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Hatching Success and Predation of Bog Turtle (*Glyptemys muhlenbergii*) Eggs in New Jersey and Pennsylvania

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Abstract. – Nest-site selection by most turtles affects the survival of females and their offspring. Although bog turtles (*Glyptemys muhlenbergii*) do not typically leave their wetlands for nesting, nest-site selection can impact hatching success and hatchling survival. Between 1974 and 2012, we monitored the fates of 258 bog turtle eggs incubated in the field and 91 eggs incubated under laboratory conditions from 11 different bogs, fens, or wetland complexes in New Jersey and Pennsylvania. Laboratory-incubated eggs exhibited the greatest hatching success (81%), but we did not detect a significant difference in hatching success between nests protected with predator excluder cages (43%) and unprotected nests (33%). However, we found significantly lower predation rates in protected nests, suggesting that while predator excluder cages successfully reduced predation, other environmental factors persisted to reduce egg survival in the field. Natural hatching success was potentially reduced by poor weather conditions, which may have resulted in embryo developmental problems, dehydration, or embryos drowning in the egg. Our results suggest that egg depredation, coupled with embryo developmental problems and infertility, are limiting factors to hatching success in our study populations. Using predator excluder cages to protect bog turtle eggs in the field, or incubating eggs in the laboratory and releasing hatchlings at original nesting areas, may be an effective conservation tool for recovering populations of this federally threatened species.

Key Words. – *Glyptemys muhlenbergii*; hatching success; infertility; mammalian predators; predator excluder cage

Poor nest-site choice by nesting female turtles can reduce hatching success and hatchling survival (Spencer and Thompson 2003; Marchand and Litvaitis 2004; Spanier 2010). For example, high predation rates of turtle eggs in upland nesting sites are well-documented (Congdon et al. 1987; Gibbons 1990; Burke et al. 2005; Warner 2005). Nest-site selection also determines the thermal regime during incubation and thus the sex ratio of hatchlings in many turtle species (Bull and Vogt 1979; Ewert and Nelson 1991; Ewert et al. 1994). Therefore, hatching success is not only dependent upon nest sites that minimize the risk from egg predators (Spencer and Thompson 2003), but the sites must also provide appropriate thermal and soil moisture conditions for successful development of both male and female hatchlings (Hulin et al. 2009; Ihlow et al. 2012).

Most gravid female freshwater turtles migrate from their semiaquatic habitat to upland nest sites (Gibbons 1990; Ernst and Lovich 2009), whereas bog turtles (*Glyptemys muhlenbergii*) do not leave their wetlands for nesting (Zappalorti 1976; Ernst 1977; Bury 1979; Zappalorti et al. 2015). Nesting areas typically have limited canopy closure, support an array of moisture-tolerant, low vegetation, and provide ample sun exposure. Bog turtles select slightly elevated sites for nesting within their marshy habitat, generally on various species of *Carex* tussocks, mosses, or beneath plant debris (Herman 1986a; Zappalorti et al. 2015). After oviposition, females often conceal their eggs by covering them with humus, moss, or other vegetative material available at the nest site (Zappalorti et al. 2015).

For most turtles, the period of greatest vulnerability occurs during the early stages of life (Heppell et al. 1996). However, apart from Whitlock (2002) and Tryon (2009), little attention has been given to predation of bog turtle eggs and hatching success in the wild. Although adult survival is known to make the largest contribution to population growth for freshwater turtles (Congdon et al. 1993; Heppell 1998), conservation actions targeting early life stages may be necessary to maintain stable populations, particularly in cases of reduced adult survival (Enneson and Litzgus 2008). Thus, the protection of nests

Table 1. Number of bog turtle nests found by state and study area at 11 wetlands in New Jersey and Pennsylvania between 1974 and 2012.

Wetland	State	County	No. of nests	No. of eggs	Years monitored
1	New Jersey	Sussex	15	48	1974–1975, 1978–1980, 1982, 2012
2	New Jersey	Morris	1	3	1987
3	New Jersey	Monmouth	16	50	1978–1979, 1982
4	Pennsylvania	Lancaster	19	60	1994, 2001
5	Pennsylvania	Lancaster	12	45	1994, 2001
6	Pennsylvania	Berks	11	35	1997
7	Pennsylvania	Northampton	5	16	1994, 1996
8	Pennsylvania	Monroe	19	72	2002–2003
9	Pennsylvania	Lehigh	1	3	1999
10	Pennsylvania	Chester	4	14	1998
11	New Jersey	Ocean	1	3	1982
Total	2	10	104	349	

with predator excluder cages and captive hatching of eggs may aid in the recovery of declining species. In the present study, we monitored bog turtle eggs and nests from 11 New Jersey and Pennsylvania study sites. To effectively guide conservation efforts for this federally threatened species, it is important to understand factors limiting the survival of eggs and hatchlings. Thus, our research was focused on two major questions. First, what factors affect the hatching success of bog turtle eggs? Second, are there differences in the hatching success of eggs from natural nests in the field, eggs from nests protected with predator excluder cages, and laboratory-incubated eggs?

METHODS

Study Sites. — Bog turtle habitat descriptions are well-documented elsewhere in the literature (Zappalorti 1976; Chase et al. 1989; Carter et al. 1999; Morrow et al. 2001; Pittman and Dorcas 2009); therefore, we only provide general habitat features present in the nesting areas (see Zappalorti et al. 2015 for more details). Between 1974 and 2012, we examined the hatching success and predation rate of 104 bog turtle nests from 11 bogs, fens, and wetland complexes in New Jersey and Pennsylvania (Table 1). To protect this federally threatened and state endangered species from exploitation, precise coordinates and specific site names are purposely excluded. Instead, the county and state names are provided and each study site is referred to numerically (Zappalorti et al. 2015). The habitat conditions at the 11 study sites met the soils, hydrology, and vegetation criteria for bog turtles as described by the US Fish and Wildlife Service (US FWS 1997, 2001). Data from 2 Pennsylvania study areas were combined because they are part of connected wetland systems. For example, Wetland 7 includes 3 bog turtle populations within a connected wetland complex and Wetland 8 includes 6 bog turtle populations within a large connected stream corridor complex. The management and protection of bog turtle habitat within the wetlands and the land adjacent to each site has been relatively stable over time. Ten of the sites (with the exception of Wetland 11) are located on protected federal, state, or nongovernmental organization sanctuaries.

Bog Turtle Nests. — Between 1974 and 1993, we conducted mark–recapture studies, including egg surveys, and monitored hatching success in the field and laboratory at the 11 study sites. Thereafter (1994–2012), nests and eggs were monitored in natural habitat. Sites were monitored for 1–7 yrs of the study period (Table 1). However, small sample sizes in each nest treatment (unprotected, protected, or lab-incubated) per site and the different monitoring schedules among sites precluded a detailed examination of interannual or interwetland variation (Fig. 1). For example, nests from Wetland 1 were monitored in the field during 4 yrs of the study, but < 10 eggs were recorded each of the years (Fig. 1). Nests from other sites were monitored in consecutive years (e.g., Wetland 8 was visited in 2002 and 2003) and we did not observe large differences in hatching success between these years. Hereafter, we primarily focus on the effects of the nest treatment types across all sites rather than changes in hatching success over time at individual wetlands.

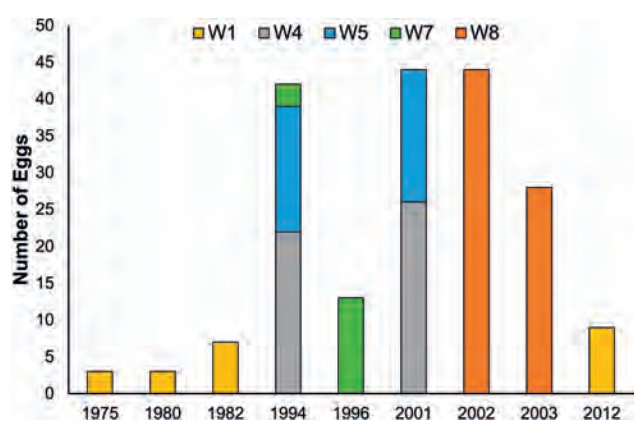

Figure 1. Number of bog turtle eggs monitored in the field (unprotected and protected with predator excluder cages) from 1975 to 2012 in New Jersey and Pennsylvania. Only sites that were monitored for $\geq$ 2 yrs are included (Wetlands 1, 4, 5, 7, and 8). Eggs that hatched in the laboratory and the years in which they were collected are not shown.

Prior to searching for nests and eggs, the hygiene protocol detailed in Zappalorti et al. (2015) was followed to avoid attracting mammalian predators to the eggs (but see Tuberville and Burke 1994; Burke et al. 2005; Kurz et al. 2011). During and after the June nesting season, bog turtle eggs were intensively searched for in *Carex, Sphagnum,* and other elevated grassy hummocks in each of the 11 wetlands. Each nest discovered was marked with a wooden stake and flagged with surveyor's tape to prevent researchers from accidently stepping on the nest or eggs. We did not expect flagging at nests to attract mammalian predators (Tuberville and Burke 1994; Zappalorti 1997; Burke et al. 2005).

Bog turtle hatching success was monitored under 3 different treatments: 1) unprotected in the field, 2) protected in the field with a predator excluder cage, and 3) in the laboratory. If eggs failed to hatch after the typical 8–9-wk period, they were monitored in the nest (in the field) or in the laboratory container for several additional weeks. By the end of the monitoring period, unhatched eggs were cut open to determine the reason for failure to hatch (i.e., infertility or developmental problems). However, because some unhatched eggs in the field were not examined, we group infertility and developmental problems together hereafter. Thus, potential sources of mortality included predation (field only) and developmental problems or infertility (i.e., eggs that did not hatch in the field or laboratory).

The following data were collected for each nest: clutch size, condition of the eggs (dented, broken, discolored), the number of depredated eggs, and hatching success in the field or laboratory. Additionally, we recorded the location and habitat structure of the nest and the surrounding vegetation type within 1 m^2. Each egg was labeled by marking the top with a unique code consisting of a nest number followed by a letter. After the eggs were marked, we covered them with the original vegetation material. If the eggs were not completely covered when originally found, we placed 2 or 3 cm of moss over the eggs to prevent dehydration (Zappalorti et al. 2015).

Between 1974 and 1993, eggs were removed from natural nests at Wetlands 1, 3, 4, 5, and 11 (n = 75 eggs) and taken to the laboratory for incubation. The eggs were oriented with the identification number up, the same way they had been found in the nest, and placed in plastic containers containing 6 cm of humus from the wetland of origin. The eggs were then carefully transported to the laboratory and covered with damp *Sphagnum* moss. A tight-fitting lid was placed on the plastic container to maintain high humidity. We checked temperatures of the eggs in the incubation containers every 3 or 4 d, alternating between 1000 and 1900 hrs. Incubation temperatures ranged from 26°C to 32°C during the day ($\bar{x}$ = 28°C), but were allowed to drop to 17°–24°C ($\bar{x}$ = 20°C) during the night to provide natural cycling temperatures. Hatchlings were weighed, measured, and permanently marked by notching the marginal scutes with stainless steel surgical scissors before being released at the original nest sites within 5–10 d after hatching, or when the yolk plug was fully absorbed into the plastron and hatchling movement was unrestricted.

Predator Monitoring. — Artificial nests and eggs have been used in previous studies to examine the vulnerability of turtle nests to predation events and can provide insights into the threats affecting recruitment in turtle populations (Wilhoft et al. 1979; Marchand and Litvaitis 2004). To identify potential egg predators, we placed egg-sized decoys made of paraffin and beeswax (50:50 mixture) alongside real eggs inside the natural nests at Wetlands 4 and 5 in 1994. If a predator bit or chewed an artificial wax egg and left it behind, impressions of tooth marks on the eggs were examined and sometimes allowed for predator identification. If a clutch had 3 bog turtle eggs, we supplemented some nests with artificial eggs by removing one real egg and replacing it with one decoy egg. If a clutch had 4 eggs, we removed 2 real eggs and substituted them with 2 decoy eggs. Thus, no nest was supplemented with more eggs than the original nest contained. The bog turtle eggs we removed were taken to the laboratory for incubation, as described above. Mammalian predators likely rely on a combination of olfactory and visual cues to detect turtle nests (Marchand and Litvaitis 2004; Strickland et al. 2010; Buzuleciu et al. 2016); therefore, we did not expect that the few artificial eggs used in this study (n = 16) would attract predators to the supplemented nests. We used decoy eggs to identify certain mammalian predators, but Wilhoft et al. (1979) also used artificial eggs (e.g., ping-pong balls) to evaluate cues used by predators to locate turtle nests.

We regularly performed visual surveys for mammal sign while monitoring bog turtle nests at the 11 sites. Additionally, we trapped for small- to medium-sized mammals in the nesting areas at Wetland 1 (New Jersey) during May of 1975 and Wetland 4 (Pennsylvania) during early May of 2003 to determine the suite of potential mammalian egg predators. We set 36 baited (peanut butter and oatmeal 50:50 mixture) Sherman aluminum live-traps (H.B. Sherman Traps, Inc., Tallahassee, FL) for mammals (e.g., meadow voles, chipmunks, and shrews) and conducted trapping during early May to avoid disturbing nesting female turtles. Traps were distributed equally in a 6×6 grid with traps 2 m apart throughout the nesting area and its edges. Traps were checked daily for 7 d at Wetlands 1 and 4 and trapped animals were released after they were identified.

To ensure protection of bog turtle eggs from small mammals, predator excluder cages were installed over 27 nests from Wetlands 1, 4, 6, 8, and 10. Predator excluder cages were installed when nests were found in June and left in place for the entire 3-mo incubation period. They completely surrounded each nest, including the tussock or hummock in which the eggs were deposited (Fig. 2). The diameter and height of each predator excluder cage varied

Figure 2. A predator excluder cage placed over a bog turtle nest. The cage was buried 6–10 cm in the mud and wooden stakes were placed on either side of the cage to prevent wind or large mammals from knocking it over. Photo taken by R.T. Zappalorti.

depending on the height of vegetation at the nest site. Predator excluders were made of 1.1-cm wire-mesh hardware cloth and the typical cage measured approximately 61 cm in height by 38 cm in width. The base of each predator excluder was buried 8–15 cm into the muddy substrate to prevent small mammals from accessing the nest. The top of the cage was covered with wire-mesh hardware cloth and secured in position with wire. Wooden stakes placed on either side of the cage prevented wind or larger mammals from knocking it over.

Data Analysis. — Data were pooled across all sites and years to examine the effects of the nest treatments (unprotected, protected, or lab-incubated) on bog turtle hatching success. We calculated bog turtle hatching success by dividing the total number of eggs that hatched by the total number of eggs from all nests of the particular treatment (e.g., all eggs from unprotected nests). We used pairwise chi-square tests of independence with a Bonferroni corrected α of 0.017 to evaluate differences in hatching success among unprotected eggs, protected eggs, and lab-incubated eggs across years. To examine egg predation rates among unprotected and protected nests, we divided the total number of depredated eggs by the total number of eggs in each field treatment and used a chi-square test of independence to test for differences in predation rates. Additionally, we compared the ordinal date of first hatching for eggs in the field (protected and unprotected combined) with that of lab-incubated eggs using the nonparametric Mann-Whitney U-test.

RESULTS

We found 104 individual bog turtle nests containing 349 eggs, with a mean of 3.4 eggs per nest (range, 1–5 eggs; Table 1). Gravid female bog turtles nested and oviposited in grassy tussocks of various *Carex* species between 2 June and 2 July. Hatching occurred from 28 July to 19 September (median hatching date = 30 August), but date of first hatching did not differ between the field (median = 31 August; mean = 1 September) and laboratory (median = 30 August; mean = 26 August) treatments ($U = 643$, $p = 0.07$).

Hatching Success. — Of the 258 bog turtle eggs monitored in natural nest sites (i.e., not laboratory hatched) in Pennsylvania and New Jersey, 161 remained in unprotected nests ($n = 55$ nests) and 97 were protected with predator excluder cages ($n = 27$ nests; Table 2).

Table 2. The fate of 349 bog turtle eggs taken to the laboratory for incubation, protected with predator excluder cages, or unprotected in the field at 11 wetlands in New Jersey and Pennsylvania between 1974 and 2012. Percentages total to 100% by row.

	No. (%)			
	Hatched	Depredated	Infertile or undeveloped	Total no.
Lab incubated	74 (81)	0	17 (19)	91
Field protected	42 (43)	6 (6)	49 (51)	97
Field unprotected	53 (33)	82 (51)	26 (16)	161
Total	169 (49)	88 (25)	92 (26)	349

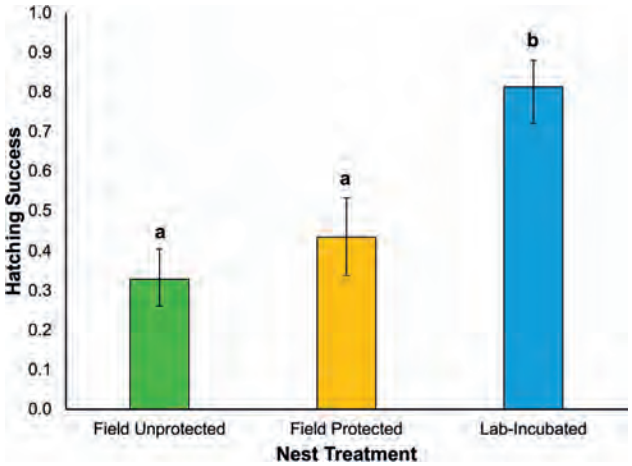

Figure 3. Hatching success of bog turtle eggs in New Jersey and Pennsylvania from 1975 to 2012. Hatching success was examined under 3 scenarios: nests unprotected in the field (n = 161 eggs), nests protected with predator excluder cages (n = 97 eggs), and lab-incubated eggs (n = 91 eggs). Different letters represent significant differences in hatching success ($p < 0.001$).

Hatching success did not significantly differ between unprotected (33%) and protected (43%) nest sites in the field ($\chi^2_1 = 2.80$, $p = 0.09$). However, we found lower predation rates in protected nests (6%) compared with unprotected nests (51%) in the field ($\chi^2_1 = 53.93$, $p < 0.001$). Furthermore, predation accounted for 11% of egg mortality from protected nests and 76% of egg mortality from unprotected nests. Infertility or developmental problems accounted for 75 eggs failing to hatch in the field, from unprotected (16% of eggs) and protected (51% of eggs) nests. Of the 91 bog turtle eggs incubated in the laboratory, 74 hatched successfully (81%), but 17 failed to hatch due to infertility. Lab-incubated eggs exhibited greater hatching success than unprotected eggs ($\chi^2_1 = 54.48$, $p < 0.001$) and protected eggs ($\chi^2_1 = 28.72$, $p < 0.001$) from the field (Fig. 3).

Predator Monitoring. — When we suspected a predation event had occurred, we observed that some eggs went missing from the nest cavity and/or found egg shell fragments in the nest with teeth marks or on the mud below the *Carex* tussock (Fig. 4). Predators removed 4 of the 16 artificial wax eggs, but despite intensive searches, none of the missing wax eggs were recovered. Some eggs were not eaten at the nests, but were carried off one at a time by small mammals. Visual observations at the 11 study areas and trapping at 2 wetlands (1 in New Jersey and 1 in Pennsylvania) yielded 16 potential bog turtle predators (Table 3). It is possible that black bears (*Ursus americanus*), long-tailed weasels (*Mustela frenata*), striped skunks (*Mephitis mephitis*), eastern chipmunks (*Tamias striatus*), and gray squirrels (*Sciurus carolinensis*) may also prey upon bog turtle eggs; we confirmed raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), northern short-tailed shrews (*Blarina brevicauda*), and meadow voles (*Microtus pennsylvanicus*) as predators of eggs and/or hatchlings.

DISCUSSION

We monitored 104 individual bog turtle nests within New Jersey and Pennsylvania and examined bog turtle hatching success under 3 scenarios: unprotected nests in the field, protected nests in the field, and lab-incubated eggs. We confirmed raccoons, red foxes, northern short-tailed shrews, and meadow voles as predators of bog turtle nests and found that predation accounted for nearly 80% of egg mortality from unprotected nests in the field. Although we did not detect a difference in hatching success among unprotected and protected nests, we found significantly lower predation rates in protected nests. Thus, our results suggest that while predator excluder cages successfully reduced predation, other environmental factors persisted to reduce egg survival in the field. Eggs incubated in the laboratory exhibited the greatest hatching success; thus, captive hatching may be an effective approach to maintain or recover declining populations of bog turtles.

Predator Monitoring. — Black rat snakes (*Pantherophis obsoletus*), northern black racers (*Coluber constrictor*), and eastern king snakes (*Lampropeltis getula*) were never observed in bog turtle nesting areas during the study, but we did observe 3 eastern milk snakes (*Lampropeltis triangulum*) in a nesting area at a New Jersey study site. These snake species are known to occur at some or all of our study wetlands and could potentially account for some of the eggs removed from nests (Knight and Lorraine 1986; Brauman and Fiorillo 1995). Mammal predator sign was evident by tracks in the mud around nests and throughout the bog turtle habitat. Although it is possible that we missed certain species during visual surveys for evidence of sign and while trapping, we believe that our strategy of using multiple detection techniques (sign, teeth indentations on eggs, and traps) enabled us to identify the mammals that likely contribute most to bog turtle egg mortality. Potential mammal predation was also observed on many adult bog turtles in several of our study areas, such as tooth marks, shell punctures, missing toes, chewed feet, and missing limbs (Burke et al. 2005; R.T.Z., *pers. obs*.).

Similar to our observations, Tryon (2009) reported that predators eliminated 12 of 36 known bog turtle nests at 2 study sites in Tennessee. In some cases, he found shredded eggshells, but often, entire clutches disappeared without evidence of nest disturbance. In North Carolina, a variety of predators, such as raccoons, snapping turtles (*Chelydra serpentina*), and herons (*Ardea herodias*), injure or kill all age classes of bog turtles (Bury 1979; Herman and Tryon 1997). Other predators prey upon nests containing eggs and neonates as well, including ants, snakes, moles, shrews, rodents, and opossums (*Didelphis virginiana*; Herman 1986b). Likewise, in Pennsylvania and New Jersey, we found destroyed eggs from the previous year, or freshly depredated nests, evidenced by remnants of chewed egg shells or egg fragments in the nest chamber or in the mud below. At many of our bog turtle nesting areas, predator

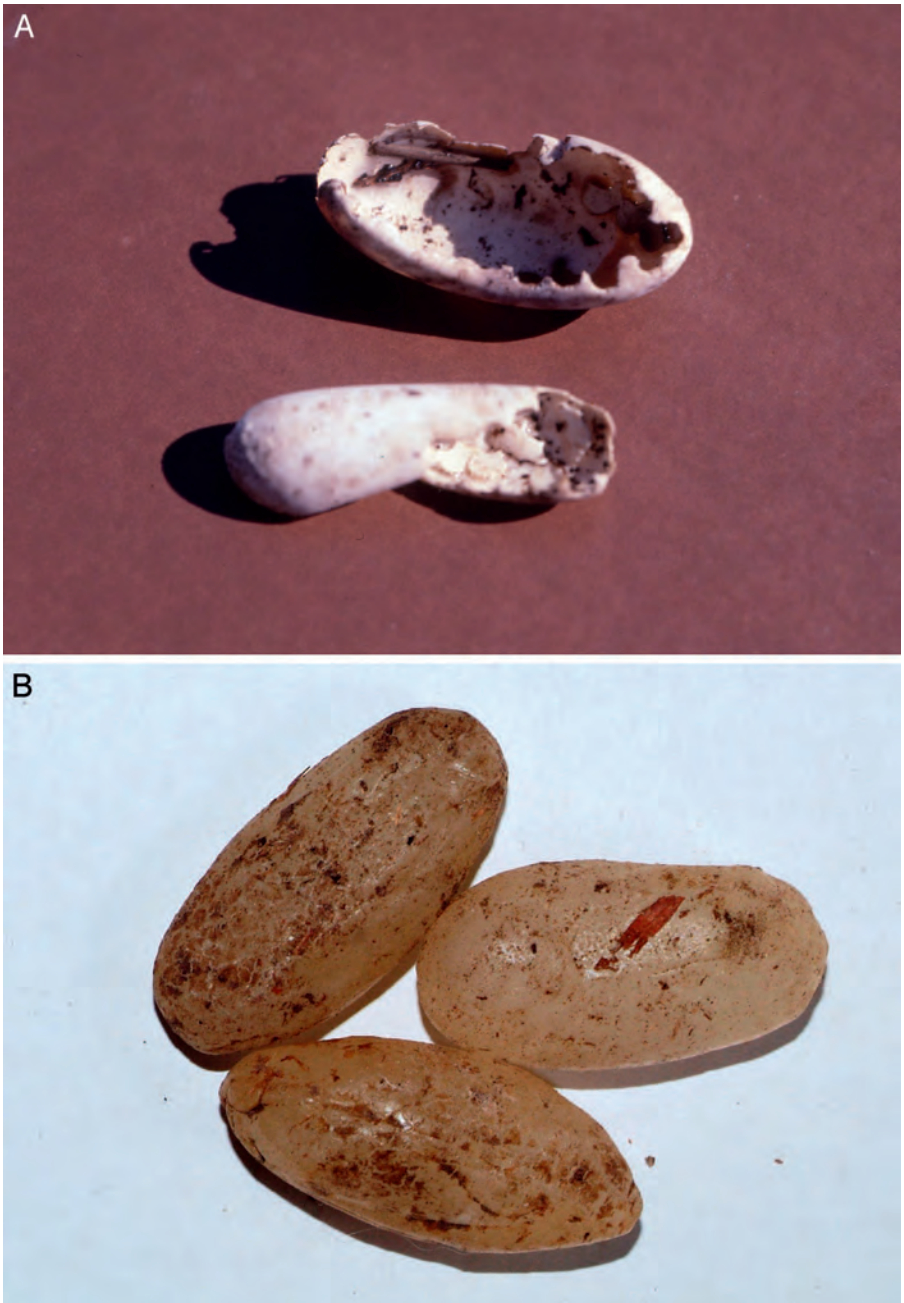

Figure 4. We monitored bog turtle nests and found evidence of egg predation, including (A) depredated bog turtle eggs in an unprotected nest at Wetland 5, Lancaster County, Pennsylvania. Note the teeth marks on the shell made by a meadow vole (*Microtus pennsylvanicus*). To identify potential egg predators, we used (B) artificial wax eggs as decoys. The wax eggs replaced eggs that were taken to the laboratory for incubation. Photos taken by R.T. Zappalorti.

numbers may have increased as a result of improved subsidized food resources scavenged from nearby agricultural fields and from residential housing developments adjacent to the habitat, as reported in other studies of turtle nest depredation (Marchand and Litvaitis 2004).

Hatching Success. — Geography, elevation, and climate influence nest temperatures during the incubation period and subsequently affect hatching success of turtle eggs, including those of bog turtles (Tryon 2009). We observed relatively low rates of hatching success at our sites (unprotected nests: 33%; protected nests: 43%) compared with other bog turtle nesting studies. For example, Tryon (2009) monitored 18 clutches of bog turtle eggs over a 3-yr period (n = 51 eggs) in Tennessee and 29 eggs hatched (57% hatching success). Furthermore, Whitlock (2002) monitored 40 clutches of bog turtle eggs (n = 122 eggs) in Massachusetts and 113 eggs hatched (93% hatching success). In our study, predation and developmental problems or infertility were serious limiting factors for hatching success in the field.

Predation. — Predation accounted for nearly 80% of egg mortality in unprotected nests across sites. Addition-

Table 3. Confirmed or potential mammalian nest predators and the number of individuals trapped, observed, or identified through the presence of sign in one or more of the bog turtle study areas in New Jersey or Pennsylvania between 1975 and 2012. Sign refers to skull or bones, identifiable droppings, scat, or tracks in mud within the 11 wetlands.

Species	No. trapped	No. observed	Sign	Confirmed predators of bog turtles	Reference or source
Shorttail shrew (*Blarina brevicauda*)	14	1	2	Yes	Confirmed by present study
Starnose mole (*Condylura cristata*)	3	1	0	Unknown	
Black bear (*Ursus americanus*)	0	2	1	Unknown	
Longtail weasel (*Mustela frenata*)	0	0	1	Unknown	
Red fox (*Vulpes vulpes*)	0	2	3	Yes	Confirmed by present study
Striped skunk (*Mephitis mephitis*)	0	2	4	Yes	M. Knoerr, *pers. comm.,* February 2017
Woodchuck (*Marmota monax*)	0	7	3	Unknown	
Raccoon (*Procyon lotor*)	0	9	17	Yes	Ernst and Lovich 2009; present study
Eastern chipmunk (*Tamias striatus*)	10	11	9	Unknown	
Eastern gray squirrel (*Sciurus carolinensis*)	1	10	2	Unknown	
Meadow jumping mouse (*Zapus hudsonius*)	12	7	3	Unknown	
White-footed mouse (*Peromyscus leucopus*)	10	4	0	Unknown	
Meadow vole (*Microtus pennsylvanicus*)	32	26	5	Yes	Confirmed by present study
Opossum (*Didelphis virginiana*)	0	3	6	Unknown	
Beaver (*Castor canadensis*)	0	3	3	Unknown	
Eastern cottontail (*Sylvilagus floridanus*)	0	24	14	Unknown	

ally, we observed large interannual variability in nest predation in the unprotected nests from Wetland 5. The egg predation rate at Wetland 5 declined from 56% (n = 27 total eggs) in 1994 to 6% (n = 18 total eggs) in 2001, despite no significant observable changes to nesting habitat over the time period. Instead, we attribute the discrepancy in nest depredation among years to natural fluctuations in predator densities, a pattern that could also affect efforts to fully address predation threats to turtle populations. We did not observe significant differences in egg hatching success among unprotected and protected nests, but we confirm previous findings that installation of predator excluder cages around nests effectively protects turtle eggs from predation (Graham 1997; Mroziak et al. 2000; Riley and Litzgus 2013).

Developmental Problems and Infertility. — In addition to predation, natural hatching success in our study was potentially reduced by poor weather conditions, which may have resulted in embryo developmental problems, dehydration, or embryos drowning in the egg. Infertility and developmental problems have routinely been documented in field studies for turtles (bog turtle: Tryon 2009; Blanding's turtle [*Emydoidea blandingii*]: Congdon et al. 1983) and we attributed most (89%) of the mortality in protected nests to these sources. We observed infertility and developmental problems in unprotected nests to a lesser degree (24% of total mortality), most likely because of nest depredation (i.e., eggs were depredated before we could determine whether they were fertile or fully developed). It is unknown whether the prevalence of developmental problems documented in the present study is typical for turtle populations because there are few studies to compare our results with. However, the unique nesting habits of bog turtles may make their eggs particularly vulnerable to mortality as a result of developmental problems. Many bog turtle nests are shallow (mean elevation above the substrate of 8.2 cm), potentially exposing nests to extreme changes in temperature or inundating nests with water during heavy rainstorms (Zappalorti et al. 2015). Furthermore, females may leave eggs covered haphazardly or completely uncovered, partially or fully exposing them to direct sunlight (Zappalorti et al. 2015). We observed the effects of harsh weather conditions and poor nest choice on bog turtle hatching success in this study. During drought years at Wetlands 5, 6, 9, and 10, some eggs showed signs of dehydration (n = 10 eggs), but we covered them with moist *Sphagnum* moss and 3 eggs hatched. At Wetlands 7 and 8, severe rainfall events flooded the low-lying nests and caused 18 of 19 eggs to drown.

Female bog turtles may be capable of sperm storage within their oviducts as documented in other turtle species (Gist and Jones 1989), but without annual copulation or sufficient sperm retention, eggs may not be fertilized. High predation rates in unprotected nests and significant developmental problems coupled with infertility in protected nests make it difficult to determine the contribution of infertility to total egg-hatching failures in the field. The egg infertility rate from the laboratory setting (19%), in the absence of predation and developmental problems, may be reflective of the natural levels of egg infertility in the wild, but there likely is variation in infertility among populations. For example, 31% of 51 bog turtle eggs in Tennessee were infertile (Tryon 2009) and only 5% of 122 bog turtle eggs in Massachusetts were infertile (Whitlock 2002).

The results of the present investigation suggest that predation on eggs, coupled with infertility and developmental problems, are serious limiting factors to hatching success in bog turtle populations in Pennsylvania and New Jersey. We found that reducing only one source of egg mortality in the field (i.e., predation) was insufficient to significantly improve hatching success at our study sites. Thus, developmental problems can be a serious limitation to hatching success and nest-site selection has important implications for egg survival. Given the high rates of nest predation and developmental problems we observed, protecting natural nests with predator excluder cages or removing eggs for captive incubation may be suitable conservation tools to maintain or recover declining bog turtle populations.

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