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Bog Turtle (*Glyptemys muhlenbergii*) Nesting Ecology and the Efficacy of Predator Excluders in New York

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Abstract - Nest predation is a conservation concern for species with low reproductive output, such as *Glyptemys muhlenbergii* (Bog Turtle). Over 4 years and across 9 sites in New York, we monitored 77 Bog Turtle nests and examined clutch size (n = 77; 1–5 eggs; mean = 3.3 eggs ± 0.92 S.D.), incubation periods (n = 27; 67–89 days; mean = 79.7 days ± 5.78) and temperatures, and the effectiveness of predator excluders. We compared nest-predation rates with (n = 53) and without (n = 24) predator excluders and assessed the effects of predator excluders on hatching rates and incubation timing. On average, protected nests lost 1.04 fewer eggs to predation than nests without predator excluders, and the predation rate (loss of 1 or more eggs) was 25% lower for protected nests (38%) than for unprotected nests (63%). However, the failure rate for eggs surviving predation was marginally higher for protected nests versus unprotected nests, and the number of viable hatchlings produced per nest was not statistically different between protected versus unprotected nests. Overall, our results underscore the need to monitor hatching rates in addition to predation rates when evaluating the success of predator-exclusion devices for turtle conservation.

Introduction

Across North America, freshwater turtle populations have declined due in large part to direct and secondary effects of encroaching human land development including road mortality, collection for the pet trade, and predation from human-commensal species (Fahrig 2003, Gibbs and Shriver 2002, Mitchell and Klemens 2000). Higher densities of predators associated with human presence (e.g., *Procyon lotor* (L.) [Northern Raccoon] and *Mephitis mephitis* (Schreber) [Striped Skunk]) can lead to increased rates of predation of turtles and their nests (Engeman et al. 2005, Garber and Burger 1995, Kurz et al. 2012, USFWS 2001, Urbanek et al. 2016). Habitat loss and fragmentation can also result in increased rates of freshwater turtle nest predation because turtle nests may be at higher densities within smaller areas with increased amounts of edge habitat (Bougie et al. 2020, Holden 2021, Kolbe and Janzen 2002, Marchand and Litvaitis 2004, Temple 1987; but see Murphy et al. 2022).

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Depending on the characteristics of a nesting habitat and the predators present within a landscape, turtle nest predation rates vary by site and year (Brown and Macdonald 1995, Congdon et al. 1983, Kolbe and Janzen 2002). For example, Kolbe and Janzen (2002) conducted a 5-year study of *Chrysemys picta* (Schneider) (Painted Turtle) nest success and found that nest-predation rates varied from 20% to 76%. However, many researchers have reported nest-predation rates of >50% for freshwater turtle species (e.g., 63% in *Emydoidea blandingi* (Holbrook) [Blanding's Turtles; Congdon et al. 1983]; 93% in *Emydura macquarii* (Gray) [Murray River Turtles; Spencer 2002]). For threatened turtle species, these high predation rates can reduce recruitment and may eventually impact the size and viability of populations (Crouse et al. 1987, Marchand and Litvaitis 2004, Mullin et al. 2020).

To reduce the effects of nest predation, conservation managers may deploy predator excluders in the form of cages or other protective coverings over turtle nests (Bougie et al. 2020, Campbell et al. 2020, Graham 1997, Kurz et al. 2012, Ratnaswamy et al. 1997, Riley and Litzgus 2013, Zappalorti et al. 2017). However, predator excluders could potentially have negative effects on hatching rates, incubation timing, and even sex ratios (for species with temperature-dependent sex determination; Bull and Vogt 1979). For example, predator excluders can shade nests and reduce nest temperatures (Breckenridge 1960), which may lead to reduced hatching rates in some cases (Garrett et al. 2010, Janzen 1993; but see Burke and Eugene 2024, Riley and Litgus 2013). Therefore, it is critical to evaluate the efficacy and potential detrimental effects of nest excluders before adopting this method as a viable conservation strategy.

For the federally threatened *Glyptemys muhlenbergii* (Schoepff) (Bog Turtle), habitat loss and fragmentation are the primary threats to persistence, and conservation managers hypothesize that landscape changes have increased the predation rates from human-commensal predators (USFWS 2001, Van Dijk 2011). USFWS (2001) discusses evidence that primary predators of both adults and nests include human-commensal species such as Northern Raccoon, Striped Skunk, and *Vulpes vulpes* (L.) (Red Fox). Additionally, Bog Turtle nest predators include small rodents (Byer et al. 2018, Whitlock 2002, Zappalorti et al. 2017), birds (Byer et al. 2018, Whitlock 2002), and insects (Byer et al. 2018, Knoerr et al. 2021, Whitlock 2002). Reported Bog Turtle egg/nest-predation rates vary across studies and years, with 12–57% egg predation at 5 sites in Pennsylvania (Zappalorti et al. 2004), 40–74% egg predation across sites in Maryland (Byer et al. 2018), 53% average egg predation across 5 sites in North Carolina (Knoerr et al. 2021), and a 33% mean nest-predation rate in a Massachusetts study (maximum of 94% in 1 year; Whitlock 2002). Knoerr et al. (2021) found evidence that greater egg survival resulted in higher recruitment of juvenile Bog Turtles, indicating that protecting nests from predation may be a viable strategy for conserving Bog Turtle populations.

In this study, we present evidence on the efficacy of predator excluders for the Bog Turtle in the northern portion of the species range, and test for adverse consequences of predator excluders. We predicted that predator excluders would substantially reduce Bog Turtle nest predation and would have no detectable

adverse effect on hatching rates or the timing of incubation. If so, this study would lend support to the installation of predator excluders wherever nest predators are identified as a potential driver of Bog Turtle population declines.

Field-Site Description

In southeastern New York State, Bog Turtles are most commonly found in calcareous wet meadows and rich graminoid fens (Kiviat and Stevens 2001, Shoemaker 2011). Our study was conducted at 9 sites (i.e., CFP, COL, EFP, SHA, SHF, SHR, SMF, WDF, WFP; Macey 2015, Shoemaker 2011) in southeastern New York over 4 years (2009–2012) (Fig. 1). Although we studied nesting at most of these sites for multiple years, only 1 site (SMF) was studied for all 4 years (see Table S1 in Supplemental File 1, available online at https://www.eaglehill.us/NENAonline/suppl-files/n31-sp12-N2059pp-Macey-s1, and for BioOne subscribers, at https://www.doi.org/10.1656/N2059pp.s1). We are herein withholding specific location information of these sites due to illegal collection for the pet trade (USFWS 2001); however, the general habitat characteristics of these sites are described.

Within the same wetland complex, CFP, EFP, WFP, and SHR are mineral-rich sloping fens composed primarily of calcareous wetland plant communities that encompasses 0.2, 0.4, 0.8, and 4.1 ha, respectively. These sites are discrete wetlands that are geographically distinct and separated by a matrix of coniferous and deciduous forests, steep embankments, ridges, and a low-traffic road. In a separate complex, SHF and SHA are separated by upland and wetland forest, cropland, pasture, and light residential/commercial land use, including a road with moderate traffic. SHF has ~1.6 ha of mineral-rich sloping fen habitat with an intermittent drainage stream dividing the habitat into 2 sections, and SHA has ~0.6 ha of fen habitat with an unpaved farm access road bisecting the habitat into 2 distinct areas.

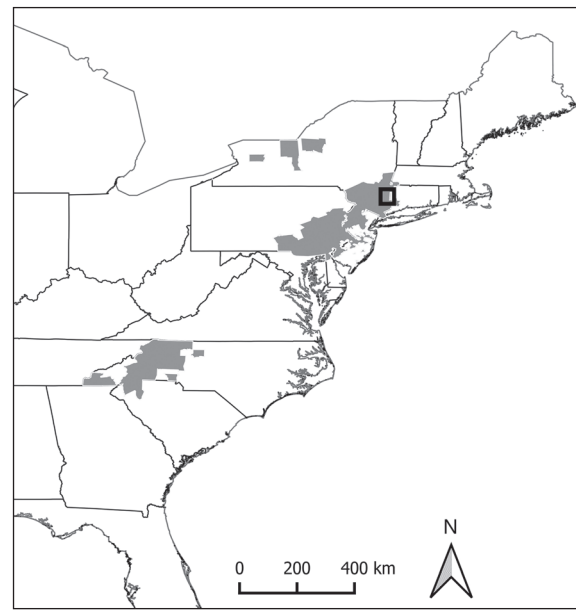

Figure 1. Map of the eastern US, illustrating the current estimated Bog Turtle range (gray polygons; USFWS 2001) and the general location of our field sites (boxed region).

SMF is found within a 110-ha continuous wetland complex. The 2.5 ha of habitat where Bog Turtles are found at SMF is characterized by *Acer rubrum* L. (Red Maple) swamps with seepage and shrub fens and an area of wet pasture primarily composed of *Phalaris arundinacea* L. (Reed Canary Grass). At the time of this study, SMF was actively grazed by *Bos taurus* L. (Cattle). COL is a 1.3-ha site within a 22-ha wetland complex. The Bog Turtle habitat comprises graminoid fen, marsh, and hardwood swamp with a series of springs and surface drainage from nearby wetlands. Prior to our study years, management at this site has included herbicide treatment of large stands of *Phragmites* spp. (common reed) and light Cattle grazing. In 2009, *Castor canadensis* Kuhl (American Beaver) activity altered a large portion of the site, flooding the habitat, including some nests. WDF is a 1.2-ha calcareous sloping wet meadow with groundwater seeps adjacent to a forested swamp. During the study, this site was actively grazed by Cattle and had agricultural modifications, including drainage swales and a livestock watering hole. Any site with active grazing had installed electrified fences to prevent grazers from entering known nesting areas during the duration of the nesting season.

Methods

Field methods

Female morphometric data collection. We surveyed and hand-captured Bog Turtles in southeastern New York each spring (late April to late May) during the 4-year study period. We assigned unique notch codes to all unmarked turtles (Cagle 1939). We determined sex based on sexually dimorphic shell and tail characteristics (Ernst and Lovich 2009). When we captured a female Bog Turtle, we measured the straight-line maximum carapace length (SCL; mm; Ernst and Lovich 2009), mass (g), and age class (i.e., juvenile, adult, old-adult) based on the number of distinct annuli found on the plastron scutes (modified from Sexton 1959), and the relative amount of carapace and plastron wear (Litzgus and Brooks 1998). For this study, we considered females with fewer than 10 annuli to be juveniles, following Whitlock (2002). "Adults" included any female with 10 or more annuli. Upon initial capture, we assessed whether females were gravid by gently palpating the inguinal region for shelled eggs (Congdon et al. 1983) and monitored any assessment of the presence of shelled eggs throughout the nesting season to confirm reproductive status.

Nest data collection. For any adult female captured, we affixed a radio transmitter (4.5 g; L.L. Electronics, Mahomet, IL) to a rear pleural scute using waterproof PC-11 epoxy (PC-Products, Allentown, PA). We tracked females using a handheld, R-1000 telemetry receiver (Communications Specialists, Orange, CA) approximately once per day between the last week of May and the end of the nesting season (mid–late June) at dusk—when Bog Turtles often exhibit nesting behavior (Ernst and Lovich 2009). After observing a female excavating a potential nest (displacing soil with hind legs), we returned to the excavation site the following day to establish if the female had deposited eggs. Additionally, we occasionally ($n = 9$) discovered nest sites opportunistically by observing females without transmitters

nesting or by searching for nests by hand (most of the time with gloves) in hummocks that appeared disturbed.

In these sites, Bog Turtles nested exclusively in hummocks, which were characterized as living structures that included the sedge tussock itself and all the vascular and non-vascular plants that colonized it. For all confirmed nests, we noted the date, counted the number of eggs, and placed a Tidbit Hobo temperature logger (Onset, Bourne, MA)—set to record the temperature on the half-hour—within the nesting hummock. We opted not to place the temperature logger within the nest cavity to avoid disturbing or altering nest conditions. Instead, we created a secondary cavity within the nesting hummock, carefully covering and camouflaging the temperature logger to avoid predator detection. Additional precautions were also taken to avoid unintentionally signaling nest locations to predators, such as avoiding placement of flagging tape directly at the nest location, using disposable gloves, and approaching nest locations circuitously (Burke et al. 2005, Rollinson and Brooks 2007, Whelan et al. 1994). From late July to late September, we monitored nests approximately once per week for egg conditions and signs of hatching. Because monitoring occurred on a weekly basis, nest hatch dates were not recorded as the day the first egg was observed hatching but as the median day between the previous monitoring date and the date hatching was observed. We deemed eggs hatched when either hatchlings were observed, or eggshell remains displayed hatching characteristics such as the clean-edged splitting of the eggshell into distinct parts (from hatchling egg-tooth; Hamilton 1940). If a nest with eggs at one monitoring event was found during the next monitoring event with no hatchlings and many indistinguishable eggshell pieces, sometimes appearing shredded, we would designate the nest as predated. During the last week in October, we deemed any remaining unhatched eggs to be unsuccessful and retrieved the temperature loggers.

Predator-excluder deployment. We originally designed this study as a 2-year study, building off the work of previous and coinciding research (Myers 2011). In 2009, all study nests but 1 were protected (protected = 21 nests; unprotected = 1 nest), and in 2010, no nests were protected (unprotected = 15) (see supplemental Table S1 in Supplemental File 1). When we elected to continue this study after 2010, we protected approximately half of the nests in 2011 (protected = 9 nests; unprotected = 7 nests) in a pair-wise manner per site (i.e., alternating between placing excluders on nests and leaving without excluders as nests were found at any particular site) (see supplemental Table S1 in Supplemental File 1). Based on preliminary assessments of predator-excluder effectiveness in reducing predation and other goals of the larger project, we protected all but 1 nest in 2012 (protected = 23 nests; unprotected = 1 nest; see supplemental Table S1 in Supplemental File 1). Unprotected nests in 2009 and 2012 were an artifact of finding the nests very late in the nesting season.

We constructed excluders using 0.64-cm (0.25-in) hardware cloth fashioned into a low profile, open-bottomed cage with a closed hardware-cloth top secured with wire (Fig. 2). We built cages in a 12 cm x 12 cm x 12 cm triangular prism shape with 4–6 cm hardware-cloth flanges extending below the base of the

Figure 2. Low-profile predator-excluder devices constructed out of 0.64-cm (0.25-in) hardware cloth, which we installed on a subset of Bog Turtle nests during our 4-year study period. The cage top had a hinge and was secured by wire ties for ease of opening and checking on egg status or removing any dense vegetation overgrowth without disturbing the integrity of the nest. The base of the cages was secured to the ground using wooden dowels with a diameter of 0.64 cm (0.25 in). Our design loosely followed Zappalorti et al. (2017).

excluders. We found a triangular shape to be easy to construct and versatile as the size of nest hummocks varied and the triangular shape reduced the need for sizing modifications (as compared to a square). Because Bog Turtles may use nesting hummocks multiple years in a row (Whitlock 2002), we aimed to avoid compromising the structural integrity of hummocks. Therefore, we did not counter-sink excluders below the surrounding substrate surface but instead secured them to nesting hummocks with wooden dowels 0.64 cm (0.25 in) in diameter inserted into the hardware cloth flanges, careful not to disturb nest cavities. Our excluders were modified from the design used in the Zappalorti et al. (2017) Bog Turtle nest predator-excluder study, which used larger gauge hardware cloth (1.1-cm), were taller (~61 cm), wider (~38 cm), secured with large wooden stakes, and buried 8–15 cm below the substrate. Other studies since 2012 have used or slightly modified our design (McCoy et al. 2021, Travis et al. 2018).

Because study nests were only monitored once per week during the hatching period, we removed the predator excluders from all nests within a site as soon as any nest within that site showed evidence of hatching (to prevent entrapping hatchlings). Therefore, during the hatching season, nests deemed "protected by predator excluders" might have had no protection for a period of a few days or, in some cases, a few weeks.

Data analysis

We first ran separate chi-squared tests to evaluate the effect of predator excluders on (1) egg-predation rate (n = 257 eggs), (2) nest-predation rate (n = 77 nests; nest predation defined as one or more depredated eggs in a nest), (3) unconditional-hatching rate (n = 257), and (4) the egg-failure rate conditional on surviving predation (n = 158) (see Table 1 for precise definitions of terminology used in this study relating to Bog Turtle nesting ecology).

Integrated model of Bog Turtle nesting ecology. To assess the many interrelated processes potentially driving egg production and hatching success (including the

Table 1. Definitions for all summary statistics used to discuss Bog Turtle nesting outcomes in this study.

Level	Statistic	Definition
Nest	Nest-predation rate	Fraction of nests for which one or more eggs were depredated
	Nest success	Fraction of nests for which one or more eggs hatched successfully
Egg	Egg-predation rate	Fraction of eggs depredated (pooled across all nests)
	Conditional egg-failure rate	Fraction of eggs that fail to hatch, conditional on surviving predation
	Conditional hatching rate	Fraction of eggs that hatch successfully, conditional on surviving predation (complement of conditional egg-failure rate)
	Unconditional hatching rate (or "hatching success")	Fraction of eggs hatching successfully

effects of predator excluders), we built a structural equation model (Grace et al. 2010) of clutch size, nest-predation rate, hatching rate (conditional on surviving predation), incubation timing, and nest temperature in our study system (Fig. 3). In this model, we assumed that egg predation and egg failure (conditional on surviving predation) were independent processes. That is, we assumed that the eggs consumed by predators would be expected to have the same hatching rate (had they not been depredated) as eggs passed over by predators.

Clutch size: We modeled clutch size as a log-linear function of maternal carapace length (CL, in mm), assuming a Poisson error distribution:

$$\text{Log}(Eggs_n) = \beta_{0eggs} + \beta_{CL} \bullet \text{CL},$$

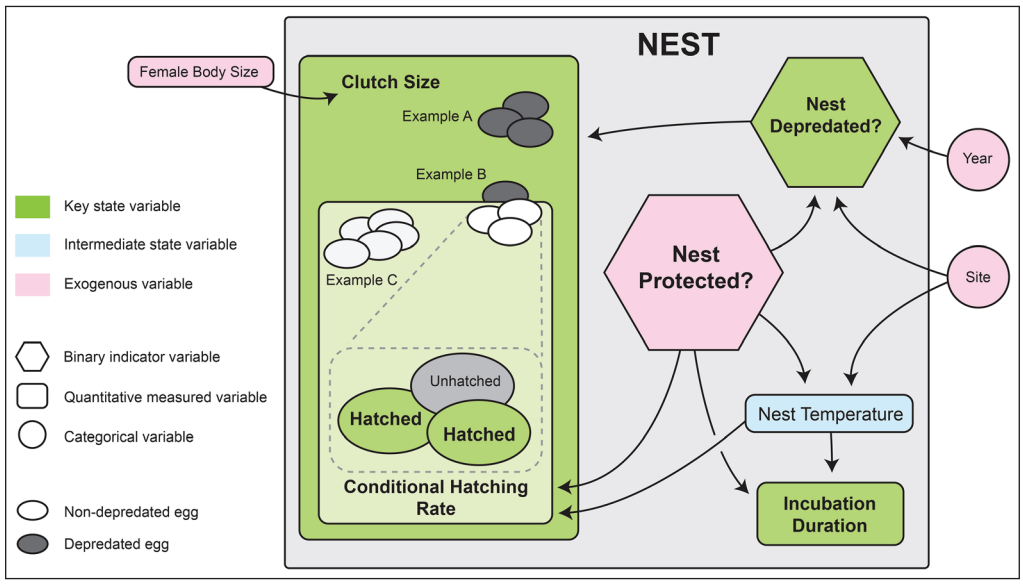

Figure 3. Schematic diagram of the integrated Bog Turtle nesting-ecology model (structural equation model) used to model the interacting components of nesting success in our study system in northeastern New York. The large box labeled "Nest" represents a Bog Turtle nest in our study (n = 77). Three example nests are shown: Example A, a fully depredated nest (dark grey ovals); Example B, a partially depredated nest (dark grey and white ovals); and Example C, a non-depredated nest (white ovals). Key state variables (shown in green) modeled for each nest include whether or not a nest was depredated ("Nest Depredated?"), the total number of eggs deposited ("Clutch Size"), and the period from egg deposition to hatching ("Incubation Period"). At the egg level, the most important state variable (only shown for Example B) was whether or not an egg surviving depredation hatched successfully (green ovals labeled "hatched" in dotted lined call-out of Example B). In the model, a clutch was first subjected to predation; any remaining eggs were then allowed to hatch or not according to the "Conditional Hatching Rate" parameter. Light pink shapes represent exogenous variables that serve as covariates or random effects within the integrated model. Nest temperature (in blue) served as an intermediate state variable, variously serving as both a response variable and a predictor variable. Arrows represent the flow of information through the model, hexagon shapes denote binary indicator variables, rectangles represent quantitative measured variables, and circles represent categorical variables.

where $Eggs_n$ represents the number of eggs in nest n (clutch size), β_{0eggs} represents the baseline clutch size (log scale), and β_{CL} represents the effect of maternal body size (carapace length [CL]) on clutch size.

Nest predation: We modeled nest predation probability as a logit-linear function of whether or not a predator excluder was deployed. We also incorporated a random-effect term to accommodate additional variance in predation among sites and years:

$$\text{Logit}(P_{pred_n}) = \beta_{0pred} + \beta_{Excl_{pred}} \bullet Excl_n + \gamma_{sy},$$

where P_{pred_n} is the probability of nest predation for nest n, $ß_{0pred}$ is the baseline nest predation probability (logit scale), $\beta_{Excl_{pred}}$ is the effect of a predator excluder device on the (logit) probability of predation, $Excl_n$ is a binary indicator variable (1 indicates predator excluder deployed at nest n, 0 is unprotected), and γ_{sy} is a random-effect term drawn from a normal distribution with a mean of zero and standard deviation σ_{pred}.

The total number of eggs depredated within each nest ($Eaten_n$) was determined following:

$$Eaten_n = \begin{cases} \text{Binomial } (Eggs_n\ ,\ p_{eaten}) & \text{if } pred = 1 \\ 0 & \text{otherwise,} \end{cases}$$

where $Eaten_n$ is zero if the nest is not depredated (Bernoulli random draw with probability equal to P_{pred_n}), and is a binomial random draw with size equal to the clutch size $Eggs_n$ and probability p_{eaten} for depredated nests.

Conditional-hatching rate: We modeled the probability of hatching for non-depredated Bog Turtle eggs (conditional on surviving predation) as a logit-linear function of the presence of a predator excluder:

$$\text{Logit}(P_{hatch_n}) = \beta_{0hatch} + \beta_{Excl_{hatch}} \bullet Excl_n + \beta_{T_{hatch}} \bullet T_n + \gamma_n,$$

where P_{hatch_n} is the probability of an egg successfully hatching, conditional on surviving predation, β_{0hatch} is the baseline (conditional) hatching rate (logit scale), $\beta_{Excl_{hatch}}$ is the effect of a predator excluder on the conditional hatching rate, $\beta_{T_{hatch}}$ is the effect of nest temperature on the conditional hatching rate, T_n is the observed nest temperature (centered and scaled) and γ_n is an over-dispersion factor (normally distributed random effect on the mean conditional hatching rate for each nest). We modeled the total number of successfully hatched eggs per nest as a binomial distribution with size equal to the number of non-depredated eggs in each nest ($Eggs_n$ - $Eaten_n$) and probability equal to P_{hatch_n}.

Incubation period: Incubation periods were calculated for any nests in which the deposition date and hatch date (median day between the first hatching observed and the previous monitoring date) were known. We modeled incubation period (Inc_n) as a linear function of the presence or absence of a predator excluder following:

$$Inc_n = Normal(\beta_{0inc} + \beta_{Excl_{hatch}} \bullet Excl_n + \beta_{T_{inc}} \bullet T_n\ ,\ \sigma_{inc}),$$

where $ß_{0inc}$ is the baseline incubation period, $\beta_{Excl_{hatch}}$ is the effect of a predator excluder device on incubation period, $\beta_{T_{inc}}$ is the effect of nest temperature on

incubation period, and σ_{inc} is the standard deviation of incubation period (assuming incubation period is normally distributed).

Nest temperature: Based on the timing of deployment and the varying success of temperature loggers in the nests, we standardized the nest temperature data across years and sites by using the same 55-day period before the first nest in a particular year had signs of hatching. For this 55-day incubation period, we first computed the mean minimum (min) and mean maximum (max) daily nest temperatures, and we then calculated the average temperature for each nest as the mean of these 2 values. We modeled nest temperature (during the 55-day period before the first nest began hatching; see above) as a linear function of whether or not a nest was installed with a predator excluder device:

$$T_n = Normal(\beta_{0T_{yr}} + \beta_{Excl_T} \bullet Excl_n + \gamma_s , \sigma_T),$$

where $\beta_{0T_{yr}}$ is the baseline nest temperature (estimated separately for each of the 4 years of the study; centered and scaled), β_{Excl_T} is the effect of a predator-excluder device on nest temperature, γ_s is a random effect of site on nest temperature, and σ_T is the standard deviation of nest temperature.

We fitted the integrated nesting-ecology model in a Bayesian framework using Markov chain Monte Carlo (MCMC) in JAGS v. 4.3.1 (Plummer 2003), which was called from R v. 4.3.1 (R Development Foundation, Vienna, Austria) using the 'jagsUI' package v. 1.6.1 (Kellner 2021). We assessed convergence of the MCMC chains by visual inspection of trace-plots and by ensuring that potential scale-reduction factors were below 1.1 for all parameters (Brooks and Gelman 1998). We assessed goodness-of-fit using a posterior predictive check in which the sum of squared error (SSE) for the observed numbers of hatched eggs per nest was contrasted with the analogous SSE for data simulated under the fitted model (Kéry and Schaub 2011). R and JAGS code for these analyses are available at https://github.com/kevintshoemaker/BT_nest_ecol.

Results

Across the 4-year study, we discovered a total of 77 Bog Turtle nests (containing 257 eggs) across 9 study sites (see Table S1 in Supplemental File 1). Mean clutch size was 3.3 eggs ± 0.92 SD with min–max = 1–5 eggs. Seventy nests were observed being laid, and the remaining 7 were discovered opportunistically (and lacked a known deposition date). For the 70 nests with known deposition dates, the earliest was 29 May (2012), and the latest was 21 June (2009). Of the 28 nests for which hatching was observed, the earliest hatch date was 4 August (2012), and the latest was 7 September (2009). A total of 27 nests had known incubation periods (both deposition date and hatch date were known). Incubation periods varied from 67 to 89 days with a mean of 79.7 days ± 5.78 (median = 80 days). Of the 77 nests, 50 had known maternity and maternal morphological measurements (i.e., age class, mass, length), and 39 had known nest temperatures. Only 9 nests had both known incubation periods and known nest temperatures.

Chi-squared tests

When each egg was treated as an independent data point, there was a strong effect of predator excluders on egg predation (n = 257 eggs; χ^2 = 21.3, P <0.001), whereby unprotected eggs had a 60% egg-predation rate versus 29% for protected eggs (Table 2). Whereas unprotected nests lost an average of 2.0 eggs to predation, protected nests lost only 0.96 eggs on average. When each nest was treated as an independent data point, nest-predation rate (loss of at least 1 egg to predation) was lower for protected nests (38% with excluders, 63% for unprotected nests; Table 2) but the lower sample size (n = 77 nests) resulted in a much weaker statistical effect of predator excluders (χ^2 = 3.15, P = 0.076). Unconditional hatching rate (Table 1) was not statistically different for eggs in protected versus unprotected nests (38% for excluded versus 30% for unprotected eggs; χ^2 = 1.16, P = 0.28, n = 257). This lack of effect appeared to be driven by increased conditional egg-failure rates (for eggs that survived predation); we observed a 47% conditional egg-failure rate with excluders versus a 25% conditional egg-failure rate for unprotected eggs (χ^2 = 4.12, P = 0.042, n = 158; Table 2). Finally, the fraction of late-season predation (nest initially depredated after mid-August) was slightly higher with excluders (9 out of 20; 45%) vs. without (3 out of 15; 20%). However, a chi-squared test indicated that this result was inconclusive (P = 0.24).

Integrated nesting-ecology model

The integrated nesting-ecology model exhibited adequate goodness-of-fit (Bayesian P-value = 0.5; see Fig. S1 in Supplemental File 1). Average clutch size was 3.3 eggs (95% credible interval [CI] = 2.93–3.76), with no apparent effect of maternal body size (posterior median = 0, 95% CI = -0.12–0.13) (Table 3). Consistent with the chi-squared tests (above), our integrated model of Bog Turtle nesting ecology indicated that predator excluders reduced the probability of nest predation (Fig. 4a), resulting in ~0.5 additional eggs per nest remaining by the end of the incubation period for protected nests versus unprotected nests (Fig. 4b). However, reduced hatching rates (conditional on surviving predation) for protected nests tended to offset these gains (Fig. 4c), resulting in little difference in the number of eggs successfully hatched between protected versus unprotected nests (Fig. 4d).

Table 2. Bog Turtle nesting summary statistics with and without predator excluders. Asterisks (*) represent statistically significant comparisons with and without excluder (chi-squared test, alpha = 0.05; see text for details). Note that conditional hatching rate is the complement of the conditional egg-failure rate.

Level	Statistic	With excluder	Unprotected	Total
Nest	Nest-predation rate	38% (20/53)	63% (15/24)	45% (35/77)
	Nest success	55% (29/53)	38% (9/24)	49% (38/77)
Egg	Egg-predation rate*	29% (51/177)	60% (48/80)	39% (99/257)
	Conditional egg failure rate*	47% (59/126)	25% (8/32)	42% (67/158)
	Conditional hatching rate*	53% (67/126)	75% (24/32)	58% (91/158)
	Unconditional hatching rate (or "hatching success")	38% (67/177)	30% (24/80)	35% (91/257)

Similar to the raw data summaries (see above), the estimated average (median) incubation period across all Bog Turtle nests was 78.0 days (95% CI = 74.3–82.0; Table 3). Nests with predator excluders took on average 2.5 days longer to hatch than unprotected nests (95% CI = -1.7–6.5), although this effect was statistically inconclusive (Fig. 5). In addition, warmer nest temperatures tended to reduce total incubation period (Fig. 5); however, with only 9 nests with both known incubation period and known nest temperature, there was limited information in this study for assessing the effects of temperature on incubation timing.

Finally, although raw nest temperatures were generally lower for protected nests vs. unprotected nests (23.4 °C vs. 25.1 °C), this effect was negligible after accounting for differences in nest temperatures among years (Table 3, Fig. 6). Nest temperatures differed substantially among years, with among-year variation tending to swamp out any effect of predator-exclusion devices.

Discussion

Overall, predator excluders were effective at reducing the rate of egg and nest predation for Bog Turtle nests at our New York study sites, with protected nests expected to lose ~1 fewer egg to predation than unprotected nests. However, this positive effect of predator excluders was offset by an increase in egg failures in protected nests (for those eggs surviving predation), such that the number of successful hatchlings emerging from protected versus unprotected nests was statistically

Table 3. Summary of parameter estimates (posterior distributions: median and 95% credible interval [CI]) from an integrated Bayesian model of Bog Turtle nesting success.

Parameter	Posterior median	CI
Mean nest temp, 2009, ˚C	23.33	22.01–24.67
Mean nest temp, 2010, ˚C	25.02	23.65–26.23
Mean nest temp, 2011, ˚C	23.86	22.7–25.02
Mean nest temp, 2012, ˚C	24.56	22.91–26.24
Sigma, nest temp (scaled)	0.82	0.64–1.07
Sigma, random site effect on nest temp	0.54	0.15–1.21
Excl. effect, nest temp	-0.23	-1.17–0.7
Baseline nest pred. rate	0.60	0.35–0.81
Excl. effect, nest pred.	-1.07	-2.35–0.09
Sigma, random site/year effect on nest pred.	0.83	0.28–1.63
Frac. of eggs eaten (depredated nests only)	0.39	0.33–0.44
Baseline clutch size	3.34	2.93–3.76
Effect of maternal SCL on clutch size	0.01	-0.12–0.13
Baseline hatching rate (non-depredated eggs only)	0.77	0.35–0.96
Nest temp effect, hatching rate	0.32	-0.84–1.47
Excl. effect, hatching rate	-1.20	-3.46–0.97
Overdispersion factor, hatching rate	2.95	1.74–4.67
Baseline incubation period, days	78.02	74.28–82.02
Nest temp effect, incubation period	-0.96	-2.94–1.07
Excl. effect, incubation period	2.54	-1.65–6.54
Sigma, incubation period (days)	5.45	3.79–7.74

indistinguishable. Our results underscore the need to monitor egg-failure rates in addition to predation rates when evaluating the success of predator-exclusion devices for Bog Turtle conservation.

Predator excluders did not fully prevent nest predation in our study; 38% of protected nests still experienced predation events. It is possible that our recorded rates of predation are inflated because we monitored nests only once per week during the hatching period and our decision to remove all predator excluders from a site as soon as hatching started in any nest left "protected" nests as unprotected for a period of time. Interpreting eggshell remains on a weekly basis was difficult because the appearance of eggshell remains after hatchlings spent time within nests (e.g., breaking up and distributing their eggshells throughout the hummock) was sometimes similar to the appearance of some nests deemed depredated. We opted to conservatively estimate hatching, and, therefore, we considered nests depredated

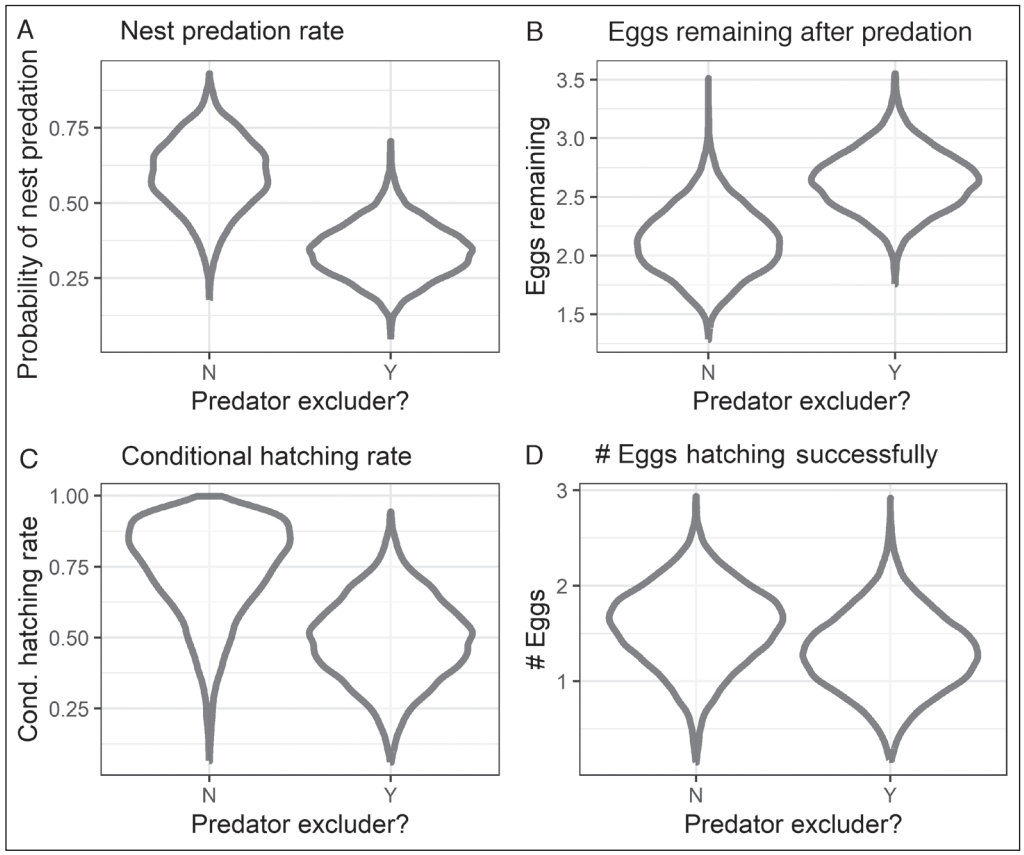

Figure 4. Nest predation and hatching success for Bog Turtle nests with and without predator excluders, illustrating (a) the probability of nest predation (one or more eggs depredated), (b) the mean number of non-depredated eggs per nest, (c) the probability of an egg hatching successfully conditional on survival predation, and (d) the mean number of eggs successfully hatched per nest. Violin plots represent posterior predictive distributions from a Bayesian integrated model of Bog Turtle nesting ecology, based on data from 77 monitored nests at 9 study sites in New York.

when no hatchlings and scattered small eggshell remains were observed. More frequent monitoring of nests in the hatching season would help prevent these issues.

Predation of protected nests was most commonly attributed to burrowing predators digging up to the nest cavity (we observed predator tunnels from the substrate directly into nest cavities) or late-season predation events after the predator excluder was removed for the hatching season. It is likely that some instances of predation of protected nests could have been avoided if predator excluders were constructed to extend further below the surface of the nesting hummock (thereby excluding burrowing predators). However, such predator excluders could compromise the integrity of hummocks, potentially resulting in unintended negative consequences for nest success in current and future years (assuming some level of nest-site fidelity; Macey et al. 2020, Whitlock 2002). We recommend that researchers rigorously assess any long-term effects that digging around hummocks may have on the quality and integrity of nesting microhabitats.

We suspected the majority of egg-predation events were caused by small mammals (e.g., mice, voles, shrews, or possibly *Mustela* spp. [weasels], though never observed at these sites) based on either the presence of small tunnels found leading from nest cavities and complete absence of eggs or the eggshell remains

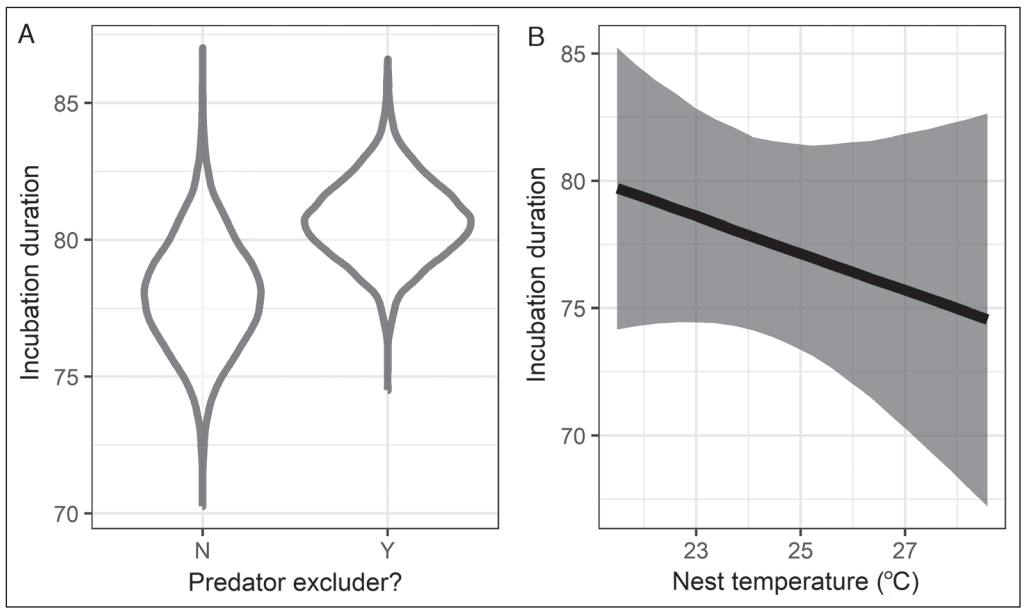

Figure 5. Mean incubation period for Bog Turtle nests in New York, visualized (a) with and without predator excluders, showing a slightly higher mean incubation period for nests with predator excluders, and (b) as a function of nest temperature, showing a general reduction in mean incubation period with higher mean nest temperatures. All plots represent posterior predictive distributions from a Bayesian integrated model of Bog Turtle nesting ecology, based on data from 28 monitored nests with known deposition-date and hatch-date across 9 study sites in New York. Note that only 9 nests in our study had both known incubation period and known nest temperature; nest temperatures for the remainder of nests were interpolated according to the model described in the main text.

displaying evidence of damage from small teeth (Byer et al. 2018, Whitlock 2002, Zappalorti et al. 2017). We observed relatively little evidence of nest-predation pressure from human-commensal predators such as Northern Raccoons and Striped Skunks, suggesting these larger mammalian predators are in relatively low densities at these sites or these predators do not target Bog Turtle nests as readily as other turtle species' nests (e.g., *Malaclemys terrapin* (Schoepff) [Diamond-backed Terrapins; Feinberg and Burke 2003]; *Graptemys* spp. [map turtles; Geller 2012]). Although most species of freshwater turtles experience the highest nest-predation pressure within the first week of being laid, when the olfactory cues from the maternal laying process are presumably the highest (Butler et al. 2004; Congdon et al. 1983, 1987; Tinkle et al. 1981), we frequently observed shell-remain evidence of predation during the hatching period. Byer (2015) similarly noted late-season predation for Bog Turtles and cited Riley and Litzgus's (2014) description of olfactory and auditory cues associated with nest hatching as a possible explanation for late-season predation.

Despite reducing predation rates, we found weak evidence that eggs experienced greater failure rates in nests with predator excluders, raising concerns that nest protection (at least of the type used in this study) may pose some unintended risks to

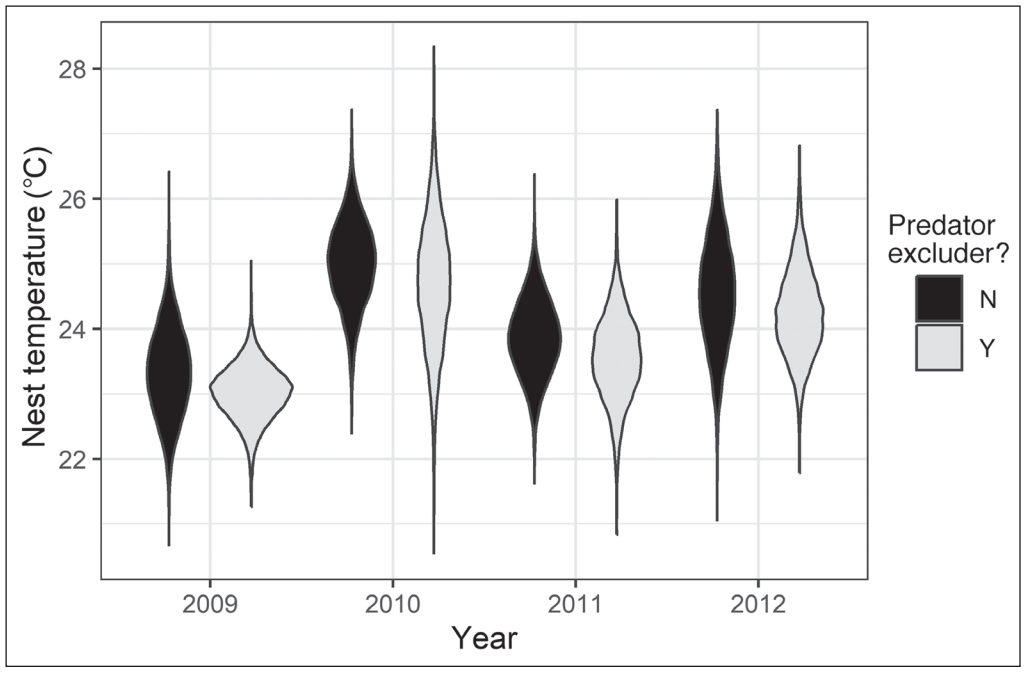

Figure 6. Mean temperatures for Bog Turtle nests in New York as a function of whether a nest was protected with a predator excluder (light gray) or unprotected (dark fill) and as a function of study year (2009 through 2012). In general, among-year variation in nest temperature tended to overwhelm any effect of nest protection. All violin plots represent posterior predictive distributions from a Bayesian integrated model of Bog Turtle nesting ecology, based on data from 29 monitored nests for which nest temperature was measured across 9 study sites in New York.

the populations we are attempting to protect. Among the suspected sources of egg failure (unrelated to mammal predation and regardless of protected or unprotected status) were infertility, incomplete development, insect predation, plant-root intrusion, exposure to temperature extremes, and flooding. However, the mechanism by which nest protection may increase egg failure remains unclear. Significant egg mortality unattributable to predation has also been observed in other studies. Zappalorti et al. (2017) found that protected Bog Turtle eggs experienced 51% mortality in the wild, compared with 19% when artificially incubated in laboratory conditions without predation pressures, physical destruction, or temperature fluctuations. Bougie et al. (2020) observed a 20% failure rate for *Glyptemys insculpta* (Le Conte) (Wood Turtle) eggs due to reasons other than predation, with high inter-annual variability suspected to be weather-driven. Garrison et al. (2023) reported a 50% hatching failure rate for protected *Clemmys guttata* (Schneider) (Spotted Turtle) nests in Massachusetts due primarily to causes other than predation.

Intuitively, any effect of nest protection on hatching rates (conditional on surviving predation) could be driven by nest-temperature differences, as temperatures are likely to be affected by any cover structure and could, in turn, affect hatching rates (but see Burke and Eugene 2024, Riley and Litzgus 2013). Although nest temperatures in our study tended to be lower in protected nests versus unprotected nests (potentially affecting egg-failure rates), this apparent difference appeared to be an artifact of inter-annual differences in temperature. In addition, vegetation can detrimentally affect Bog Turtle eggs, as we observed some eggs that appeared to be killed by plant-root growth. Soil disturbances caused during the installation of predator excluders may potentially affect the rate of root intrusion into Bog Turtle eggs. Although few studies have parsed the contributions of different sources of egg mortality for freshwater turtles, causes other than depredation seem to play a significant role and merit further investigation.

Importantly, our deployment of predator excluders did not follow a rigorous (e.g., paired) experimental design every year, making it difficult to conclude that the observed differences in egg-failure rates were caused by the excluders themselves and not due to environmental differences that were not controlled for in our study. For example, 2 protected nests in our study were flooded due to American Beaver activity, resulting in 100% egg failure in these nests. Therefore, we strongly recommend that future studies on the efficacy of predator excluders for Bog Turtles use a paired experimental design whereby each protected nest is paired (to the extent possible) with an unprotected nest laid at a similar time and place (thereby controlling for confounding factors).

Mean clutch size of ~3.3 eggs in the present study is similar to that recorded in other Bog Turtle studies (Byer et al. 2018, Ernst and Lovich 2009, Whitlock 2002). Clutch size varied by year and body condition (BCI); perhaps yearly conditions and resource availability impacted BCI and, therefore, clutch size (Gibbons et al. 1982). Whitlock (2002) observed variation in clutch size of 19 female Bog Turtles monitored multiple years, suggesting that there are yearly effects of resources on a female's clutch size or that perhaps reproductive output of 1 year influences

the reproductive output of the female the following year (Broderick et al. 2003, Gibbons et al. 1982, Litzgus et al. 2008, Shine 1980). Considering females have relatively small clutch size and may not nest every year (Whitlock 2002) and do not lay multiple clutches per year (Ernst and Lovich 2009), Bog Turtles have a relatively low reproductive output as compared to other turtle species (Gibbons et al. 1982). Predation of nests may be of greater concern for turtle species, such as Bog Turtles, with low annual reproductive output as compared to those with larger annual reproductive outputs (Smith et al. 2013).

Considering the low reproductive output of Bog Turtles, predator excluders may benefit populations, especially if recruitment in populations is chronically low due to nest predation (Crowder et al. 1994, Reed et al. 2009). Although predator excluders did not improve the production of hatchlings in this study, we observed a 56% reduction in predation rates in protected versus unprotected Bog Turtle nests. If further studies document that predator excluders (possibly of a different design than used in this study) can reduce predation rates without having a detrimental effect on hatching rates for surviving eggs, predator excluders may be a viable strategy for improving recruitment rates for some populations. However, we caution that the time and expense of finding nests, deploying predator excluders, and monitoring hatching may not always be cost-effective when compared with other conservation strategies.

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