
B)
62F17C
07-01-2017 04:02:47
C)
06-24-2017 22:57:54
D)

Figure 2.

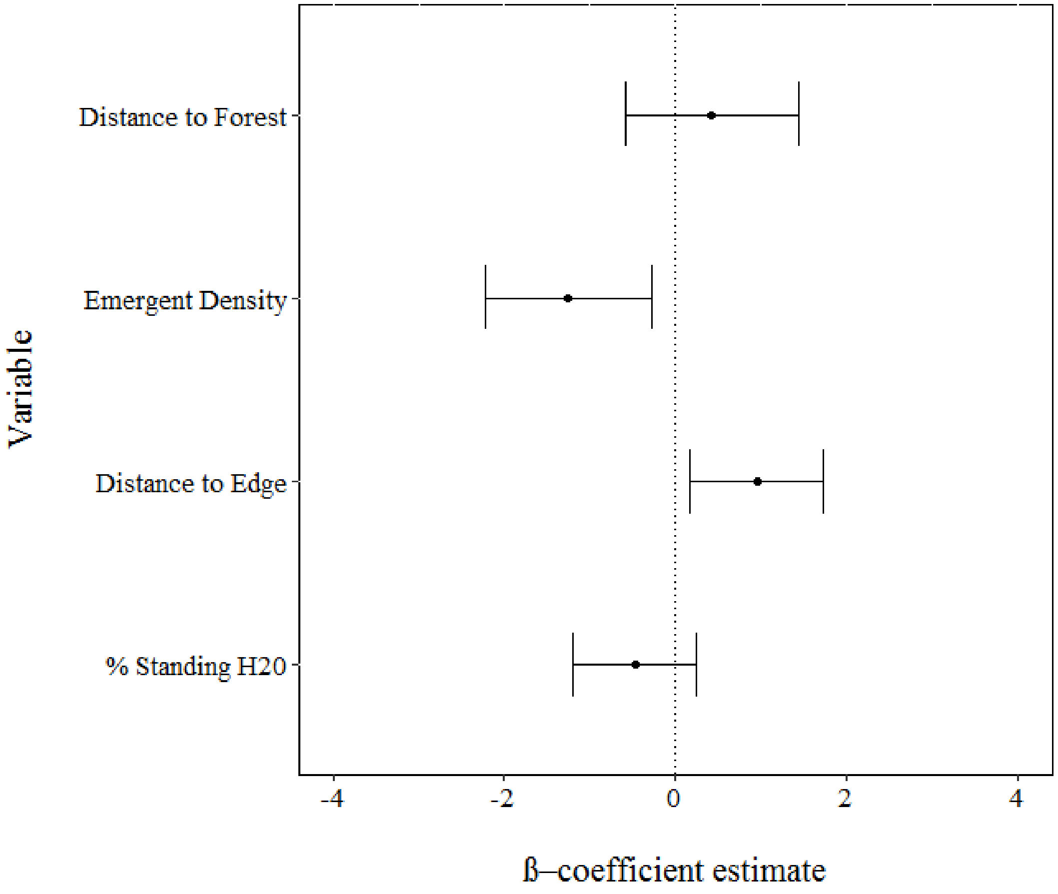

Variable
Distance to Forest
Emergent Density
Distance to Edge
% Standing H20
-4
-2
0
2
4
ß–coefficient estimate

Figure 3.

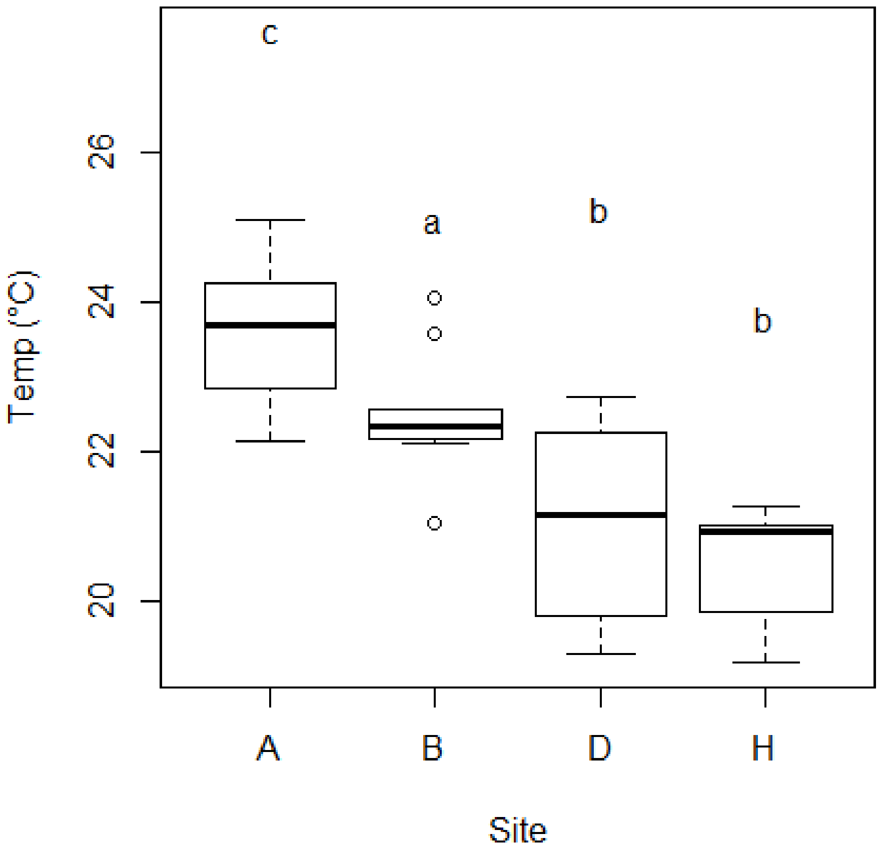
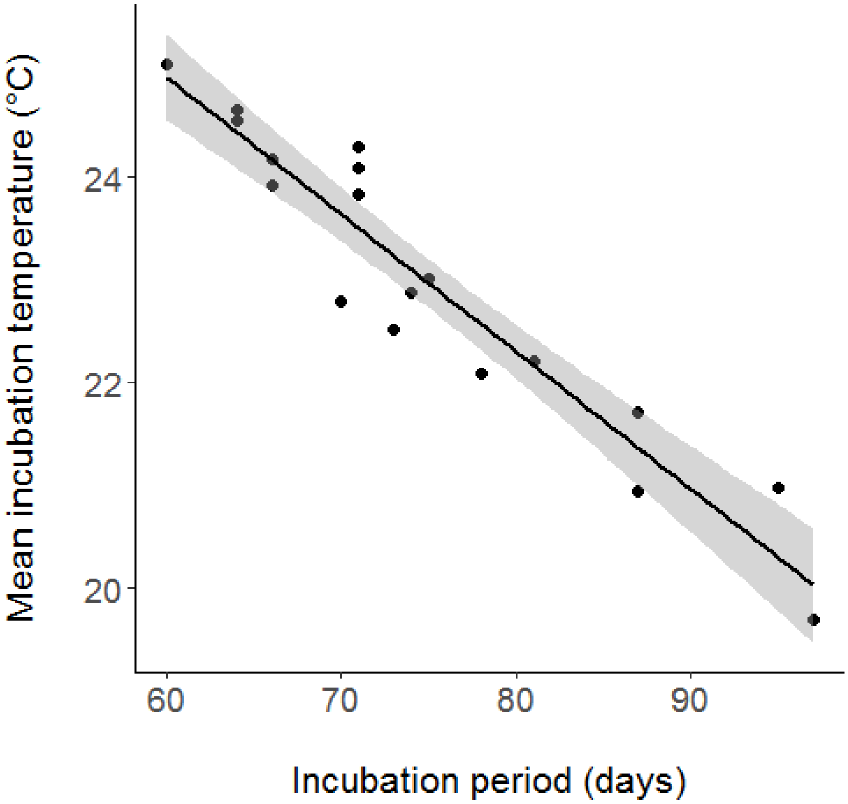


Figure 4.


Mean incubation temperature (°C)
24
22
20
60
70
80
90
Incubation period (days)

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CHAPTER 2

POPULATION MODELS REVEAL THE IMPORTANCE OF MANAGEMENT INTERVENTION FOR AN ENDANGERED TURTLE SPECIES

Abstract. — Demographic models are useful for estimating 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 a stage-based matrix model to estimate population growth and to assess potential management scenarios for five populations of federally threatened bog turtle in North Carolina. Only two of the five populations modeled were stable or growing under current vital rates. The declining populations share many characteristics with many other populations in the region. Elasticity analysis revealed small changes in adult survival have the largest effect on population growth. These models also highlighted the synergistic effects of multiple inflated or deflated survival rates on population growth rates. Our results demonstrated that management scenarios targeting increased recruitment (especially a head-start scenario) may substantially contribute to some populations reaching stability. Population growth rates will likely be dramatically higher when these efforts coincide with wetland restoration efforts that increase survival and site fidelity at other life stages.

Introduction

Effective conservation plans for species of concern can often be developed through knowledge of species–habitat relationships or positive identification and remediation of species-specific threats (Joyal et al. 2001; Lawler et al. 2002). Nevertheless, there are many species, especially those with few remaining individuals or subpopulations, where information on population dynamics is critical to promote the best use of limited conservation resources (Dahlgren et al. 2016). For this latter group, accurate vital rate estimations offer a starting point for identifying conservation opportunities and assessing their long-term costs and benefits.

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 (Carslake et al. 2009). Population projection matrices (PPM) classified by age (Leslie 1945) or stage (Lefkovitch 1965) are commonly used to determine population growth rates and to conduct perturbation analyses (Heppell et al. 2000; Sibly & Hone 2002; Unger et al. 2013). Stage-based PPM allow for more flexibility when modeling the population dynamics of long-lived species that may exhibit similar vital rates across ages or when age is not easily discernible. Most importantly, stage-based PPM are the most readily interpretable for management purposes; they allow wildlife managers to compare the effects of proposed conservation interventions for each life stage. For example, they have been applied widely to inform sustainable harvesting plans (Zimmer-Shaffer et al. 2014) and explore the potential demographic impacts of conservation actions (Crowder et al. 1994; Reed et al. 2009).

Long-term demographic data is critical to understand population trends of species with long generation times, such as freshwater turtles. It is well documented that long-lived species are slow to recover from demographic perturbations (Wheeler et al. 2003; Enneson & Litzgus 2008). There also may be time lags between reductions in vital rates to unsustainable levels (particularly of early life stages that are difficult to monitor) and observed population declines, complicating efforts to identify populations at risk for extirpation.

The bog turtle (*Glyptemys muhlenbergii*) 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; Zappalorti et al. 2017). Bog turtles are highly cryptic, semi-aquatic turtles that occupy open-canopy freshwater wetlands (e.g., bogs, fens, and wet meadows) in the eastern United States. The bog turtle is one of the most rare and imperiled turtle species in North America (Herman & Tryon 1997; USFWS 1997; Seigel & Dodd Jr 2000; Rosenbaum et al. 2007) and is recognized as critically endangered on the IUCN Red List (van Dijk 2011). Although detailed quantitative range-wide estimates are not available, a 90% decline in species level abundance over the course of the 20th century is likely (van Dijk 2011). The species is affected by multiple stressors (e.g., poaching and human-subsidized predators), but habitat fragmentation, degradation and loss primarily limit population persistence (USFWS 2001). The bog turtle's geographic range is discontinuous, split into a northern population network (extending from Massachusetts to Maryland) and a southern population network (extending from southern Virginia to northern Georgia (Ernst & Lovich 2009). Although bog turtles are listed as federally threatened in the United States, the two population networks receive different levels of protection under the Endangered Species Act. Bog turtles in the southern population network are protected from poaching as a result of their "similarity in appearance" status to turtles in the northern population network, but do not receive federal protection from destructive activities affecting their habitat (USFWS 1997).

Life history theory suggests that because turtles display high egg mortality and delayed sexual maturity, high adult survivorship is critical to population persistence (Congdon et al. 1993; Pittman et al. 2011). However, Tutterow et al. (2017) found relatively low annual adult survival for eight intensively studied North Carolina bog turtle populations as compared to northern bog turtle populations (Shoemaker et al. 2013) and other closely-related species such as the spotted turtle (*Clemmys guttata;* Enneson & Litzgus 2008). The effects of low adult survival on population growth rate (λ) has not been estimated for these populations; however, the urgency for doing so is further bolstered by observations that many populations in North Carolina are dominated by older turtles with few to no juveniles encountered in recent decades (Tutterow et al. 2017). It has been suggested that a combination of low adult survival and low recruitment has driven population declines of bog turtles and other species (Haskell et al. 1996; Hays et al. 1999; Spinks et al. 2003; Kuhns 2010; Crawford et al. 2014; Tutterow et al. 2017).

Population models that incorporate survival estimates for each bog turtle life-stage would therefore be useful for testing these suggestions.

Although the mechanisms behind the reduced recruitment observed in many North Carolina bog turtle populations is not well understood, the early stages of life are often the most vulnerable for many turtle species. Nest and hatchling survival are dramatically low for many species and may dampen recruitment rates (Congdon et al. 1993). It is well documented that survival of hatchlings is significantly lower than that of juvenile and adult turtles (Iverson 1991a; Heppell et al. 1996; Green 2015). Although small changes in adult survival are known to make the largest improvements to population growth for freshwater turtles (Congdon et al. 1983; Heppell 1998), protection of early life stages may be necessary to maintain stable populations, particularly when adult survival is reduced (Enneson & Litzgus 2008; Spencer et al. 2017). The factors most limiting the survival of these life stages (i.e., predation) are also the most readily addressed by management interventions (Heppell et al. 1996). One of the possible management strategies to aid in the recovery of declining turtle populations is to increase recruitment by collecting eggs from the wild and rearing hatchlings to larger sizes to boost survival probabilities (i.e., head-starting). Several publications have been critical of head-starting as an effective tool to stabilize turtle populations (Mrosovsky 1983; Crouse et al. 1987; Woody 1990; Frazer 1992; Crowder et al. 1994; Heppell et al. 1996) as modeling demonstrated that population growth rates are far more sensitive to changes in adult survivorship than earlier life-stages. Recent research has suggested that head-starting may be an effective management tool to speed up recovery time for diminished populations, to increase underlying abundance, and to establish new populations of imperiled aquatic turtle species (Spinks et al. 2003; Mitrus 2005; Vander Haegen et al. 2009; Kuhns 2010; Buhlmann et al. 2015; Green 2015; Masin et al. 2015; Michell & Michell 2015; Penaloza et al. 2015; Spencer et al. 2017).

We used stage-based population projection matrices to examine the effects of estimated annual survival rates on bog turtle population growth and to evaluate population growth response to recruitment augmentation in the form of nest protection, lab-incubation of eggs, and a head-start scenario. Population growth rates provide managers with a base line to categorize the status of populations. Altering specific vital rates to mimic potential management efforts can illustrate the effects of various management scenarios. Comparisons of growth rates and the effects of management intervention across five bog turtle populations illustrate a wide spectrum of population status across the region.

Study Area

We built matrix models for five bog turtle populations located in western North Carolina, USA. The exact locations of these populations have been withheld due to poaching concerns. These sites are a part of a long-term monitoring effort (>15 years) initiated by Project Bog Turtle and the North Carolina Wildlife Resources Commission. These sites range from high elevation populations in the Blue Ridge Mountains, to lower populations just off the Blue Ridge Escarpment. One highly isolated population exists in the NC piedmont. Each site varies in size and degree of connectivity to other wetlands, from larger wetlands (1.25 ha) existing within mostly intact watersheds characterized by a mosaic of wetland, woodland and pasture, to small (0.3 ha) isolated wetlands nestled within developed areas. These wetlands are hydrologically complex, but all maintain a strong groundwater connection, and are thus most accurately described as fens, although they are generally referred to as mountain bogs amongst land managers. Within these wetlands, limited nutrient availability has historically prohibited highly competitive wetland and woody plants from dominating these systems. The result is a highly diverse and iconic open canopy vegetative community. Several of these wetlands are dominated by sphagnum and are vegetatively complex with patches of woody shrubs interspersed amongst emergent vegetation. Cattle graze some of these fens while others are periodically managed with fire or manual vegetation thinning. These properties are in private ownership or owned and/or managed by land conservancy organizations.

The five focal sites are a subset of sites evaluated in Tutterow et al. (2017). To facilitate comparison and future study we follow their naming convention. Compared to other known bog turtle sites in North Carolina, Sites A and B represent 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 416–547 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 declining populations (Sites D & E; Tutterow et al. 2017). Sites A and B experienced successful recruitment in each of the last 10 years, as evidenced by counting scute annuli over the 2016 and 2017 field seasons. The highest egg survival was also observed at these sites (average = 0.52 egg survival) over both field seasons (Chapter 1).

Sites D & H are high elevation populations (approximately 954 and 869 m, respectively). Site D is one of the three most robust populations known in the state. Both populations are dominated by older turtles (median age >25 years) with an obvious recruitment event having also occurred 10 – 12 years ago at both sites. Juveniles represent 10 – 20% of total encounters at Site D from 2003 – 2017 and site H from 1992 – 2017. Similar to Daigle & Jutras (2005) we believe that the low proportion of juveniles encountered likely reflects poorer recruitment (we define recruitment as turtles entering every life stage, e.g. eggs to hatchlings, hatchlings to juveniles, juveniles to adults) in these populations. Juvenile survival is estimated at 0.49 at site D and is not empirically available for Site H. Egg survival (n = 106) was <0.01 at Site D across 2016 and 2017 due to catastrophic predation (Chapter 1). Egg survival at Site H was 0.15 in 2018.

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 – 2015, this population appears be primarily comprised of older adults (median estimated age > 25 y). 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). It is estimated that fewer than 10 turtles existed in this wetland as of 2018.

Collectively, these sites represent the broadest range of demographic states for North Carolina bog turtle populations, from highly abundant populations that display annual recruitment to a nearly extirpated population with no recruitment observed in recent decades (Tutterow et al. 2017). It is likely that the demography and status of these populations (particularly Sites H & E) are representative of many others in the region.

Methods

Matrix Model: We parameterized deterministic 3x3 stage-based population projection matrices to examine the 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 et al. 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 suggests that many turtles reach 80 mm CL by approximately year seven. We define the egg/hatchling stage as beginning when eggs are laid and persisting until the following May (approximately 10 months). The stage-based matrix (A) contained the following parameter structure:

$$A = \begin{bmatrix} 0 & 0 & F_3 \\ P_{12} & P_{22} & 0 \\ 0 & P_{23} & P_{33} \end{bmatrix}$$

F_3 is the fertility of adult females and P_{ji} is the probability that individuals in class j survive and transitions into stage i (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 (Enneson & Litzgus 2008; Hyslop et al. 2012; Zimmer-Shaffer et al. 2014).

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: Eighty-three bog turtle nests were found across both field seasons primarily via performing radio-telemetry on gravid female turtles in the evenings, as well as by following thread bobbins, opportunistically observing nesting events of gravid females not on radio-telemetry and nest searching (Chapter 1). The number of eggs in each nest was recorded at first discovery, generally (>80%) within 12 hours of nesting, providing an estimation of clutch size. Site-specific and regional average egg survival was estimated by monitoring egg fate throughout the summer with camera trap and visual inspection (Chapter 1). Four of the five sites modeled in this manuscript were monitored for egg survival. To our knowledge, this nest dataset is the largest yet compiled on the fate of naturally incubated bog turtle nests. As adult female abundance is so low at Site E to limit inference of egg survival, this site was excluded from the nest study. Thus, we set Site E egg survival to the regional average.

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

$$F_3 = (avg.\,clutch\ size) \times (avg.\,clutch\ frequency) \times (adult\ survival) \times 0.5$$

Where clutch frequency (0.85) was derived by palpating all adult female turtles in the month of June 2016 and 2017 in our most intensively monitored populations to determine whether they were gravid (Chapter 1). We generated site-specific clutch sizes (2.96 – 3.77) for sites where we detected at least eight nests. As encounter data are slightly female biased, Tutterow et al. (2017) estimated annual adult survival for each NC bog turtle population individually and found no evidence of sex-specific differences in survival in the population. Considering also that bog turtle sex is genetically determined (Literman et al. 2017), differences in survival may exist at the juvenile stage (Tutterow et al. 2017). For the purposes of the model, we assume a 1:1 sex ratio, thus the estimate of annual fertility was halved as we used a females-only model.

Bog turtle hatchling survival has not been empirically estimated from this or any study. Yet it is well documented that hatchling turtle survival is significantly lower than that of later life-stages and Shoemaker et al. (2013) estimated egg/hatchling survival to be low (0.33) for stable New York bog turtle populations. With this in consideration, we calculated hatchling survival as 0.40 times the site-specific juvenile survival estimate. Subsequent sensitivity analysis (Fig. 1) suggested the results was not greatly influenced by our choice of parameter value for hatchling survival. 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_{12}).

A previous study leveraged long-term recapture data to produce site-specific juvenile and adult apparent survival estimates (Tutterow et al. 2017). We obtained annual estimates of adult survival within the five populations using Cormack-Jolly-Seber models by incorporating the 2016 – 2017 recapture data into a size-based analysis described by Tutterow et al. (2017) (Table 6). P_{33} was set equal to the annual adult survival rate as 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 the juvenile (<80 mm CL, corresponding to approximately 1 – 6 years) to the adult (> 80 mm CL, corresponding to approximately 7+ years) stage during each annual sampling period to estimate juvenile survival probabilities (σ_j) and juvenile transition probabilities (ψ) for Sites A, B, D & E. We used the top-ranked CJS model to inform our multistate analyses (Tutterow et al. 2017). As 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 confident 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:

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

Next, we calculated the matrix element P_{23} as the product of ψ and σ_j, representing the probability of transitioning from the juvenile to adult stage, conditional on survival (Morris & Doak 2002).

$$P_{23} = \psi * \sigma_j$$

Parameterizing the stage-based matrix: We generated three alternative stage-based matrix parametrizations to model three egg survival scenarios for each of the five NC bog turtle populations. First, we generated site-specific lambda (λ) values by using site-specific parameters. 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 these wetlands. In the cases of Sites A and B, the observed proportion of juveniles encountered 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 & B for those sites ("High") and the regional average egg survival for the remaining sites ("Average"). We refer to this as "High vs. Average" egg survival model (see Appendix 1).

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

Each recruitment augmentation scenario assumed 0.70 of available nests are recovered for management intervention in each respective wetland (except for the largest population Site A, where we modeled 0.40 nest recovery), which translates to a maximum of 25 nests recovered when incorporating site-specific abundance estimates and clutch frequency. For protected eggs, we model 0.40 average hatch success, 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 they were at Sites A & B), the protected egg survival estimate was arbitrarily set 10% beyond 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. Both head-start scenarios also assume 0.81 average egg survival and 0.95 hatchling survival during captivity (M. Ogle, 2018, Pers. comm. 10 March). As released head-started turtles would be approximately equal in size to wild 3-year old bog turtles, we set released head-start survival probabilities equal to the site-specific juvenile survival estimate. We also arbitrarily increased head-start model transition probabilities by 1.17 times the site-specific estimate as we predict these turtles will spend 2-3 fewer years in the juvenile stage. Finally, survival of eggs not recovered for management efforts (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 sites A (where proportion of eggs recovered = 0.40 and eggs remaining in their wild state = 0.60):

$$P_{21} = \left(\left(\sigma_{art.incubation} * \sigma_{captive\ hatchling}\right) * .7)\right) + \left(\left(\sigma_{\mathrm{good/avg\ egg}} * \sigma_{8\ month\ hatchling}\right) * .3)\right)$$

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 – 100%). We recalculated λ after each perturbation trial.

Results

Average clutch size for the 83 nests recorded across the region was 3.28 eggs. 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 /adult survival and transition probabilities are provided in Appendix 1.

The stable stage distribution results estimated via the “High vs. Average” egg survival model suggests that the greatest proportion of individuals should be in the egg/hatchling stage for Sites D & E (~0.52; Table 1), whereas Site A would have the lowest proportion in the egg/hatchling stage (0.40). Sites A & 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/hatchlings, these estimates translate to approximately 48% juveniles at Site B and 20% at Site D, a slightly higher proportion than what we have observed in field encounters.

The reproductive values of juveniles and adults were similar for Sites A and B, with juveniles contributing approximately four times more to future generations than eggs/hatchlings, and adults contributing 10-13 times more to future population growth than eggs/hatchlings. The reproductive value of the adult class for Sites D, E, & H were drastically greater, with adults contributing 36-96 times more to future generations than eggs/hatchlings (Table 2).

Elasticity analyses indicated that the survival of the adult class (P_{33}) proportionally contributed the most to population growth (Table 3), with adult survival elasticities above 0.7 for all sites. The matrix element corresponding to juvenile survival (P_{22}) was also considered important for population growth of Sites A and B (Table 3). Juvenile survival elasticities ranged from 0.22 at Site B to 0.025 at Site D.

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). Site D, E, & H all appear to be experiencing 6 – 10% annual decline ($\lambda = 0.94$, 0.90 & 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 dramatic nest predation (D & H), caged nest scenarios increased population growth rates by approximately 2%. The lab-incubated egg scenario more substantially improved λ for Sites A, B, D, & H, which exhibited 3 – 5% increases in population growth (Figure 2). The head-start scenario was the only potential management strategy modeled that stabilized or grew all populations except Site E (Figure 2).

For the two sites (A and B) with $\lambda > 1$, we estimated the parameters values that is estimated to lead to negative population growth (Table 4). 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. Population growth rates for all remaining sites were estimated to be < 1 (Table 5). For each of these sites, substantial increases (see Table 5) would be required in any one stage to yield population growth, and in some cases no amount of increase at a given stage resulted in $\lambda > 1$ (assuming other parameters were held constant). Site E would require particularly dramatic intervention, with a 10% increase in adult survival or a 90% increase in egg and hatchling survival needed to provide positive population growth. Site D was notable for its catastrophically low egg survival, thus egg and hatchling survival would have to increase >99% from this deflated rate (0.003 to 0.5) to stabilize the population.

The sensitivity curves demonstrated the proportional effects of vital rate perturbations on λ and corroborated that a small change to adult survival results in the greatest change to λ (Fig. 1). These effects become more dramatic as a population experiences greater decline. At Site D for example, a 10% decline in adult survival reduces λ by approximately 10%, while a 10% decline in egg/hatchling survival reduces λ by approximately 1%. However, with the exception of Site E, high survival of egg/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/hatchling survival, Site A experienced 22% annual growth compared to 18% and 11% annual growth under scenarios of 100% juvenile survival or 100% adult survival. For Site E, egg/hatchling survival had limited effect on population growth and population stability only occurred when juvenile or adult survival approached 100% (Fig. 1).

Discussion

Of the five NC bog turtle populations modeled, we found only two that are likely to exhibit stability or growth under current conditions. The three other populations were estimated to be in decline. Sites A and B appear to be growing or stable under current rates and have robust abundance estimates, suggesting that they should be highly prioritized in a regional-scale conservation plan. As evidenced by capture data, recruitment has been continuous for at least a decade at Sites A and B, and this likely results from reduced nest predation, moderate incubation temperatures (Chapter 1) 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 is moderately deflated (Fig.1, Table 4). For both of these populations, survival estimates for the egg and juvenile life stage and transition probabilities are high, effectively compensating for low to moderate adult survival. Although both populations are estimated to be stable or growing, Site B appears to be in a more precarious state as demonstrated by the small vital rate adjustments required to produce a $\lambda < 1$ (Fig. 1, Table 4). Nearly any decreased survival at any stage is projected to lead to population decline.

Long-term population viability is unlikely for the majority of the sites modeled here. Several studies that involved population modeling of turtle species has shown that small increases in adult mortality may destabilize populations (Crouse et al. 1987; Heppell et al. 1996; Heppell 1998; Enneson & Litzgus 2008). 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. Estimated population growth rates varied greatly among sites, with some estimates low enough to suggest dramatic management intervention will be necessary to stabilize populations. Sites D & H may stabilize via targeted efforts to increase recruitment (Fig. 1 and 2; Table 5). If these management actions were to occur, we would expect the populations to produce sensitivity curves similar to Sites A and B (Fig. 1). Site E had such low underlying vital rates that it is likely to continue precipitous decline under the management scenarios presented here unless multiple increases in survival occur at other life-stages (Fig. 1; Table 5).

Estimating reasonable survival probabilities for head-started turtles in comparison with their wild counterparts was critical to assessing the effect of these efforts on population growth rates. Several sources have recorded comparatively high survival for head-started turtles relative to hatchlings in the wild (Kuhns 2010; Michell & Michell 2015). Head-started 9-month old turtles in Tennessee are similar in size to their 3-y old wild counterparts (M. Ogle, 2018, Pers. comm. 10 March), thus we also adjusted the estimate of transition probability to reflect the reduced time in the juvenile life stage. In addition, our use of transition probabilities from multistate capture-recapture analysis did not provide reasonable estimates for Sites D and H. We derived a method of adjusting the estimates (see Methods) that we deemed as preferable to other means for generating transition probabilities (Crouse et al. 1987; Caswell 1989). The approach taken by these authors would have resulted in dramatically more conservative transition probabilities, and as a result these early methods may have contributed to the historical perspective that head-start programs have limited conservation utility (Heppell et al. 1996).

Turtles are slow to mature, long lived and iteroparous. These life history traits help to buffer populations against the characteristically vulnerable early stages of life (Enneson & Litzgus 2008). Natural predation on eggs is historically high and hatchling survival is generally low for most turtle species (Congdon et al. 1983; Mitchell 1988; Frazer et al. 1990, 1991; Iverson 1991a; Paterson et al. 2012; Dragon 2015; Spencer et al. 2017). Substantial longevity allows them to persist through harsh years and compensate with higher fecundity during favorable years (Litzgus 2006), effectively smoothing inter-annual changes in population growth. This evolutionary strategy is generally considered dependent upon extremely high adult survival (Congdon & Gibbons 1990; Van Buskirk & Crowder 1994; Heppell et al. 1996). Shoemaker et al. (2013) concluded that stable NY bog turtle populations had annual adult survival estimates of ~96%. It was estimated that adult survivorship needs 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 low adult survival and associated λ values estimated for some NC bog turtle populations suggests that these historical estimates may be representative benchmarks (Tutterow et al. 2017; Fig. 2). The populations modeled to be stable in this study also demonstrate that some level of lower adult survival can be tolerated when survival is inflated at other life-stages (Fig. 1).

Estimated λ values from this study for several populations suggest that both site-specific and regional average egg survival may result in annual population declines when compounded by low juvenile/adult survival rates (Fig. 2). While acknowledging that these manipulations are a symptomatic treatment of a larger conservation problem (Spencer et al. 2017), management plans targeting increased recruitment may contribute substantially to some populations reaching stability in a given year. Of the recruitment augmentation scenarios investigated, head-starting is the most effective management tool to stabilize these populations.

The literature on the effects of head-start efforts on long-term population viability is mixed. The historical perspective on the utility of turtle head-start programs to stabilize populations has generally been critical (Mrosovsky 1983; Crouse et al. 1987; Woody 1990; Frazer 1992; Crowder et al. 1994; Heppell et al. 1996). Frazer (1992) viewed head-starting as a “halfway technology” that does not ameliorate the actual threats driving population decline and thus places more turtles into degraded environments in which their parents have failed to flourish. Several authors concluded that caging nests and head-starting were ineffective conservation tools as modeling demonstrated that population growth rates are far more sensitive to changes in pre-adult or adult survivorship than earlier life-stages (Crouse et al. 1987; Crowder et al. 1994; Heppell et al. 1996; Shoemaker 2011). Some critiques of the approach appear to be based on strict assumptions, such as Shoemaker (2011), where head-started bog turtles were assumed to have survival rates equal to their same-aged *in situ* cohort. This author concluded that a “10-year head-start program” for a NY bog turtle population would have negligible effect on 100-year extirpation risk.

More recent studies on head-starting freshwater turtles have concluded that it may be a valuable tool to address recruitment problems, increase turtle numbers, and stave off extinction threats (Spinks et al. 2003; Mitrus 2005; Vander Haegen et al. 2009; Kuhns 2010; Moore et al. 2013; Buhlmann et al. 2015; Green 2015; Masin et al. 2015; Michell

& Michell 2015; Penaloza et al. 2015; Spencer et al. 2017). The Turtle Survival Alliance has targeted head-started several freshwater turtles, including several within the highly imperiled *Batagur* genus; these efforts appear to be highly effective at staving off immediate extinction threats (Goldstein et al. 2017). Enneson and Litzgus (2008) conducted a stage based matrix analysis on a stable spotted turtle population in Ontario, Canada. These authors concluded that protection of eggs may be an efficient conservation strategy when egg or juvenile survivorship was dramatically low (below 0.29 and 0.69, respectively). Head starting programs have also have empirical or model support for Illinois Blanding's turtle (Kuhns 2010) and eastern long-necked turtles (Spencer et al. 2017). These authors suggest that head-starting could be an effective and cost-efficient primary management tool in a broad-scale, integrated plan. Importantly, these analyses suggest that when survival is not increased elsewhere, turtle populations will begin to decline immediately after head-start initiatives had ceased.

Among the sites we modeled, a head-start scenario is likely to boost λ at all locations. Nevertheless, the increase to population growth at Site E is likely to be insufficient for long-term persistence, as this declining population has such a low abundance estimate (<10 adult turtles) that the probability of stochastic extinction in very high regardless of the annual λ value (Shoemaker et al. 2013). If population persistence is the goal, we suggest careful consideration of all population augmentation tools available to avoid local extinction. Presuming the wetland scale drivers of decline have been amended, translocation of head-started individuals from highly abundant stable populations into populations with dramatically low abundance may be an effective strategy to limit immediate extinction threats.

Management Implications

Only two of five well-studied NC bog turtle populations modeled appear to be stable or growing under current estimates. These populations likely represent the demographic spectrum of bog turtle population status. The declining populations share similar vital rate and abundance characteristics with many other bog turtle populations in the region.

These models suggest that management plans targeting an endangered freshwater turtle will likely need to be tailored to site-specific dynamics. For some sites, increased recruitment (especially a head-start scenario) may substantially contribute to declining populations (Sites D & H) reaching stability (Fig. 1 & 2). For example, sensitivity curves for all sites except Site E suggest when other life-stages are held constant, large increases in survival at the egg and hatchling stage will result in the highest population growth rates (Fig. 1). If 33 and 50% of all available eggs and hatchlings survive until their second summer, we would expect population stability at Sites D and H (Table 5). Population growth will likely be dramatically higher when these efforts coincide with management to increase survival and site fidelity at other life stages (such as addressing hydrological issues and woody encroachment). Site E is not expected to stabilize via any in-site recruitment augmentation efforts alone (Table 5, Fig. 2). For sites with dramatically low abundance (such as Site E), the probability of extinction is extremely high regardless of population growth trajectories. Deciding whether translocation (Cope & Waller 1995; Menges 2008; Schwartz et al. 2012; Dresser et al. 2017) is a viable tool for such populations is an open question since regional and local habitat issues may have created a population sink. Determining where such issues exist and whether or not they can be ameliorated is a critical next step. Our research highlights the need for managers to consider site-specific demography and vital rates in order to create effective management plans. As financial resources are limited, choosing conservation actions at one site may preclude action at others (Wilson & Law 2016). These analyses help managers make informed decisions as to where they might invest limited resources to maximize conservation outcomes in a region-scale management plan.

Table 1. Stable stage distributions (the right eigenvector) from stage-based population projections models for five North Carolina bog turtle populations utilizing the “High vs. Average” egg survival model.

Site	**Egg/Hatchling**	**Juvenile**	**Adult**
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

Table 2. Reproductive values (the left eigenvector) from stage-based population projections models for six North Carolina bog turtle populations utilizing the “High vs. Average” egg survival model. The reproductive value is the relative contribution to future population growth an individual in a particular class is expected to make; values for juveniles and adults should be interpreted relative to the contribution of eggs/hatchlings.

Site	**Egg/Hatchling**	**Juvenile**	**Adult**
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

Table 3. Elasticities of vital rates for three North Carolina bog turtle populations show the proportional contribution of each stage class to overall population growth (λ) utilizing the "High vs. Average" egg survival model.

Site	**Egg/Hatchling**	**Juvenile**	**Adult**
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

Table 4. Values of stage-specific annual survivorship resulting in a decreasing population growth rates (λ <1) when other survivorship values are held constant in a stage-based matrix model for two growing North Carolina bog turtle populations (Sites A & B, observed λ = 1.058 and 1.004). Fertility values were adjusted in accordance with adult survival.

	Observed Parameter	**Parameter value resulting in λ < 1**	**% change resulting in λ < 1**
Site A			
Egg Survival	0.560	0.236	0.578
Hatchling Survival	0.474	0.200	0.578
Egg + Hatchling Survival (8 months) (P_{12})	0.266	0.112	0.578
Juvenile Survival + Persistence (P_{22})	0.642	0.160	0.751
Adult Survival (P_{33})	0.935	0.860	0.081
Site B			
Egg Survival	0.450	0.426	0.054
Hatchling Survival	0.458	0.433	0.054
Egg + Hatchling Survival (8 months) (P_{12})	0.206	0.195	0.054
Juvenile Survival + Persistence (P_{22})	0.654	0.640	0.021
Adult Survival (P_{33})	0.902	0.895	0.008

Table 5. Values of stage-specific annual survivorship resulting in an increasing population ($\lambda > 1$) when other survivorship values are held constant in a stage-based matrix model for three declining North Carolina bog turtle populations (Sites D, E, H, observed λ = .937, .903, .934). Fertility values were adjusted in accordance with adult survival. NA refers to no value possible.

	Observed Parameter	**Parameter value resulting in $\lambda < 1$**	**% change resulting in $\lambda < 1$**
Site D			
Egg Survival	0.009	NA	NA
Hatchling Survival	0.337	NA	NA
Egg + Hatchling Survival (8 months) (P_{12})	0.003	0.500	0.994
Juvenile Survival + Persistence (P_{22})	0.435	0.997	0.563
Adult Survival (P_{33})	0.937	0.999	0.062
Site E			
Egg Survival	0.276	NA	NA
Hatchling Survival	0.443	NA	NA
Egg + Hatchling Survival (8 months) (P_{12})	0.094	0.900	0.896
Juvenile Survival + Persistence (P_{22})	0.443	0.942	0.529
Adult Survival (P_{33})	0.057	0.999	0.102
Site H			
Egg Survival	0.150	NA	NA
Hatchling Survival	0.404	NA	NA
Egg + Hatchling Survival (8 months) (P_{12})	0.061	0.330	0.816
Juvenile Survival + Persistence (P_{22})	0.549	0.916	0.327
Adult Survival (P_{33})	0.913	0.983	0.075

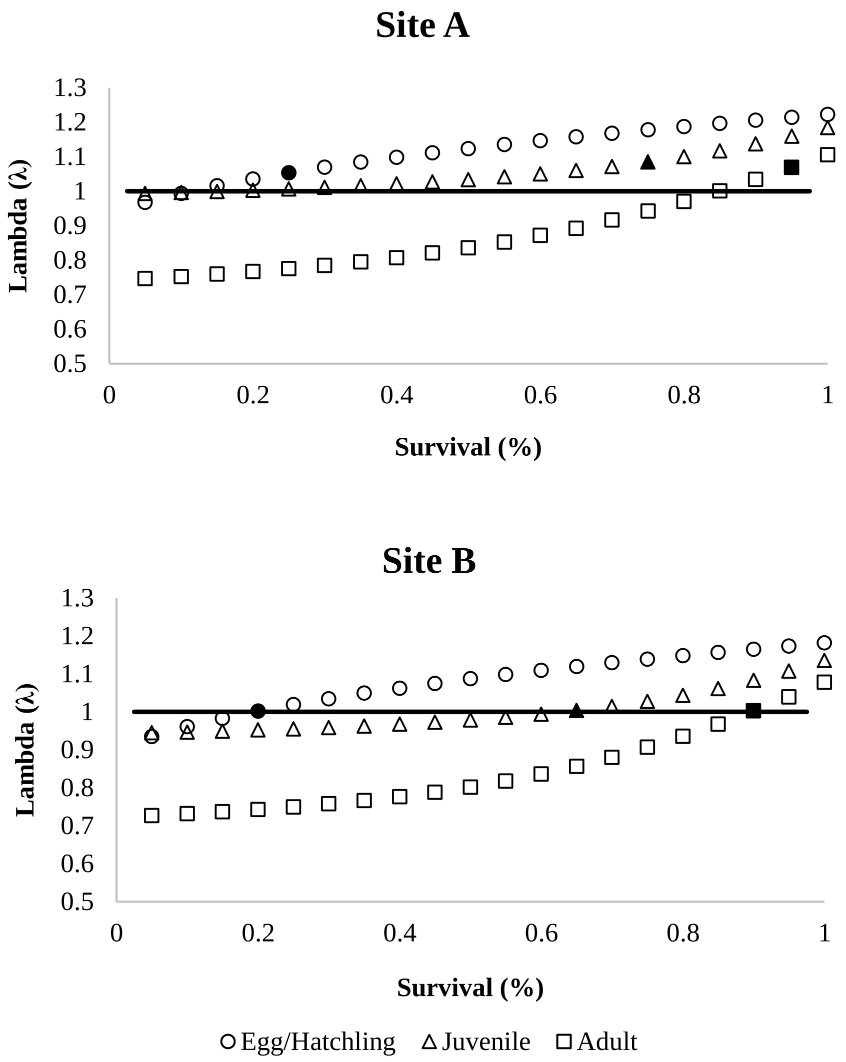
Table 6. Annual apparent survival and transition estimates were derived from the dataset analyzed in Tutterow et al. 2017 and re-analyzed by size-class incorporating 2016 and 2017 encounter data for sites A, B, D & H. Adult apparent survival were estimated using Cormack-Jolly-Seber models. Juvenile survival and transition probabilities were estimated using multistate capture–recapture analyses (Lebreton & Cefe 2002) as described under the methods section.

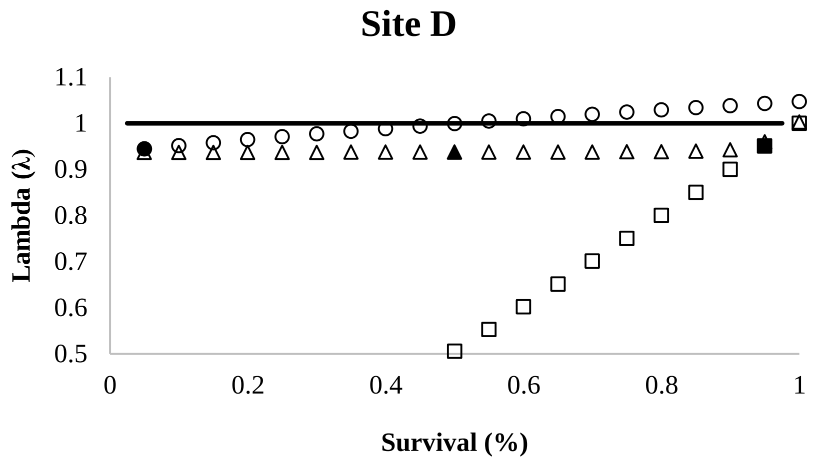
Adult Survival (size based >80mm CL)						
Site	**Phi**	**LCI**	**UCI**	**SE**	**Model**	**Year Range**
A	0.935	0.903	0.957	0.014	Phi(.)p(t)	1996-2017
B	0.902	0.868	0.928	0.015	Phi(.)p(t)	1996-2017
D	0.937	0.908	0.958	0.013	Phi(.)p(t)	2003-2017
E	0.887	0.846	0.918	0.018	Phi(.)p(t)	1992-2015
H	0.913	0.852	0.951	0.024	Phi(.)p(t)	1992-2017
Juvenile Survival (size based <80mm CL)						
A	0.815	0.721	0.882	0.041	Phi(.)p(t)ψ(.)	1996-2017
B	0.773	0.678	0.847	0.043	Phi(.)p(t)ψ(.)	1996-2017
D	0.493	0.257	0.732	0.132	Phi(.)p(t)ψ(.)	2003-2017
E	0.501	0.238	0.764	0.149	Phi(.)p(t)ψ(.)	1992-2015
H	0.646	NA	NA	NA	NA	NA
Juvenile Transition Probability (size based <80mm CL)						
A	0.212	0.143	0.302	0.041	Phi(.)p(t)ψ(.)	1996-2017
B	0.155	0.093	0.247	0.039	Phi(.)p(t)ψ(.)	1996-2017
D	0.112	NA	NA	NA	NA	NA
E	0.113	NA	NA	NA	NA	NA
H	0.148	NA	NA	NA	NA	NA

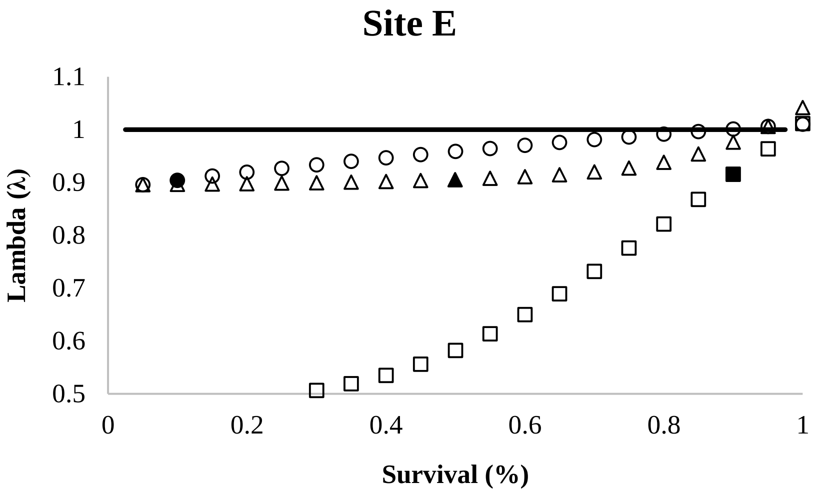
Figure 1. Sensitivity curves demonstrate incremental (from 0-5%) perturbations to each vital rate (egg/hatchling, juvenile, adult) and the effects to λ in stage-based matrix models for five North Carolina bog turtle populations. Solid symbols represent site-specific observed survivorship values. The vital rate estimates at other life-stages are held constant at these observed values when perturbations are made.

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 eggs combined with head-started turtles) on λ for five bog turtle sites in North Carolina. Management scenarios assume that 40% of available nests at Sites B, D, E, and H and 70% of nest at Site A are recovered for management purposes.

Figure 1.


Site A
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
Lambda (λ)
0
0.2
0.4
0.6
0.8
1
Survival (%)
Site B
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
Lambda (λ)
0
0.2
0.4
0.6
0.8
1
Survival (%)
○ Egg/Hatchling
△ Juvenile
□ Adult


Site D
Lambda (λ)
1.1
1
0.9
0.8
0.7
0.6
0.5
0
0.2
0.4
0.6
0.8
1
Survival (%)


Site E
Lambda (λ)
1.1
1
0.9
0.8
0.7
0.6
0.5
0
0.2
0.4
0.6
0.8
1
Survival (%)

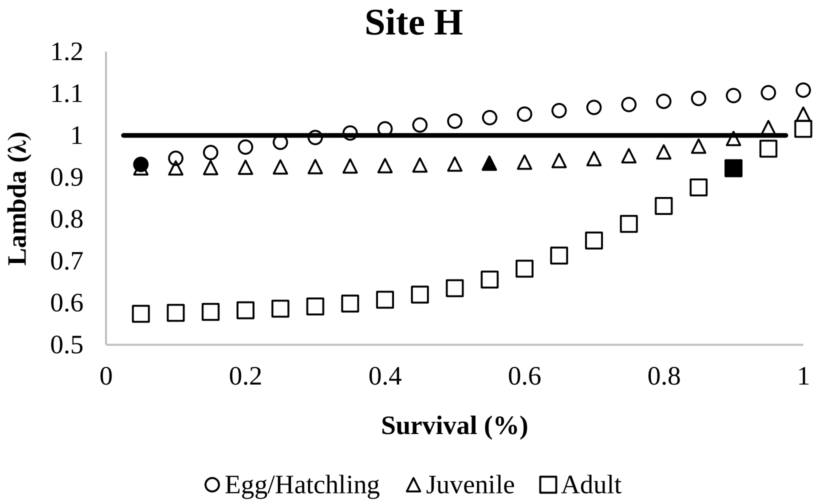
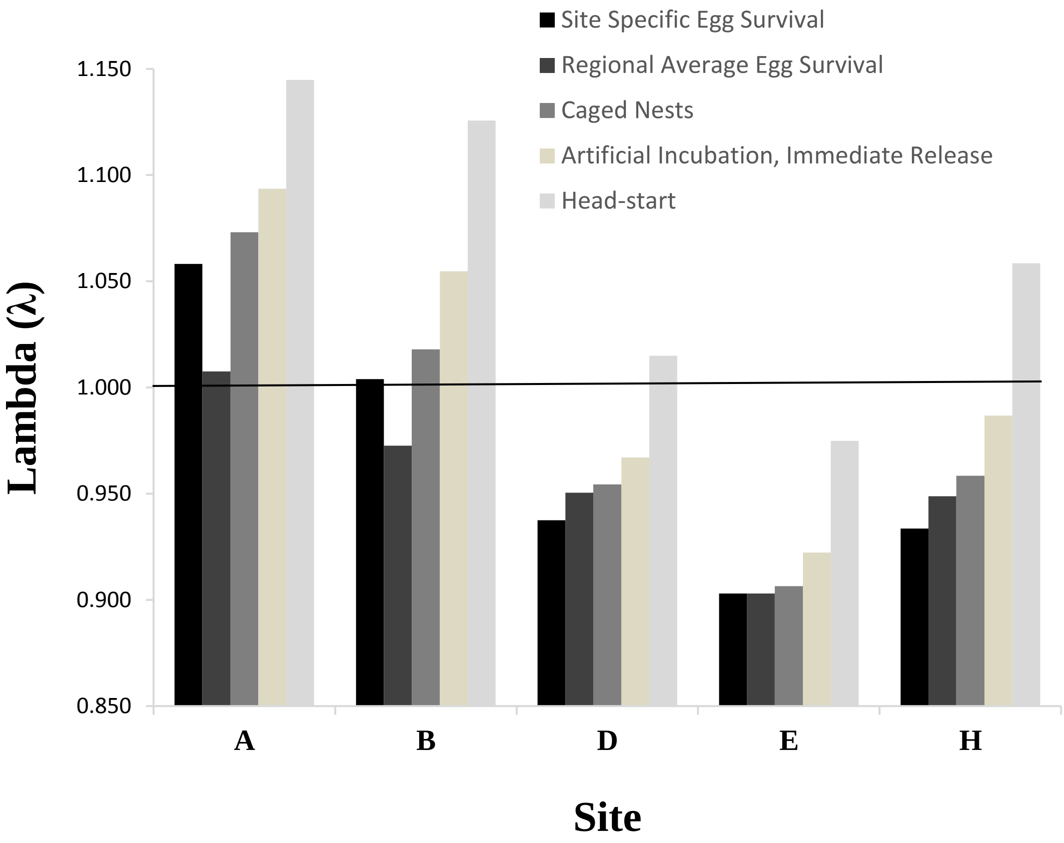

Site H
Lambda (λ)
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0
0.2
0.4
0.6
0.8
1
Survival (%)
○ Egg/Hatchling
△ Juvenile
□ Adult

Figure 2.



Site Specific Egg Survival
Regional Average Egg Survival
Caged Nests
Artificial Incubation, Immediate Release
Head-start
1.150
1.100
1.050
1.000
0.950
0.900
0.850
Lambda (λ)
A
B
D
E
H
Site

Appendix 1. Vital rates used in the stage-based matrix population models for five well-studied bog turtle populations in North Carolina. Non-underlined values are site-specific estimates while underlined values originated from other studies. The bold values are estimates derived from other sites (see text for details).

	Site A	**Site B**	**Site D**	**Site E**	**Site H**	**Source**
Site-specific Egg Survival	0.56	0.45	0.009	**0.276**	0.15	Chapter 1
Regional Avg. Egg Survival	0.276	0.276	0.276	0.276	0.276	Chapter 1
High vs. Average Egg Survival	0.516	0.516	0.276	0.276	0.276	Chapter 1
Caged Egg Survival	0.4	0.4	0.4	0.4	0.4	Macey 2017, Zappalorti et al. 2017
Artificially Incubated Egg Survival	0.81	0.81	0.81	0.81	0.81	Macey 2017, Zappalorti et al. 2017
Hatchling Survival	0.33	0.31	0.20	0.20	0.26	Derived from Juv. Survival, Tutterow et al. (2017)
Site-specific Egg + Hatchling Survival (8 Months) (P_{21})	0.266	0.206	0.003	0.094	0.061	Chapter 1, Tutterow et al. (2017)

Regional Avg. Egg + hatchling Survival (8 Months) (P_{12})	**0.131**	**0.126**	**0.093**	**0.094**	**0.112**	Chapter 1, Tutterow et al. (2017)
Caged Egg + Hatchling Survival (8 Months) (P_{12})	0.272	0.247	0.122	0.124	0.147	Macey 2017, Zappalorti et al. (2017)
Art. Incubated Egg + Hatchling Survival (8 months) (P_{12})	0.301	0.331	0.219	0.221	0.263	Macey 2017, Zappalorti et al. (2017)
Juvenile Survival	0.815	0.773	0.490	0.500	**0.645**	Updated from Tutterow et al. (2017)
Juvenile Survival + Persistence (P_{22})	0.642	0.654	0.435	0.443	**0.549**	
Juvenile Transition	0.212	0.155	**0.112**	**0.114**	**0.148**	
Juvenile Transition (conditional on survival) (P_{23})	0.1725	0.1200	**0.055**	**0.057**	**0.095**	
Adult Survival (P_{33})	0.935	0.902	0.937	0.887	0.913	Updated from Tutterow et al. (2017)
Fertility (F_3)	1.18	1.45	1.28	**1.24**	1.28	Knoerr et al. (in prep), Tutterow et al. (2017)

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