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Research Article

Hatch Success and Recruitment Patterns of the Bog Turtle

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ABSTRACT Researchers suggest that several bog turtle (*Glyptemys muhlenbergii*) populations in North Carolina, USA, are in decline and have few remaining individuals and low annual survival probability. Most populations are dominated by older adults with few juveniles encountered; however, the proportion of juveniles encountered in 2 populations is higher. It is unknown why the juvenile:adult ratio varies among populations. We conducted a nest monitoring study in 2016 and 2017 to test the hypothesis that sites with fewer juvenile encounters would be where nest predation was highest. We documented the fate of 272 eggs from 83 nests encountered across 7 sites in North Carolina. On average 28% of eggs hatched across all sites over both years, but we observed large variation in hatch success among sites. Predation by mesopredators and small mammals was the primary cause of nest failure. The probability of nest predation decreased with greater emergent vegetation density and increased with greater distance to the edge of the wetland. Cooler temperatures, which prolonged incubation and thus increased predation risk, may also hinder recruitment at higher elevation sites. Our observations are consistent with the hypothesis that nest predation would be highest at sites with fewer juvenile encounters. Managers concerned about low bog turtle recruitment rates should consider the role of nest predation and the potential benefits of management that increases hatch rates. © 2020 The Wildlife Society.

KEY WORDS bog turtle, demography, egg predation, egg survival, *Glyptemys muhlenbergii*, mesopredator, North Carolina, recruitment.

Habitat loss and degradation are leading causes 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 also increase secondary threats such as genetic isolation, road mortality, and predation by human-commensal mammals on turtles and their nests (Mitchell and Klemens 2000, Gibbs and Shriver 2002, Marchand and Litvaitis 2004, Steen and Gibbs 2004). Semi-aquatic turtle species are particularly susceptible to decline because they often require intact landscapes to meet life-history requirements and to facilitate movements. The propensity for large movements between wetlands and adjacent uplands makes many turtle populations vulnerable to habitat alteration (Litzgus and Brooks 2000, Litzgus and Mousseau 2004, Pittman and Dorcas 2009).

The bog turtle (*Glyptemys muhlenbergii*) is a semi-aquatic species found in bogs, wet meadows, swamp forest-bog complex, and fens (Ernst et al. 1994, Buhlmann et al. 2009, Pittman and Dorcas 2009). In the southern portion of the species' range, bog turtles exist within the Southern Blue Ridge Ecoregion of the Appalachian Mountains and surrounding foothills. The wetlands they occupy are collectively referred to as Southern Appalachian mountain bogs. These wetlands are among the most critically endangered ecosystems in the United States today (Noss et al. 1995). Residential development, road construction, and wetland drainage for agriculture has resulted in an 80–90% decline in mountain bogs with <400 ha remaining (Weakley and Schafale 1994, Noss et al. 1995, Herman and Tryon 1997). Many remnant bogs are moderately to highly degraded because of a range of factors (Lee and Norden 1996, Drexler and Bedford 2002, Bedford and Godwin 2003, Tesauro and Ehrenfeld 2007, Stratmann 2015).

Bog turtles are one of the most imperiled chelonians in North America (Seigel and Dodd 2000, Rosenbaum et al. 2007). Although quantitative range-wide estimates are not available, it is likely that a 90% decline in bog turtle populations has occurred during the twentieth century (van Dijk 2011). A recent study of several bog turtle populations (Tutterow et al. 2017) in North Carolina, USA, reported adult survival probabilities were lower than those of some northern populations of bog turtles (Shoemaker et al. 2013) and closely related species such as the spotted turtle (*Clemmys guttata*; Enneson and Litzgus 2008). Low estimates of apparent adult survival indicate that certain bog turtle populations in North Carolina may be in decline

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because small changes in adult survival have the greatest effect on population growth rate for turtles (Congdon et al. 1993, Heppell 1998). Records of juveniles are also absent or rare in most of the bog turtle-occupied wetlands in North Carolina except in 2 populations, where >40% of encounters over >2 decades have been juveniles (Tutterow et al. 2017). The mechanisms responsible for the different proportion of juveniles encountered among populations is not well understood but may be linked to variation in fecundity, nest success, hatchling survival, or juvenile survival (Tutterow et al. 2017). Extended recruitment failures (i.e., turtles transitioning from eggs to hatchlings, hatchlings to juveniles, or juveniles to adults) compounded by low survival at the adult stage may destabilize populations (Congdon et al. 1983, Daigle and Jutras 2005, Knoerr 2018). Thus, the mechanisms influencing the disparity in the juvenile fraction have become an important limiting factor for many bog turtle populations (Tutterow et al. 2017).

Nest and hatchling survival are low for most turtle species (Mitchell 1988, Frazer et al. 1990, Iverson 1991, Paterson et al. 2012) and predation is as a major cause of freshwater turtle nest failure (Congdon et al. 1983, Marchand and Litvaitis 2004, Schwanz et al. 2010). Although multiple taxa prey on turtle nests (Buhlmann and Coffman 2001, Butler et al. 2004, Draud et al. 2004), mesopredators may be the greatest source of nest predation in many systems (Congdon et al. 1983, Christens and Bider 1987, Robinson and Bider 1988, Feinberg and Burke 2003). Changes in vegetation and hydrology may decrease available nesting area and likely elevate mesopredator densities, both of which may further increase the probability of nest predation above the historical norm (Temple 1987, Kolbe and Janzen 2002*b*, Marchand and Litvaitis 2004). Infertility, flooding, heat stress, and an inadequate thermal environment are additional sources of nest failure (Christens and Bider 1987, Warner et al. 2010) and may be linked to weather patterns, connectivity to adjacent populations, impermeability of surfaces in the surrounding landscape, riparian condition, and vegetation characteristics (Schwanz et al. 2010, Strickland et al. 2010).

We investigated egg survival in bog turtles in western North Carolina. We hypothesized that reduced egg survival would be influenced primarily by mesopredators and predicted that nest predation would be highest at sites where we observed fewer juvenile bog turtles. We also hypothesized that certain wetland-scale habitat characteristics, including hydrological and vegetative characteristics, would increase predator access to and detection of bog turtle nests. In addition, because our focal populations occurred across a wide elevation gradient, we predicted that a colder thermal nest environment would result in longer incubation periods that reduce egg survival probabilities.

STUDY AREA

We monitored bog turtle nests at 7 wetlands located in western North Carolina from May 2016–October 2017. The exact locations of the studied wetlands are withheld to prevent poaching of turtles. The study sites ranged from high elevation populations in the Blue Ridge Mountains (869–1,039 m) to populations at lower elevations off the Blue Ridge Escarpment (365–547 m). The area has a temperate seasonal climate and is characterized by frequent snowfall in from 1 December through 28 February, and temperatures from June until August rarely exceeding 31°C. High levels of precipitation (125–130 cm annual) are also characteristic of the area. The wetlands in our study ranged in size from a 0.2-ha isolated wetland existing within a residential area to a 3.1-ha wetland existing within a mosaic of pasture, wet meadow, and woodland. Each wetland maintained a strong groundwater connection. The inundated hydric soil was generally a soft and muddy substrate. Commonly observed fauna in these wetlands included ribbon (*Thamnophis sauritus*) and northern water snakes (*Nerodia sipedon*), wood (*Lithobates sylvaticus*) and pickerel frogs (*Lithobates palustris*), dusky salamanders (*Desmognathus* spp.), eastern newts (*Notophthalmus viridescens*), American robins (*Turdus migratorius*), ravens (*Corvus corax*), coyotes (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), and small rodents (eastern gray squirrel [*Sciurus carolinensis*], eastern chipmunk [*Tamias striatus*], and mice [*Peromyscus* spp.]). The plant community was characteristically open canopy with patches of woody shrubs interspersed amongst emergent vegetation. The area and density of both woody and emergent vegetation was variable and was related to the scale of disturbance or management. Most sites were under active management via cattle grazing, prescribed burns, or manual thinning of plants. Each site was owned privately or by a land conservancy organization.

We collected nest data at 7 sites; however, the bulk of our study focused on 4 primary sites. Sites A and B were off the Blue Ridge Escarpment, contained 2 of the most robust bog turtle populations in the state, and had a high proportion of juveniles encountered (43–54%) in 1995–2014 (Tutterow et al. 2017). Sites D and H were at higher elevation in the Blue Ridge Mountains. Site D had a high abundance of bog turtles with proportionally fewer juveniles (24%) detected between 2002 and 2014. Site H possessed a moderately abundant population and proportionally fewer juveniles (9%) were detected between 1992 and 2014 (Tutterow et al. 2017). Collectively, the study sites contained distinct populations that represented a range of bog turtle population demography. Although other sites in North Carolina have bog turtle populations at greater risk of extirpation, the abundance in those populations is so low that our ability to draw inference as it relates to egg survival is limited. Therefore, intensive nest monitoring took place only at sites where encounter data over the past 10–15 years suggested an abundance of ≥15 adult turtles (G. J. Graeter, North Carolina Wildlife Resources Commission, unpublished data).

METHODS

Field Methods

We acquired all necessary state wildlife permits (North Carolina Wildlife Resources Commission 18-ES00464, 18-SC01069), and all procedures were approved by the Clemson University Institutional Animal Care and Use Committee (AUP 2017-043). We conducted intensive nest monitoring over 2 years. We found bog turtles primarily by probing, an activity that involves tapping submerged turtles with wooden dowels (Carter et al. 1999) and by searching for active and exposed individuals. We also trapped turtles at lower abundance sites with non-baited wire-mesh traps that we placed in rivulets and other wet areas (Somers and Mansfield-Jones 2008). We partially submerged (1–2 cm) the bottom of the traps in water and covered them with vegetation to prevent overheating of trapped turtles. We checked the traps daily. We searched each wetland an average of 30 hours/week from 15 May–15 June in both years. We determined age by counting carapace annuli (this age estimation technique is relatively precise for juvenile turtles but becomes less reliable as the turtles mature). We palpated all females and inspected the inguinal region for shelled eggs or follicles (Congdon et al. 1987) in May, June, and July to determine whether they were gravid. We monitored most female turtles that were of adequate size or had signs of gravidity via a very high frequency (VHF) radio-tag (model R1680, 3.6 g; Advanced Telemetry System, Asanti, MN, USA; 39 individuals in 2016; 56 individuals in 2017) attached with epoxy putty (J-B Weld-WaterWeld, Atlanta, GA, USA) to the mid-posterior pleural scutes. We tracked the 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 used a bobbin with 150 m of thread to aid in locating the nests. We wrapped the bobbins in cellophane and Plasti Dip® (Plasti Dip, Blaine, MN, USA; Wilson 1994) and placed them on the posterior marginal and pleural scutes using a 5-minute 2-part epoxy (Devcon, Milpitas, CA, USA). The thread bobbins weighed approximately 3 g attached. We tied the end of the thread to vegetation and it unraveled as the female moved. To limit weight-related stress, we kept the devices (7 g combined) to ≤6% of the turtle's weight (Schubauer 1981; Pittman and Dorcas 2009); thus, we only used this combination on turtles that weighed ≥115 g. Because the gravid turtles frequently made within-wetland movements during the nesting period, we replaced 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. We used red headlamps after dusk to limit disturbance to nesting turtles. An active turtle at or after dusk suggests nest location searching or laying behavior (digging nests, depositing eggs, covering eggs). Thus, once we observed the nesting turtle, we placed a flag on vegetation 1–2 m away from the turtle to aid in nest identification 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 with nitrile gloves where we had observed her the previous night. If we did not find a nest, 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. We also found 20 nests opportunistically by observing females without transmitters laying eggs or by carefully searching in nesting areas.

Once we found the nest, generally within 12 hours of laying, we recorded nest characteristics and counted the number of eggs. At each nest site, we visually estimated (to within 10%) the percent of standing water within 2 m of the nest and the percent of scrub within 0.5 m of the nest. We assessed density of emergent vegetation in a 0.2-m^2 area around the nest by assigning a score from 0–5, where 0 indicated no emergent vegetation and 5 indicated thick and consistent coverage of the area. We measured density of woody stems in a 0.5-m^2 area; scores were based on the same scale as vegetation. 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, we placed a sealed (Plasti Dip®) thermochron iButton (Maxim Integrated, Addison, TX, USA; 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 the eggs began to hatch. If the nest was depredated, we left the iButton in place until other nests within the wetland hatched to generate comparable thermal measurements. We placed a trail camera (Bushnell Trophy® Cam HD Essential E2, Philadelphia, PA, USA) on a stake approximately 1–3 m from the nest to record nest predation events. We periodically checked the trail camera photographs and surface of the nests for evidence of predation (obvious disturbance or egg fragments) through the incubation period. Through the hatching window (Aug–Oct), we periodically exposed the eggs to document their hatching status. To assess fertility, we opened eggs that had failed and showed evidence of decomposition to determine whether an embryo was present.

Analysis Methods

We categorized the fate of all nests throughout the incubation period. Because predation was the primary source of all nest failure, we used binary logistic regression (generalized linear model [GLM] function) to test hypotheses about the relationship between nest predation (as defined as ≥1 egg was eaten) and environmental conditions within and among sites. We evaluated 5 models that represented various hypotheses about the environmental factors influencing nest predation (Table 1). Before analyzing the data, we evaluated all bivariate correlations among variables, and eliminated 1 variable from any pair with a correlation coefficient >0.70. We also converted all covariate measurements to z-scores prior to analysis. This standardization creates a common scale for predictor variables (mean = 0 and SD = 1) and allows for direct comparison of model coefficients. To generate an overdispersion parameter, we evaluated the global model using a quasibinomial distribution. Because the estimate of the overdispersion parameter was approximately 1 in that model, all subsequent models used a binomial distribution (Demétrio et al. 2014). We compared the relative support for all models using

Table 1. Akaike's Information Criterion corrected for small sample size (AIC_c) values ranking 5 models of bog turtle nest predation across 4 wetlands in western North Carolina, USA, 2016–2017 (data pooled between sites and years). The predator access model included all factors hypothesized to influence mesopredator access to a nest (% standing water, distance to wetland edge, emergent vegetation density, distance to forest edge). The predator detection model included factors hypothesized to influence mesopredator nest detection (woody stem density, % scrub shrub, and emergent vegetation density). The site model represents the latent variable and allows for nest predation to vary by wetland.

Model	K^a	AIC_c	ΔAIC_c	AIC_c weight	Cumulative model weight	Log-likelihood
Predator access + site	8	86.12	0.00	0.42	0.42	−34.01
Predator access	5	86.64	0.52	0.32	0.74	−37.90
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	1.00	−41.81

[a] Number of parameters.

Akaike's Information Criterion corrected for small sample size (AIC_c; AICtab function, AICcmodavg package in R; Mazerolle and Mazerolle 2017). We subsequently used the modavg function to average the parameter estimates appearing in the top models ($\Delta AIC_c < 2$). We validated models using leave-one-out cross-validation (Davison and Hinkley 1997).

We compared the thermal environment of nests across the 4 intensively monitored sites over 2 years where we had thermal data for ≥7 nests. We considered 7 different measures of the thermal environment; however, after eliminating correlated variables ($|r| > 0.7$), we used only 3 in our analyses: mean daily nest temperature, mean minimum nest temperature, and mean daily range of nest temperature. We first used an analysis of variance (ANOVA) to assess the effect of site on temperature variables for 56 nests. Temperatures were warmer across most sites in 2017; however, we were primarily interested in evaluating site comparisons across years. If we established a difference existed amongst the means, we used 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 56 available thermal datasets where incubation period was known (glm function, Gaussian family; Car package in R; Fox and Weisberg 2011). Specifically, we modeled incubation period as a function of mean temperature, mean minimum temperature, and the mean thermal range.

RESULTS

Most turtle observations (>300 distinct individuals) came from 4 study wetlands in 2016–2017, sites identified as A, B, D, and H in Tutterow et al. (2017). The remainder came from sites J, K, and L. At sites A and B, age estimated by counting scute annuli over the 2016 and 2017 field seasons indicated successful recruitment in each of the last 10 years. Juveniles were highly represented in populations at sites A and B (observed juvenile fraction >0.4). Compared to sites A and B, Sites D and H appear to possess populations that are dominated by older turtles (median age >25 yr) with an obvious recruitment event having also occurred approximately 12 years ago at both sites. Juveniles represent 0.2 of total individuals at site D and 0.1 at site H during this study period.

We found 83 bog turtle nests (272 eggs) across both field seasons across 7 sites. Seventy-eight of those nests (252 eggs) came from the 4 focal sites (A, B, D, and H; Table 2). Approximately 28% of eggs (75 eggs) hatched across all sites over both years. Average egg survival by site ranged from <1% to 56% over both years. The highest egg survival observed at 1 site (site A) in a given year was 60%.

Predation accounted for the greatest source of nest failure (Table 2). The 2 sites with robust data (≥25 eggs/season) over both field seasons showed limited inter-annual change in egg predation; site A had 12% and 22% predation and site D had 96% and 84% predation in 2016 and 2017, respectively. As evidenced by 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 (*Mephitis mephitis*) accounted for 92% (48/50) of depredated eggs and 84% (47/56) of egg failure at site D over both field seasons. Raccoons and Virginia opossums also depredated nests and were responsible for 10 depredated eggs across 4 events (an event is defined as all depredated eggs consumed or destroyed by the same individual animal in a single night at a site). Of nests with known lay dates, mesopredator events took place 3–59 days after egg laying ($\bar{x} = 18.6$ days).

Small mammals accounted for approximately 31% of all depredated eggs and 100% of depredated eggs at site H in 2017

Table 2. Bog turtle egg fate across 4 wetlands in western North Carolina, USA, 2016–2017. We included only sites with ≥8 nests with a known fate in the summary. We defined destroyed eggs as non-predated eggs smashed or broken by animals, infertile as eggs with no evidence of embryonic development (from visual inspection), developmental problems as those that died after some period of development or while hatching without signs of inundation or heat stress, drowned as eggs that became submerged during observed inundation events, and heat stress as desiccated eggs that failed after multiple days of temperatures >32°C as evidenced by iButton data.

Site	Number of eggs	Hatched	Depredated	Destroyed	Infertile	Developmental problems	Drowned	Heat stress
A	71	0.56	0.18	0.03	0.13	0.04	0.06	
B	49	0.45	0.23	0.04	0.08	0.10		0.10
D	106	0.01	0.90		0.09	0.01		
H	26	0.15	0.81			0.04		

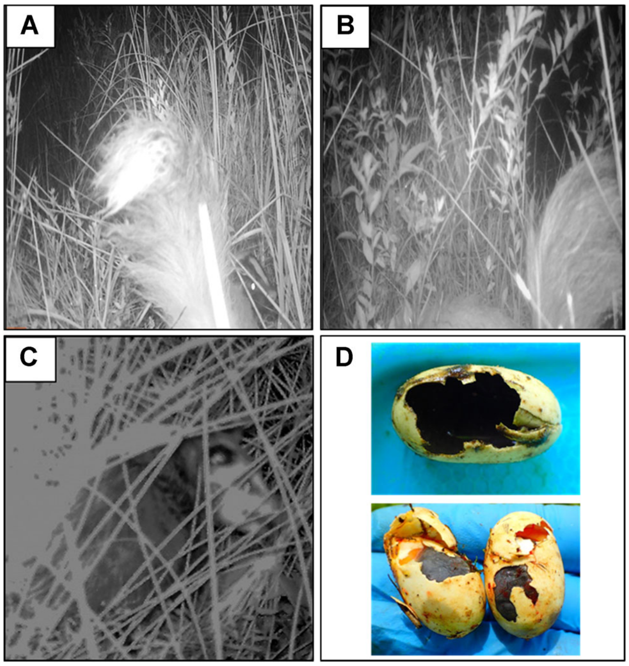

Figure 1. Sample camera trap photos depicting bog turtle nest predation events by striped skunks (A, B) and Virginia opossum (C), western North Carolina, USA, 2016–2017. Predation events by small mammals (D) were evident from the damage pattern on eggshells.

(85% of the eggs documented at that site). Multiple small-mammal species may have been responsible because we observed a wide range of predation signs: all eggs missing with no obvious disturbance, single eggs missing, or egg(s) partially chewed on (Fig. 1). Of nests with known lay dates, small-mammal predation events (as defined above; $n = 15$) took place from the night of egg laying through egg piping (1–94 days, $\bar{x} = 54$ days). Other animal sources of nest destruction included trampling by cows ($n = 5$) and 1 case where a nest was exposed and partially depredated by a crayfish (*Cambarus* spp.) while excavating its burrow. In some cases, we observed eggs being consumed by insects such as ants and the root systems of a grass (as evidenced by a root entering through a pinhole and completely filling the interior of an eggshell). Although it is possible that insect predation of living embryos occurred, we chose to place eggs with these characteristics within the infertile or developmental problems categories because the limited evidence supported opportunistic scavenging. Other apparent sources of egg failure included flooding, heat stress, infertility, and developmental problems (Table 2).

Among nests lost to predation, 2 models (predator access and predator access + site) received substantial support. Both models collectively represented 74% of the Akaike weight of all models (Table 1), and each had high classification accuracy based on leave-one-out cross validation (predator access = 73% and predator access + site = 78% accuracy). For the variables shared between the 2 models, 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. Among the 4 habitat variables shared between the top models (% standing water, distance to wetland edge, density of emergent vegetation, distance to forest edge, only emergent density ($\beta = -1.26 \pm 0.50$ [SE]) and distance to wetland boundary ($\beta = 0.95 \pm 0.40$) had statistically significant effect sizes. The probability of nest predation decreased with higher emergent vegetation density and increased with greater distance to the edge of the wetland (Fig. 2).

Mean incubation temperature for the 56 nests with thermal data ranged from 20.45–23.57°C and we rejected the null hypothesis of no statistical difference among sites (ANOVA, $F_{3,52} = 27.5$, $P \leq 0.001$; Fig. 3A). Mean daily minimum temperatures ranged from 16.9–20.0°C, and we again were able to reject the hypothesis that values were not statistically different across sites (ANOVA, $F_{3,52} = 28.8$, $P \leq 0.001$; Fig. 3B). A comparison of mean daily thermal range across sites (6.95–8.66°C) reveled no evidence that sites were statistically different [ANOVA, $F_{3,52} = 1.35$, $P = 0.27$; Fig. 3C). Pairwise comparisons using Tukey's honestly significant difference for the 2 significant ANOVA tests (mean and mean daily minimum) revealed differences between low (sites A and B) and high elevation sites (sites D and H; Fig. 3). Of 18 nests with known incubation periods and thermal data, incubation periods ranged from

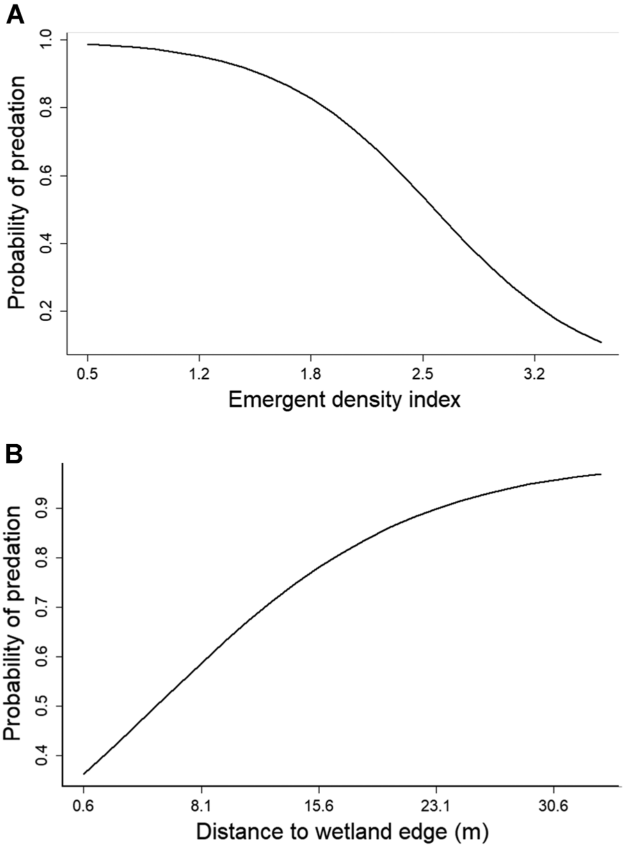

Figure 2. Predicted probability of nest predation for bog turtle nests across 4 sites in western North Carolina, USA, 2016–2017. The predator access model included 4 variables; however, only density of emergent vegetation (A) and distance to edge (B) had a statistically significant effect. The emergent density index was for a 0.2-m^2 area around the nest and ranged from 0–5, where 0 indicated no emergent vegetation and 5 indicated thick and consistent coverage of the area.

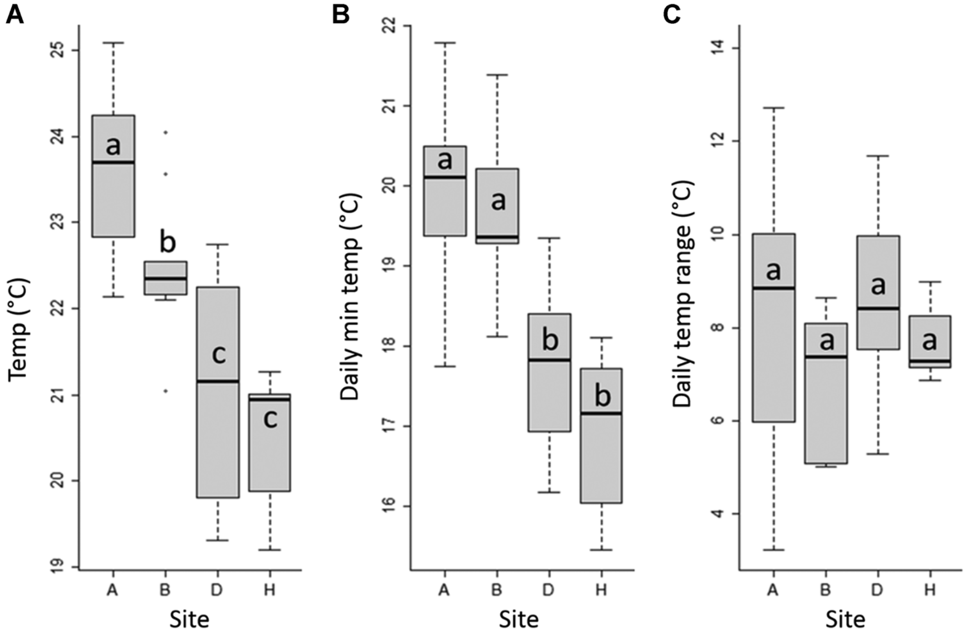

Figure 3. Mean daily temperature (A), mean daily minimum temperature (B), and mean daily temperature range (C) for 56 bog turtle nests with known or hypothesized incubation periods; these nests were located at 4 sites in North Carolina, USA, 2016–2017 (site A = 20 nests; site B = 10 nests; site D = 19 nests; site H = 7 nests). We continued to measure temperatures at failed nests using mean incubation periods for hatched nests within the wetland ($n = 38$). Letters within bars represent statistically significant differences in pairwise comparisons based on Tukey's honestly significant difference test ($\alpha = 0.05$). The ends of the box are defined by the extent of the 25th and 75th quartile values, and the black line represents the median. Whiskers extend 1.5 times the interquartile range.

60–95 days ($\bar{x} = 75$ days). Among the 4 nests in sites with elevations >869 m (sites D and H), incubation periods were approximately 21 days longer than nests ($n = 14$) at lower elevations (<548 m; sites A and B). Mean nest temperature was the only significant predictor of incubation period (GLM, $P \leq 0.001$, df = 14, $\beta = -7.23 \pm 1.16$ [SD]). This model predicted an incubation period that was 3.6 days shorter for every 0.5°C increase in average temperature (between 19.7 and 24.7°C) during the incubation period, assuming the mean value for other modeled covariates. Eggs with lower mean temperatures during their incubation had longer incubation periods (Fig. 4).

DISCUSSION

Status assessments, including assessments of survival at early life stages, are needed for bog turtles and other globally imperiled turtle species (van Dijk et al. 2014). A limited but growing body of research has been conducted on bog turtle egg survival across its range (Whitlock 2002, Macey 2015, Zappalorti et al. 2017, Byer et al. 2018). Within this North Carolina study, bog turtle hatch success varied widely among the 4 sites that we intensively monitored; however, egg survival was relatively consistent within sites between 2016 and 2017. Nest predation was the most prevalent cause of nest failure and, among those nests depredated, most were consumed by mesopredators. Human-commensal predators (e.g., northern raccoon, striped skunk, red fox [*Vulpes vulpes*]) have been reported as the largest sources of increased bog turtle predation in altered habitats (U.S. Fish and Wildlife Service 2001) and we positively identified mesopredators as bog turtle nest predators. At site D, a striped skunk or skunks systematically depredated 27 of 33 nests across multiple nights and over both years. The skunk(s) depredated nests nearly exactly 1 year apart, with the 2016 episode occurring 2 and 3 July and the 2017 episode occurring 31 June–1 July.

Researchers have reported a neutral or negative relationship between nest visitation or nest flagging and the probability of nest predation (Tuberville and Burke 1994, O'Grady et al. 1996, Burke et al. 2005, Edmunds et al. 2018), so we do not think that our activity increased

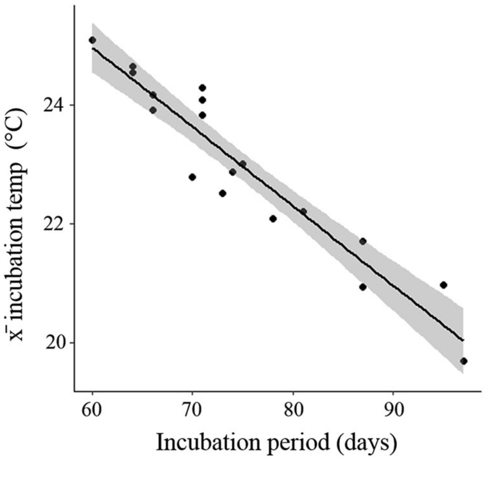

Figure 4. The effect of mean nest temperature on incubation period for 18 bog turtle nests at 4 sites in North Carolina, USA, 2016–2017, with known lay and hatch dates. The shaded area represents the 95% confidence interval.

nest predation. The consistent variability in egg survival across sites appears to mirror observed recruitment patterns and suggests that observed egg survival may reflect longer-term trends and not research-augmented predation. Observations during the 2016 and 2017 field seasons broadly validated the site-specific disparities in abundance and age structure depicted in Tutterow et al. (2017).

Factors that influence a predator's access to nests best predicted nest predation among the wetlands we surveyed. Several researchers demonstrated that mammalian predation is higher along ecological edges (Wilcove 1985; Temple 1987; Paton 1994; Kolbe and Janzen 2002*a*, *b*). Contrary to those studies, but consistent with Byer (2015), nest predation may be lower along wetland boundaries and higher in the interior of the wetland for bog turtles. We believe this contrast is a function of the micro-topography in our focal wetlands. Each wetland has variable complexity in topography that generates wet and dry areas throughout. Rivulets and rivulet edges reduced emergent vegetation and facilitate predator access into the wetland interior. Coincidentally, a large proportion of nests at site D were within 2 m of rivulets. Emergent vegetation density was also part of our predator access model; we predicted it would be inversely related to predation risk. Many turtle species nest in open areas where higher nest temperatures accelerate embryonic development (Janzen 1994, Wilson 1998, Janzen and Morjan 2001, Kolbe and Janzen 2002*a*, Micheli-Campbell et al. 2013). Because mesopredators use linear search patterns (Congdon et al. 1993), it is possible that turtles may be selecting to nest in the very same areas that are preferred predator corridors. Although research is mixed (Burger 1977, Robinson and Bider 1988, Valenzuela and Janzen 2001, Marchand and Litvaitis 2004, Escalona et al. 2009), the risk of large predation events may be exacerbated if nests are clustered linearly along these interior wetland edges.

Similar to other researchers, we documented nest predation events by small mammals (Whitlock 2002, Macey 2015, Zappalorti et al. 2017, Byer et al. 2018). Small predator species may include short-tailed shrew (*Blarina brevicauda*), star-nosed mole (*Condylura cristata*), various mice species, and American mink (*Neovison vison*). We also observed black racers (*Coluber constrictor*) within sites A and B, so it is possible that snake predation may account for some of the missing eggs. These predation events occurred from the night of laying through pipping 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 ($\bar{x} = 30.4$ days) in comparison with other aquatic turtle species (Tinkle et al. 1981, Spencer 2002, Butler et al. 2004, Riley and Litzgus 2014). Similar to observations by Byer (2015), nest predation remains a threat for bog turtles across the entire incubation period, with mesopredators posing a significant threat, particularly early in the incubation period, and small mammals acting as sources of continued predation until hatch.

Average egg survival (0.28) was comparable to northern populations of bog turtles (range = 15–33%; Whitlock 2002, Macey 2015, Zappalorti et al. 2017, Byer et al. 2018; Table 3). As in our study, predation was the primary cause of egg failure across all previous studies and ranged from 51–73% (Table 3) by study, site, and year. Whitlock (2002) observed egg predation rates from 0.05–100%, and Zappalorti et al. (2017) recorded hatch success as high as 83% in a given season. Whitlock (2002) and Byer et al. (2018) both documented substantial nest predation events, but the predators were not identified.

Although egg failure was primarily influenced by predation, we also identified other sources of failure. The true proportion of eggs potentially affected by other variables (destroyed, infertility, developmental problems, flooding, and heat stress) may have been higher had nest predation rates been lower. Of those eggs that were not depredated, approximately 10% did not develop across all sites; a state we attributed to infertility. Two nests were in areas of high emergent density and subsequently were buried atypically in the thatch of dead rush (*Juncus* spp.). Both nests experienced extreme and extended thermal variability as evidenced by iButton data and likely failed because of heat stress. Similar to Zappalorti et al. (2015), we also documented bog turtle egg mortality associated with inundation. Although risk of failure from inundation was much lower than from nest predation, the effects of landscape and flooding may be an important consideration at some sites.

Our study sites represented a wide elevation gradient, so the thermal environment experienced by bog turtle eggs was different across sites. Our data are consistent with the assumption that lower temperatures during incubation extend the incubation period (Fig. 4). Because we recorded high rates of predation at our high elevation sites, we were unable to observe egg survival trends as they relate to the thermal environment in a statistically significant way. Several

Table 3. Studies on the fate of wild, non-protected bog turtle eggs summarized by study, research years, and states. We combined data from all sites involved in each study and present it as a proportion of each total.

	Byer et al. (2018) 2013–2014 MD	**Knoerr et al. (this study) 2016–2017 NC**	**Macey (2015) 2008–2012 NY**	**Whitlock (2002) 1994–1997 MA**	**Zappalorti et al. (2017) 1974–2012 NJ, PA**
Number of eggs	135	272	80	150	161
% eggs depredated	0.70	0.53	0.60	0.73	0.51
% other sources of failure	0.15	0.19	0.10	0.07	0.16
% eggs hatched	0.15	0.28	0.30	0.19	0.33

researchers reported that colder incubation temperature reduces embryonic survival, body size, and performance, and increases time to maturity in turtles (Bobyn and Brooks 1994, Wilson 1998, Du and Ji 2003, Schwanz et al. 2010). Longer incubation periods may result in greater opportunity for nest predation events (Whitlock 2002), thermal extremes, and flooding. High emergent vegetation densities at higher elevation sites may further increase risk of failure by forcing atypical nesting placement in suboptimal conditions. Collectively, a cooler climate 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). 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.

Important data gaps remain to be filled to promote effective and targeted conservation strategies. The number of years between successful recruitment episodes a population can tolerate is currently unknown but likely depends upon underlying vital rates. 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 or juveniles may also be different enough across sites to influence recruitment success. Future research that identifies the linkages between nest predation rates and the surrounding land use would likely benefit conservation efforts for bog turtles. Because reduced survivorship at multiple life-stages appears characteristic of many North Carolina bog turtle populations, research that calculates the effects of age- or state-specific survival on demography and population growth rate will offer insight to management strategies (Knoerr 2018). Calculating the scale of those effects will aid managers in evaluating the potential for various management options to stabilize bog turtle populations. A rigorous decision framework for evaluating the suitability of population manipulation actions will be an important component in the development of a strategic conservation plan for the species.

MANAGEMENT IMPLICATIONS

High nest predation rates may reduce recruitment and eventually effect the size and viability of bog turtle populations. Given that nest predation threatens population persistence, we suggest the following potential solutions: vegetative and hydrological management that increases viable nesting area and wetland site fidelity, predator removal, protection of nests, and head-start programs that are spatially and temporally explicit. With adult abundance so low at some sites, the number of hatchling turtles produced is limited regardless of time and financial investment; therefore, we would also suggest considering alternative methods of augmenting populations, such as captive breeding and translocation of young turtles.

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