Applying Lessons from Avian Ecology to Herpetological Research: Techniques for Analyzing Nest Survival due to Predation

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Abstract.—Estimating and characterizing patterns in reproductive rates is a research priority for many animal taxa given the importance of reproduction for population persistence. For nest-laying organisms such as birds and turtles, nest depredation is often the primary cause of poor recruitment. The avian literature features many statistical techniques, ranging from descriptive estimators to more complicated modeling frameworks, specifically designed to quantify patterns of nest survival. Although these techniques are broadly accepted and commonly used by avian ecologists, they have not been widely adopted in herpetological research. Here, we provide an overview of nest survival analyses developed in the avian literature to highlight their potential utility in herpetological studies. We then apply the logistic exposure model to estimate and characterize patterns of nest survival for Blanding's Turtles (*Emydoidea blandingii*) and Bog Turtles (*Glyptemys muhlenbergii*), both of which are species of conservation concern. Using this model, we documented strong effects of spatiotemporal factors on nest depredation that would have been difficult to identify using traditional approaches employed by herpetologists. We suggest that more modern nest success analysis techniques, such as the logistic exposure model and the Program MARK nest survival model, will be useful to herpetologists interested in examining patterns of nest depredation and success. Applying these models will facilitate the development of conservation priorities and approaches for managing nest survival in herpetofauna.

Importance of Quantifying Nest Survival

Reproductive output is an important component of fitness and is frequently measured on a per-female basis by either counting the number of eggs that hatch or young that are born in a given period (Le Boeuf 1974; Pianka 1976). For egg-laying vertebrates such as birds and many non-avian reptiles, nest survival is a driver of population-level recruitment rates (Aldridge and Brigham 2001; Nur et al. 2004). Nest depredation is one of the dominant sources of nest failure in many species, although its impacts often vary in intensity among taxa with different life histories and breeding strategies (Lack 1954; Ricklefs 1969; Angelstam 1986). High rates of nest depredation have been observed in both birds (Lack 1954; Ricklefs 1969; Wilcove 1985) and reptiles (Congdon et al. 1983; Brooks et al. 1992) and sustained high levels of depredation can depress recruitment rates and threaten population viability (Crouse et al. 1987; Congdon et al. 1993, 1994; Crowder et al. 1994; Heppell 1998). Thus, substantial research effort has been devoted to determining spatial and temporal patterns of nest depredation rates and evaluating how

environmental factors, such as land cover and climate variables, influence nest depredation (Dinsmore et al. 2002; Shaffer 2004).

Detailed knowledge of nest depredation is necessary for estimating overall nest survival using statistical techniques and models (Mayfield 1961, 1975), which have frequently been applied in avian systems (Mayfield 1961; Johnson 1979; Dinsmore et al. 2002; Shaffer 2004). These methods range from relatively simple and unbiased calculations that incorporate the number of exposure days between nest checks (Mayfield 1961) to more complicated modeling approaches that accommodate time-varying covariates (Dinsmore et al. 2002; Shaffer 2004). Collectively, these more sophisticated analysis techniques have led to a deep understanding of the ecological processes and environmental factors associated with nest survival and depredation in avian systems by summarizing nest survival rates as daily survival probabilities. Yet, these approaches have not been readily adopted by herpetologists interested in questions related to nest depredation and survival. In the few cases where herpetological studies have extended nest survival

analyses beyond simple descriptive metrics of nest survival, researchers have used methods such as Kaplan-Meier survivorship curves or Cox proportional hazards models (Leighton et al. 2011; Wirsing et al. 2012; Riley and Litzgus 2014). While these methods allow for the modeling of effects of environmental factors on nest depredation rates, they require precise knowledge of nest age and failure date, which may be unrealistic for some studies (Nur et al. 2004; Johnson 2007a). Recent techniques for analyzing nest depredation and survival introduced in the avian literature (e.g., Dinsmore et al. 2002; Shaffer 2004; Converse et al. 2013) provide more analytical flexiblity that potentially may be more suitable for studies of nest depredation and survival in reptiles, as they can accommodate mixed model structures and a broader range of survey designs, with or without precise knowledge of nest age and failure date. Furthermore, these methods can be used to investigate a wide variety of environmental factors, including climatological, spatial, temporal, or vegetational covariates, and can thus be applied to nearly any possible question related to the timing, frequency, and intensity of nest depredation through time (Shaffer 2004).

In this paper, we review the history and utility of nest survival analysis techniques commonly applied to nest depredation data in the avian ecology literature with the aim of illustrating methods available to herpetologists interested in evaluating the effects of spatial and temporal factors on nest depredation and survival. We also employ nest depredation data collected on two species of conservation concern, the Blanding's Turtle (*Emydoidea blandingii*) and the Bog Turtle (*Glyptemys muhlenbergii*), to illustrate how these underutilized techniques can provide insights into factors affecting fitness for turtles beyond what could be learned using traditional approaches, such as group-level comparisons of nest survival rates. We applied the logistic exposure model developed by Shaffer (2004) in our example for two reasons: first, it is one of the most frequently used nest survival models in avian ecology, and second, it can accommodate varying intervals between nest checks, a common limitation of many herpetological field studies. The logistic exposure model may represent the most useful starting point for herpetologists interested in applying more sophisticated nest survival analyses to their nest depredation datasets.

A Brief Review of Nest Survival Analysis Techniques

Below we provide a broad overview of commonly used statistical models for nest survival data, how they have been applied in avian ecology, and their potential use in herpetological research on nest depredation and survival. We divide this historical overview into three roughly chronological sections, meant to capture the gradual increase in analytical sophistication and flexibility of these methods. This review is by no means exhaustive and represents our synthesis of the most commonly applied and cited techniques for analyzing nest depredation datasets. For those interested in a more thorough treatment of the history, application, and intricacies of these methods in the context of avian research, Studies in Avian Biology, Volume 34 contains a number of excellent and thorough overviews of these methods. In particular, we direct readers to both reviews by Johnson (2007a, b), which provided foundational information that guided our review.

We define a successful nest as one that produces at least one surviving hatchling and define nest depredation as the consumption of eggs by avian, mammalian, and insect predators, which can generally be identified by the presence of chewed or otherwise damaged eggs in and around the nest cavity. For much of the discussion and analysis that follows, nest failure is generally assumed to be due entirely to nest depredation, as visible signs of nest depredation are usually much easier to diagnose than more subtle signs of nest failure due to other factors (such as inundation, poor thermal conditions, or other complicating factors); furthermore, we caution that most of the literature reviewed herein focuses almost entirely on reductions in nest survival due to depredation. In addition, we follow Dinsmore et al. (2002) in using nest survival to describe the probability that an individual nest will produce at least one surviving hatchling, and nesting success to describe the probability that an individual will produce a nest that produces at least one surviving hatchling during a season. While these two terms are functionally synonymous for species that lay one nest per season, this distinction is important when considering species that lay multiple nests per season.

Throughout this review, we emphasize the study design limitations that have motivated the development of these techniques. While the design of studies investigating nesting ecology in avian systems differs from that employed for herpetological field studies, we assert that the flexibility of these methods can be used to accommodate a wide variety of study designs. To this end, following the historical overview of methods, we critically examine how typical herpetological studies of nests may best benefit from reviewed techniques and provide a step-by-step guide to selecting among techniques. Following this appraisal of common herpetological study designs, we illustrate the application of this guide to technique selection with nest depredation data for two turtle species.

1960s to 1970s: early methods to account for left truncation.—Before 1961, the most common method for summarizing nest success involved simply dividing

the number of successful nests by the total number of nests found during a given period, often called apparent nest success (Jehle et al. 2004; Johnson 2007a) or the traditional method (Johnson 1979). Although this technique is simple, it was criticized for its inability to account for differences in detection between successful and unsuccessful nests. In many systems, it is typically impossible to detect nests if they are depredated prior to nest searches, which means that datasets are composed of a biased sample of nests. Failing to account for this phenomenon, which is known as left-truncation, leads to positively biased estimates of nest success (Mayfield 1961, 1975; Jehle et al. 2004; Johnson 2007a).

The Mayfield estimator (Mayfield 1961, 1975) was developed as an unbiased alternative to apparent nest success that incorporates the number of exposure days (that is, the time that nests have been under observation) into a relatively straightforward calculation of daily survival rates. This method, unlike calculations of apparent nest success, does not require monitoring of every nest from the date of egg-laying, and is considered a more powerful, flexible, and unbiased estimator of nest success (Johnson 1979; Hensler and Nichols 1981). However, the Mayfield estimator makes several restrictive assumptions, most notably: (1) constant daily nest survival rate over time, (2) constant survival among nests, and (3) knowledge of the timing of nest failure, or the assumption that failure occurs midway between visits (Jehle et al. 2004; Johnson 2007a). Johnson (1979) created a more general version of the Mayfield model that allows for unknown timing of failure and is among the first publications to recognize that generalized maximum likelihood estimators can be developed based on the Mayfield estimator.

1980s to 1990s: incorporating age effects.— Although the methods outlined above are widely considered to be unbiased methods for analyzing nest survival data that were superior to traditional apparent nest survival calculations, they did have a number of limitations. Most importantly, it was difficult to describe how daily nest survival probability varies over time with these early approaches (Klett and Johnson 1982). Although Hensler and Nichols (1981) took the first steps towards considering age-dependent survival rates by incorporating encounter probabilities into their model, Klett and Johnson (1982) presented, to our knowledge, the first model intended to address these limitations explicitly by designing their model to allow daily survival probabilities to depend on age (Johnson 2007a).

The development of approaches to calculate age-dependent survival probabilities flourished throughout the 1980s and 1990s and led to the recognition that estimating age-dependent nest survival probabilities is difficult when the age of nests cannot be determined precisely. Here, we briefly note several illustrative examples. Pollock and Cornelius (1988) developed the first approach to calculate age-dependent nest survival when nest age can only be approximated within a range of dates; however, their model was found to be biased high and is thus not frequently used (Heisey and Nordheim 1995). Heisey and Nordheim (1995) also developed a model that can calculate age-dependent survival when nest age is not known and they designed this model to directly address the biases found in the Pollock and Cornelius (1988) method by estimating age-dependent nest discovery and nest survival parameters in a likelihood framework. While the Heisey and Nordheim (1995) model was infrequently used due to its complexity, the likelihood structure used in this model formed the basis for a number of other approaches (e.g., Stanley 2000, He 2003).

1990s to present: methods to incorporate nest-level effects.—Starting in the late 1990s, and perhaps spurred by concurrent computational and statistical advances, the predominant trend in the avian nest survival literature was towards flexible approaches that can accommodate a wide range of covariates, including group-level, time-level (like age), and nest-level. The logistic regression model of Aebischer (1999) is perhaps the first approach that could accommodate all three classes of covariates and did so by treating each day during which a nest is vulnerable to depredation (a nest-day; Shaffer 2004) as a Bernoulli trial (1 = successful, 0 = unsuccessful). This model can be used to examine survival differences between groups of nests stratified by simple covariates but can only be reasonably applied when nests are checked every day and the nest failure date is known (Aebischer 1999; Shaffer 2004). This same year, Natarajan and McCulloch (1999) developed a pair of random effects modeling approaches designed to account for heterogeneity in survival rates due to measured and unmeasured sources of variation. Similar to Aebischer (1999), Natarajan and McCulloch (1999) also considered the effects of measured covariates using logistic regression.

The 21st Century ushered in a suite of even more flexible and generalizable methods for analyzing nest survival data. Dinsmore et al. (2002) presented a more flexible analytical model that allows intervals between nest checks to vary. This model can be implemented in Program MARK (White and Burnham 1999) and uses the encounter histories of individual nests to model daily nest survival based on explanatory covariates that vary across time, among nests, or among groups of nests (Shaffer 2004). Shaffer (2004) created a flexible logistic exposure model, which uses a modified link function and incorporates the number of days between

consecutive nest checks. Similar to the method of Dinsmore et al. (2002), this technique allows intervals between nest checks to vary, and can accommodate categorical, time-specific, and nest-level covariates (Shaffer 2004). The only assumptions underlying this model are independence of fates between nests and homogeneity of daily survival rates for nest days that share the same values for explanatory covariates (Shaffer 2004). Despite similarities between the methods presented in Dinsmore et al. (2002) and Shaffer (2004), the two approaches differ markedly in their treatments of time-varying covariates. Shaffer (2004) averages these covariates over each nest check interval, whereas Dinsmore et al. (2002) incorporate covariate values for the day of the nest-check into likelihood approximation. This distinction, while unimportant for studies during which nest checks are made at small intervals (such as every day), can lead to differing results for studies with long intervals between nest checks (Shaffer 2004). Several approaches (He 2003; Converse et al. 2013) have also been developed that use Bayesian inference; while we do not go into detail of these techniques here, Bayesian approaches yield estimates comparable to those obtained using likelihood methods and may be more appropriate in situations involving uncertainty in measurement of predictor covariates (Converse et al. 2013).

SELECTING THE RIGHT METHOD: CONSIDERING STUDY DESIGN AND PURPOSE

As shown above, the development of a diverse array of techniques over the past 65 y for analyzing avian nest depredation and survival data has mainly been a response to constraints imposed by avian nesting ecology, study designs, and research questions. In this section, we discuss similarities and differences in these constraints between avian and herpetological studies and provide guidance for herpetologists interested in selecting an optimal nest survival analysis technique for their study. The technique by which nests are initially identified has important downstream consequences for the analysis of nest depredation and survival data. Birds actively attend their nests, and avian nest survival data is generally collected by flushing birds from nests, manually probing in potential nest cavities, tracking a bird to nesting areas, or visually searching for nesting birds (Johnson 2007b). These survey methods typically limit sampled nests to only those that are active at the time of nest searching and exclude nests that failed before this time leading to the issues of left-truncation and unknown nest ages described above. A wide variety of amphibians and reptiles also attend their nests, including some snakes (e.g., *Liasus fuscus* and *Python sebae*; Shine 2003), a skink (e.g., *Mabuya longicaudata*; Huang 2006), some

anguid lizards (Greene et al. 2006), some geckos (Mateo and Cuadrado 2012), a salamander (e.g., *Plethodon cinereus*; Tornick 2010), and a tortoise (e.g., *Gopherus agassizii*; Agha et al. 2013), leading to similar issues (left-truncation and unknown age at discovery) as those occurring in avian studies when nests are discovered based on active attendance.

Most amphibian and reptilian species, however, do not attend their nests. For these species, nests can still be discovered by tracking gravid females and monitoring nesting areas. In studies where nests are identified by direct observation of oviposition, the issues of left-truncation and unknown nest age will be minimized and will be more tractable to analyze using nest survival techniques developed outside of the avian literature that do not take these factors into account. Even so, if studies do not incorporate nests laid outside of survey times, truncation issues will in some sense persist and may bias estimates of overall nest depredation and survival if these issues are not accounted for statistically. Direct observation of oviposition may also be extremely difficult or impossible for some species and may limit the sample size available. In this case, including nests discovered using indirect indicators (e.g., disturbed soil or eggshells) may improve sample size. At the same time, however, using indirect evidence to locate nests may reduce certainty in nest age and may lead to additional biases (i.e., well-concealed nests may be more difficult to find using indirect methods and may have a lower probability of depredation than poorly concealed nests) that can be accounted for using techniques from the avian literature, such as the logistic exposure model.

Monitoring of nests after oviposition introduces additional complications to the study of nest depredation and survival. Ideally, nest fate is monitored at consistent time intervals (daily if possible), and the timing of nest failure is known. However, logistical constraints can make consistent daily monitoring difficult or impossible. The extended incubation times exhibited by many reptilian species in particular may further challenge efforts at keeping a consistent monitoring schedule. Incubation times for most birds are less than one month (Rahn and Ar 1974), but incubation periods of greater than two months are common in reptiles (Birchard and Marcellini 1996), and some species may incubate for close to a year (*Sphenodon punctatus*; Thompson 1990), making consistent nest monitoring over the entire incubation period extremely difficult. Automated nest monitoring using cameras (e.g., Geller 2012) may improve the consistency of monitoring schedules, although cameras may fail or affect predator behavior (Herranz et al. 2002).

Despite potential challenges, we believe that avian nest depredation and survival analyses provide many advantages over traditional techniques used by

herpetologists, including: (1) flexible accommodation of varying sampling regimes, (2) incorporation of nests of unknown age into samples, (3) the ability to account for imperfect detectability of nests of different fates, which could allow nests located after they have failed to be included in samples with nests that were found after egg-laying, (4) estimation of the effects of exposure time on nest survival (in other words, how nest survival varies through time), and (5) incorporation of time-specific, individual-level, and group-level covariates, with potential to model interactive effects between these covariates. These advantages will make these approaches particularly attractive for herpetologists interested in evaluating the effects of spatial and temporal factors on nest depredation and nest survival. We recommend the following steps for selecting the most appropriate nest survival analysis. First, study questions and hypotheses should be explicitly stated, and an appropriate plan for collecting field data should be designed. Second, the limitations imposed by these field methods should be identified. This may take the form of a series of targeted questions: (1) Will nests be discovered after oviposition, and will age be unknown for some nests; (2) Will nest detection depend at least partially on the fate of that nest (for example, will successful nests be easier to find than unsuccessful nests); (3) Will nests be checked sporadically or infrequently? If the answer to any of these questions is yes, then it may be wise to consider avian nest depredation and survival analyses, as traditional methods based on calculating apparent nest survival may be biased. Some methods may be better suited to certain combinations of study design limitations than others and it is important to choose the correct method to accommodate each scenario (Table 1). At this point, the last step would involve selecting methods based on covariates of interest, as methods also vary in their ability to accommodate different types of covariates (Table 1).

APPLYING THE LOGISTIC EXPOSURE METHOD TO NEST SURVIVAL DATA

To illustrate how statistical models can be used to gain insight into patterns of nest success in herpetological studies, we applied these approaches to nest depredation data collected for two species of conservation concern: Blanding's Turtles in Wisconsin, and Bog Turtles in Maryland. We used the Shaffer (2004) logistic exposure model because this model does not assume precise knowledge of failure dates or homogeneity of survival over time. Using this model, we aimed to examine the factors influencing nest depredation for each species and identify species-specific drivers of nest depredation. For each species, we calculated nest days elapsed between checks, where one nest day is equivalent to a single nest observed for a single day. We stopped counting nest days when a given nest no longer had any surviving eggs, and only considered whole number nest days, as opposed to half or quarter days. As in Shaffer (2004), we consider sample size (n) to be the total number of intervals during which nests were observed. Similar to Shaffer (2004), nests were only monitored for visible

TABLE 1. Subset of available avian nest survival analysis techniques. Yes/No refers to whether a given technique can accommodate that constraint (study design constraints), and whether a given technique can incorporate that covariate type (covariate types).

	Study Design Constraints				Covariate Types		
Method	Left truncation	Unknown nest ages	Unknown nest fates	Inconsistent visitation schedule	Temporal covariates	Group-level covariates	Nest-level covariates
Apparent Nest Survival	No	Yes	No	Yes	No	Yes	No
Mayfield (1961, 1975)	Yes	Yes	Yes	Yes	No	Yes	No
Johnson (1979)	Yes	Yes	Yes	Yes	No	Yes	No
Hensler and Nichols (1981)	Yes	Yes	Yes	Yes	No	Yes	No
Klett and Johnson (1982)	Yes	No	Yes	Yes	Yes	No	No
Heisey and Nordheim (1995)	Yes	Yes	Yes	Yes	Yes	No	No
Aebischer (1999)	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Natarajan and McCulloch (1999)	No	Yes	No	No	Yes	Yes	Yes
Stanley (2000)	Yes	No	Yes	No	Yes	No	No
Survival Time (Aldridge and Brigham 2001; Nur et al. 2004)	No	No	Yes	Yes	Yes	Yes	Yes
Dinsmore et al. (2002)	Yes	No	Yes	Yes	Yes	Yes	Yes
Shaffer et al. (2004)	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Converse et al. (2013)	Yes	Yes	Yes	Yes	Yes	Yes	Yes

signs of depredation by predators and not for other potential sources of nest failure.

Methodology for Blanding's Turtles.—Nest data for Blanding's Turtles were collected in 2011–2013 and 2015 across seven sites 2–12 km apart as part of a long-term population monitoring study conducted in central Wisconsin, USA. Details pertaining to this study are provided in Reid et al. (2016), although the daily nest survival data analyzed here are drawn from an expanded study area and incorporate an additional year of nest survival data (2015). Briefly, nesting female turtles were located through evening surveys of nesting areas such as unpaved roads and road shoulders, open prairie/savannah areas, and exposed sandy quarries. Females located in the act of oviposition were left undisturbed and the location of the nest was recorded. Thread packets were attached to other gravid females found during nesting surveys, and nests were located afterwards via thread-tracking (see Reid et al. 2016 for details). Nests were marked with flags placed > 1 m from the nest to avoid alerting predators to exact nest locations. Evening nesting surveys were conducted for approximately three weeks each year (from late May to late June) encompassing the period during which more than approximately 95% of gravid females nested, and over the course of nesting surveys, all surviving nests were checked each morning for signs of depredation; in this way, nests were checked every day until the end of the nesting season (when no females were seen nesting for multiple consecutive nights; usually late June). After the completion of evening nesting surveys in late June, nests were checked sporadically (every 1–13 d), with the goal of monitoring all nests for at least two weeks after oviposition. It is important to note that the goal of this study was to quantify nest depredation rates and not overall nest success; therefore, due to this goal and logistical constraints, nests were not followed to hatching, and nest depredation events later in incubation could not be detected by this survey design. However, previous studies have found that depredation events late in incubation are relatively rare for this species (Congdon et al. 1983, 2000). Oviposition date was known for all nests.

Methodology for Bog Turtles.—We collected data on nest survival for Bog Turtles in 2013 and 2014 at two sites in Maryland (referred to throughout as BA030 and HA411; Byer et al. 2017, 2018) as part of a study of the spatial and nesting ecology of Bog Turtles. In each study year, we captured turtles in April and May, and attached radio transmitters to all adult female turtles. We then tracked turtles every evening from late May to late June to determine nest placement,

because nests are typically placed in tufts of grass and are thus difficult to locate (Ernst and Lovich 2009). We marked located nests with orange flags > 1 m away from cavity locations. We briefly monitored nests for external signs of nest depredation at least twice per week (every 1–4 d) from June through August. Because nests were typically buried under several cm of substrate and eggs were often exposed, we also inspected each egg within each cavity for any signs of depredation approximately once every two weeks to determine more subtle instances of depredation. These inspections were conducted while wearing nitrile gloves to minimize human scent. Approximately 50–70% of observed nests were only covered by loose vegetation, with eggs clearly visible from above; in rare cases where substrate disturbance was required to observe individual egg fates, we always carefully replaced substrate after these checks. In addition, rubber waders were always worn by researchers at each study site to minimize human scent, and researchers varied transit paths to minimize habitat disturbance. We acknowledge that these methods could influence nest survival rates; however, human scent generally does not appear to influence nest survival rates for most turtles (Burke et al. 2005), and infrequent substrate disturbance was deemed necessary for this study to detect subtle cases of nest depredation by insects and calculate precise rates of nest depredation (Byer et al. 2018). Although we cannot rule out the possibility that repeated manipulation with nitrile gloves deposited chemicals (Gutleb et al. 2001) that could have attracted predators, such phenomena have not yet been documented in reptilian nests.

Nests were monitored through to hatching. Because nests are laid very close to the surface of nesting substrates, a small number of nests (nine across both years) were discovered incidentally and thus had unknown oviposition dates; for these nests, oviposition dates were approximated as the midpoint between the start of the nesting season (8 June in both years) and the date of nest discovery (8–22 June). While these oviposition dates are only approximations, the limited duration of nesting for this species (8–22 June; Ernst and Lovich 2009) means that estimated nest oviposition dates are likely within 3–4 d of actual nest oviposition dates. We monitored nests of Bog Turtles during the entire incubation period (42–80 d; Ernst and Lovich 2009; Zappalorti et al. 2017; Byer et al. 2018), which allowed us to consider nest depredation rates throughout the study season. Because these nests were generally open and most eggs were visible from above, we were also able to detect depredation events that are typically more difficult to notice, such as egg depredation by subterranean mammals and insects. In most cases, we were also able to locate hatchlings before they left the nest cavity.

TABLE 2. Model statements used for each species. Abbreviations are S = site; Y = year; A = nest age in days; R = date of nesting relative to first nesting in a given year; T_{max} = maximum daily temperature; T_{min} = minimum daily temperature; P = daily precipitation; K = number of parameters in a given model, with subscripts indicating the species for which parameters were summarized (K_{Bog} = Bog Turtles, K_{Bland} = Blanding's Turtles). Model number provided to facilitate in-text model references.

#	Model	K_{Bog}	K_{Bland}
1	S	1	6
2	Y	1	3
3	A	1	1
4	R	1	1
5	T_{max}	1	1
6	T_{min}	1	1
7	P	1	1
8	A+R	2	2
9	Y+A	2	4
10	Y+R	2	4
11	S+Y	2	9
12	S+Y+T_{max}	3	10
13	S+Y+T_{min}	3	10
14	S+Y+P	3	10
15	S+Y+A	3	10
16	S+Y+R	3	10
17	S+Y+A+T_{max}	4	11
18	S+Y+A+T_{min}	4	11
19	S+Y+A+P	4	11
20	S+Y+R+T_{max}	4	11
21	S+Y+R+T_{min}	4	11
22	S+Y+R+P	4	11
23	S+Y+A+R	4	11
24	S+Y+A+R+T_{max}	5	12
25	S+Y+A+R+T_{min}	5	12
26	S+Y+A+R+P	5	12

Covariates.—For nests of both Bog Turtles and Blanding's Turtles, we included site (S) and year (Y) as categorical covariates to account for potential year-to-year and site-related variability in nest survival, given that nest survival is often found to vary spatially and temporally for both birds (e.g., Shaffer 2004) and turtles (e.g., Congdon et al. 1983; Kolbe and Janzen 2002). We also included two daily temporal covariates for nest survival at each nest check interval: nest age (A; number of days between the date of a given nest check and the date of oviposition for a given nest) and relative nesting day (R; number of days between the date of a given nest check and the first observation of nesting for a given year). Previous studies have found that turtle nests are most likely to be depredated within the first several days post-nesting (Tinkle et al. 1981; Congdon et al. 1983), and that nests laid early and late in the season have similar patterns of depredation (Congdon et al. 1983), and we expected to see both trends for both species. Variation in temperature and precipitation has been linked to patterns of nest depredation in birds (Dinsmore et al. 2002; Shaffer 2004) and nesting behaviors in turtles (Congdon et al. 1983; Bowen et al. 2005). To investigate the link between weather patterns and depredation rates in Bog and Blanding's turtles, we included three weather-related covariates: minimum daily temperature (T_{min}), maximum daily temperature (T_{max}), and daily precipitation (P). Weather data were downloaded from the National Centers for Environmental Information (National Centers for Environmental Information. 2017. Climate Data Online. National Oceanic and Atmospheric Administration. Available from https://www.ncdc.noaa.gov/cdo-web/datasets [Accessed 15 January 2017]). Data for study sites of Bog Turtles were obtained from the closest station to a given site (station USC00185934, 13.87 km from site BA30 and station USW00013701, 18.23 km from site HA411), while data for sites of Blanding's Turtles were obtained from a single station (USW00054903, 28.8 km from study sites). For both species, when the interval between nest checks was greater than one day we used the mean of each weather covariate (i.e., the sum of daily values divided by the number of nest days), as in Shaffer (2004). When the interval between nest checks was only one day, we used two different strategies for summarizing weather covariates. As depredation events for nests of Blanding's Turtles were associated with nocturnal nest predators and thus occurred the night before a given nest check, we used weather data from the previous day as covariates for nest fate at a given daily nest check. Timing of depredation was unknown for nests of Bog Turtles, so weather covariates were taken from the same day as each nest check.

Analysis.—While all-combinations model parameterization continues to be a popular approach, we believe that selection of models before data analysis reduces the possibility of uninterpretable or nonsensical parameter estimates that may weaken conclusions drawn from top models (Burnham and Anderson 2002). Therefore, we decided to formulate 26 possible *a priori* models based on combinations of spatial and temporal factors hypothesized to affect nest success in each of the two species (Table 2). Because sample sizes were relatively small, we avoided overfitting by limiting the number of fixed effect covariates in *a priori* model statements to fewer than six. While the logistic exposure model does allow for the inclusion of interactive effects, we decided to include only additive effects in

all model statements to facilitate model interpretation. The simplest models considered the effects of each co-variate in isolation (Models 1–7, Table 2), and we also included two-covariate models that considered only observation-specific temporal covariates (Model 8), a mix of group-level and observation-specific temporal covariates (Models 9 and 10), and group-level spatial and temporal covariates (Model 11). Because spatial and temporal variation in nest depredation probability has been observed by a variety of studies (Congdon et al. 1983; Kolbe and Janzen 2002; Shaffer 2004), we predicted that site and year effects would exist for both datasets, and that these effects would be important for consideration in higher-order models, particularly those that include climatological covariates. In addition, given that the aim of our analysis is also to illustrate the flexibility of this modeling approach for accom-modating covariates of different types, we wanted higher-order models to always include a mix of simple group-level covariates (site and year) and nest-level and time-varying covariates (climate covariates, age, and relative nesting day). Therefore, all models with three or more covariates always included additive effects of site and year, and additional covariates included in these models considered additive effects of additional temporal and climatological covariates. Given that T_{min}, T_{max}, and P were highly correlated ($|r| > 0.6$), we decided *a priori* to not allow climate covariates to coexist in the same model. Three-covariate models (Models 12–16) included S, Y, and climatological (Models 12–14) or observation-level temporal covariates (Models 15–16, Table 2). Four-covariate models (Models 17–23) al-ways included S, Y, one of the two observation-level temporal covariates (A and R), and climate covariates, whereas five-covariate models (Models 24–26) included S, Y, A, R, and one climate covariate. In this way, *a priori* models were selected to include most combina-tions of covariate types while controlling for correlation between climate covariates.

We implemented the modified link function used by Shaffer (2004) using code provided in the documentation for package brglm (Kosmidis 2013). All subsequent analyses were implemented in R (version 3.2.0; R Core Team 2015) using function glm. In each model, the response covariate was the status of the nest at each nest check day, coded as 0 for a nest that still contained eggs at a given nest check and 1 for a nest that had experienced complete depredation by that nest check. Because it was possible for nests to experience partial depredation but not fail entirely, we only assigned a 1 to nest checks where all eggs were confirmed to have been depredated. Because partially depredated nests could still produce surviving hatchlings, this allowed for more accurate estimation of the proportion of nests that produce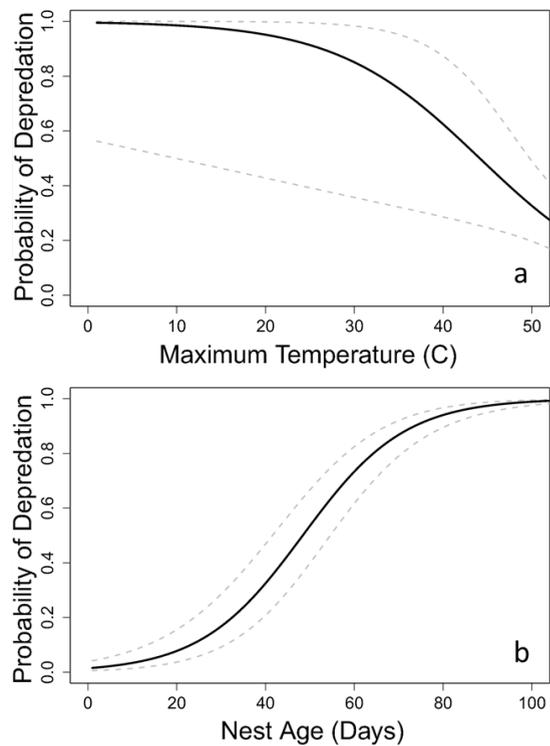d at least one hatchling. Because there were > 2 levels for the Site and Year covariates in Blanding's Turtles, we set one site (nesting area NB) and one year (2011) as the reference levels for these covariates and estimated coefficients for other sites and years relative to these. We then calculated Akaike's Information Criterion scores corrected for sample size (AICc; Sugiura 1978; Hurvich and Tsai 1991) to rank and compare the level of support among models. We considered the model with the lowest AICc the most supported model, and we considered all models within 2 AICc units of the top model (ΔAICc < 2) potentially supported alternative explanations of the data (Burnham and Anderson 2002). For all top models, we examined 95% confidence intervals for fixed effects to judge biological relevance of parameter estimates and calculated McFadden's pseudo-R^2 to judge model fit (McFadden 1974). We visualized the effects of year and site on nest depredation for Blanding's Turtles by plotting predicted depredation probabilities over the course of the nesting season for each year and site (holding all other covariates constant). In cases where covariates in top models had 95% confidence intervals that overlap with zero, we retained these uninformative parameters in model selection tables but only interpreted biological relevance for relevant covariates. We acknowledge that this modeling procedure has the potential to allow uninformative covariates into top models (Arnold 2010); however, given that our goals are both to illustrate the flexibility of these models and to explore the effects of *a priori*-formulated combinations of covariates on nest survival, we chose to pair this modeling approach with a detailed discussion of biologically-relevant covariates.

Top Blanding's Turtle models.—We located 111 total nests for Blanding's Turtles. We located one nest extremely late in the season (late June), at which time surveys became infrequent, and so we excluded it from final analyses. The number of nests per year that we found for Blanding's Turtles across all nesting areas ranged from 18 to 36, with the greatest number of nests (n = 36) located in 2013. We found approximately 37% (n = 41) of these nests in a single nesting area (area NB) with fewer numbers (5–20, or 4–18%) found in the other nesting areas. We monitored these 110 nests for a total of 1,538 nest days across 734 nest checks. Approximately half of these nests (56 of 110 total nests, or 51%) were completely depredated by early July (the end of the study period). The best model had reasonably strong support relative to all other models (ΔAICc = 5.68 compared to the second-best model; Table 3), had moderate fit (McFadden pseudo-R^2 = 0.311) and included site, year, nest age, relative nesting day, and minimum temperature (Fig. 1). This model predicted lower depredation rates with increased nest age (β_A = -0.651, 95% CI = -0.866 to -0.436; Fig. 1) and with increased minimum daily temperatures (β_{Tmin} = -0.179, 95% CI = -0.304 to -0.054;
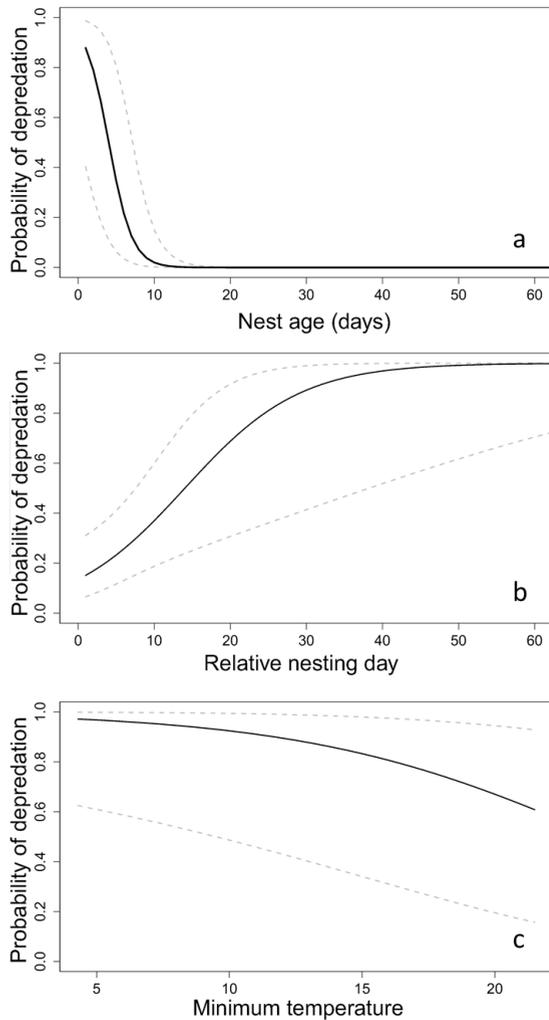
Figure 1. Probability of depredation versus (a) nest age, (b) relative nesting day, and (c) minimum temperature for the top model for Blanding's Turtles (*Emydoidea blandingii*). For each plot the predictor of interest was varied over the range of values observed in the study while the other covariates were held constant at fixed values across all observations (at nest age = 1, day of season = 29, minimum temperature = 12.9, year = 2011, and site = AR). Solid lines indicate estimated effects, and dashed lines indicate 95% confidence intervals.

Figure 2. Probability of depredation versus (a) maximum temperature and (b) nest age for the top model for Bog Turtles (*Glyptemys muhlenbergii*). The predictor of interest was varied over the range of values observed in the study while other covariates were held constant at a fixed value for that covariate across all observations (at nest age = 30, temperature = 28.5, year = 2014, and site = HA411). Solid lines indicate estimated effects, and dashed lines indicate 95% confidence intervals.

different from NB. Estimated depredation rates were lowest in 2011 and highest in 2013 (Fig. 3b). Year-level coefficients were significantly different from zero for 2013 (β_{2013} = 1.665, 95% CI = 0.609 to 2.721) and 2015 (β_{2015} = 1.381, 95% CI = 0.238 to 2.524) but not for 2012 (β_{2012} = 0.772, 95% CI = -0.367 to 1.911), indicating that nest survival rates for 2013 and 2015 were significantly different from 2011.

Top Bog Turtle models.—We used 36 nests for nest survival analyses of Bog Turtles, and we located fewer nests at BA030 (five in 2013, 11 in 2014) than HA411 (nine in 2013, 11 in 2014). We monitored these 36 nests for a total of 2,152 nest days over 574 nest checks. Of these 36 nests, 27 (75%) were depredated. The best model had moderate support relative to all other models (ΔAICc = 2.25 compared to the second-best model; Table 4), had excellent fit (McFadden pseudo-R^2 = 0.727), and included site, year, nest age, and max temperature (Fig. 2). This model predicted higher depredation rates in older nests (β_A = 0.087, 95% CI = 0.074 to 0.103) and on days with lower daily maximum temperatures

Fig. 1), higher depredation rates for nests laid later in the nesting season (β_R = 0.132, 95% CI = 0.038 to 0.226; Fig. 1). Nesting area NB had the highest estimated depredation rate, and area SB had the lowest rate (Fig. 3a). Site-level coefficients were significantly different from zero for areas SB (β_{SB} = -2.022, 95% CI = -3.413 to -0.629) and QU (β_{QU} = -1.365, 95% CI = -2.337 to -0.392) but not for the other sites (β_{BP} = -0.819, 95% CI = -1.762 to 0.13; β_{BR} = -1.012, 95% CI = -2.43 to 0.405; β_{WR} = -0.52, 95% CI = -1.505 to 0.465; β_{AR} = -0.392, 95% CI = -1.844 to 1.061), indicating that nest survival rates at sites BP, BR, WR, and AR are not significantly

Figure 3. Probability of nest depredation versus relative nesting day (a) across sites and (b) across years for the top model for Blanding's Turtles (*Emydoidea blandingii*). The predictor of interest was varied over the range of values observed in the study while other covariates were held constant at a fixed value for that covariate across all observations (at nest age = 1, temperature = 12.9, and site = AR).

(β_{Tmax} = -0.247, 95% CI = -0.447 to -0.067). Site (β_S = -0.048, 95% CI = -0.625 to 0.537) and year (β_Y = 0.378, 95% CI = -0.189 to 0.947) had confidence intervals that overlapped with zero and are thus considered to be uninformative parameters.

FACTORS INFLUENCING NEST DEPREDATION

We used a flexible nest survival analysis approach, developed originally for avian species by Shaffer (2004), to examine factors that influence nest depredation for Bog and Blanding's turtles. One of the primary strengths of this model (as well as many of the more recently developed analytical techniques presented in Table 1) is the ability to incorporate categorical, continuous, and time-varying explanatory covariates, which allowed us to evaluate statistical support for a wide range of model structures. Many of the covariate combinations that we included in our *a priori* model statements would have been difficult or impossible to accommodate using traditional herpetological nest survival analysis approaches, such as logistic regression, as these more frequently-used approaches do not consider how nest

survival probability varies over time. Because many of the approaches reviewed above focus on calculating the probability of a nest surviving a given interval of time, covariates can be summarized for groups of nests,

Table 3. Model selection results for Blanding's Turtle (*Emydoidea blandingii*). All models with weight (w_i) ≥ 0.01 are shown. Abbreviations are AICc = Akaike's Information Criterion corrected for sample size; ΔAICc = AICc of a given model minus AICc of best model; wi = relative likelihood of a given model, LL = log likelihood. S = site; Y = year; A = nest age in days; R = date of nesting relative to first nesting in a given year; T_{max} = maximum daily temperature; T_{min} = minimum daily temperature; P = daily precipitation; K = number of parameters in a given model.

Models	K	AICc	ΔAICc	w_i	LL
S+Y+A+R+T_{min}	12	307.09	0.00	0.82	-140.29
S+Y+A+T_{min}	11	312.77	5.68	0.05	-144.17
S+Y+A+R	11	313.07	5.98	0.05	-144.32
A+R	2	313.3	6.21	0.04	-153.63
S+Y+A+R+T_{max}	12	313.59	6.50	0.04	-143.5441
S+Y+A	10	314.45	7.36	0.02	-146.0419
S+Y+A+R+P	12	315.13	8.04	0.01	-144.3121
S+Y+A+T_{max}	11	315.75	8.66	0.01	-145.6595

TABLE 4. Model selection results for Bog Turtle (*Glyptemys muhlenbergii*). All models with weight (w_i) $\geq$ 0.01 are shown. Abbreviations are AICc = Akaike's Information Criterion corrected for sample size; ΔAICc = AICc of a given model minus AICc of best model; wi = relative likelihood of a given model, LL = log likelihood. S = site; Y = year; A = nest age in days; R = date of nesting relative to first nesting in a given year; T_{max} = maximum daily temperature; T_{min} = minimum daily temperature; P = daily precipitation; K = number of parameters in a given model.

Models	K	AICc	ΔAICc	w_i	LL
S+Y+A+T_{max}	4	179.68	0.00	0.60	-84.76
S+Y+A+P	4	181.93	2.25	0.20	-85.88
S+Y+A+T_{min}	4	184.40	4.72	0.06	-87.12
S+Y+A	3	185.13	5.45	0.04	-88.51
A	1	185.45	5.77	0.03	-90.70
S+Y+A+R	4	185.98	6.30	0.03	-87.91
S+Y+R+T_{max}	4	186.22	6.54	0.02	-88.03
A+R	2	186.98	7.30	0.02	-90.45

individual nests, or individual days for which nests were monitored. In addition, the assumptions underlying this model (i.e., independence of fates between nests and homogeneity of survival rates for days representing the same levels of explanatory covariates) are considerably less restrictive than those underlying the Mayfield estimator and its extensions. Below, we discuss specific insights gleaned from this analysis.

Influence of year and site on nest depredation.—Temporal variability in nest depredation can occur both within the nesting season and among nesting seasons. Previous long-term studies of nest depredation patterns have shown that the intensity of depredation can vary substantially from year to year, sometimes increasing over time (Congdon et al. 2000) and sometimes without a predictable pattern (Kolbe and Janzen 2002; Schwanz et al. 2010). This indicates a large potential role for temporal variability in the distribution and behavior of predators in determining predation risk and emphasizes the need to account for this variability when assessing other factors associated with depredation risk.

Our analysis of Blanding's Turtle nest survival indicated that both year and site had effects on depredation probability, as both of these effects were in the top model and confidence intervals for these effects did not overlap with zero. At the site level, the highest depredation risk was observed at the site in which the largest number of nests was found. Although we did not characterize the absolute number of nests or density of nests in any area (as nests were not located for all females observed at each site), this result suggests that nest predators for Blanding's Turtle (typically Raccoons, *Procyon lotor*, and Coyotes, *Canis latrans*) may target areas where large numbers of females are nesting. A promising area of future research could

involve incorporating density effects into these analyses of nest depredation probability. This would require incorporating temporal variability in nest density (due to addition and depredation of nests), which was ultimately beyond the scope of this manuscript; however, development and inclusion of density estimates could facilitate a more complex understanding of how nest placement affects nest depredation probability. Annual variability in reproductive success, such as that exhibited by Blanding's Turtles here, could also drive the evolution of compensatory longevity in this and other turtle species (Gibbons 1987), and further investigations into the relationship between longevity and temporally varying depredation rates may clarify this link.

The effects of site and year were not as pronounced for Bog Turtles as confidence intervals for these effects overlapped with zero. This is perhaps because depredation in this species is more likely due to small, ubiquitous invertebrate species that happen upon nests by chance rather than behaviorally complex mammals. In addition, it is important to recognize that we collected data for this species only across two years and sites. Application of these modeling approaches to Bog Turtle nesting datasets with more sites and years of data may find stronger signals of spatial and temporal variation in nest depredation.

Influence of nest age on depredation.—A number of herpetological studies have investigated how depredation varies with nest age (Burke et al. 2005; Geller 2012; Wirsing et al. 2012), and the most frequent pattern of nest depredation observed for turtles is high depredation risk within the first 24–72 h post-nesting that declines rapidly over time (Legler 1954; Tinkle et al. 1981; Congdon et al. 1983). This pattern is generally attributed to substrate disturbance and olfactory cues left behind by nesting turtles (Legler 1954; Congdon et al. 1983; Burke et al. 2005; Strickland et al. 2010) and observed rapid declines in depredation risk with time may be attributable to the decay of cues used by predators to locate nests (Burke et al. 2005; Strickland et al. 2010; Wirsing et al. 2012). For Blanding's Turtles, we identified several predictor covariates potentially affecting nest depredation probability (including weather and timing of oviposition); however, nest age had by far the largest effect on nest survival, and modeled nest depredation probabilities as well as actual occurrence of nest depredation were extremely low for nests of Blanding's Turtles that survived for more than a few days regardless of the values of these other predictor covariates. Nests of Blanding's Turtles that were not depredated during the study period were monitored to a maximum of 58 d (median = 25 d), while the average incubation period for Blanding's Turtles is roughly 80 d (Ernst and Lovich 2009). As nests were

monitored only for visible signs of depredation and not for other potential causes of failure (such as depredation by burrowing mammals, flooding, desiccation, or root infiltration; Congdon et al. 2000), these events and any depredation occurring after the cessation of monitoring but before hatching would have been missed, and the nest depredation probabilities provided here thus represent minimum estimates of nest failure. However, nests in this species are usually depredated within 5 d of oviposition (Congdon et al. 1983; Congdon et al. 2000) and depredation accounts for approximately 80% of total embryo mortality (Congdon et al. 2000). The dominance of nest age as a predictor of nest success lends support for the prevailing role of depredation early after oviposition in determining nest success in turtles.

Despite the prevalence of this early depredation pattern in the turtle literature, several studies have found persistent depredation risk late in incubation (Snow 1982; Brooks et al. 1992; Riley and Litzgus 2014) and, indeed, we documented a gradual increase in nest depredation probability with nest age for Bog Turtles. Riley and Litzgus (2014) suggested that these late-incubation predation events may be due to temporal fluctuations in predator population densities, olfactory cues caused by either embryonic fluids released near hatching or rotting eggs, or auditory cues given off by hatching turtles. Several lines of evidence suggest that the late incubation depredation events observed in this study were influenced by some combination of olfactory and auditory cues given off by eggs that are close to hatching, as well as potential olfactory cues given off by rotting eggs; although egg fates other than depredation were not included in our model, we will discuss these potential effects below. First, the logistic exposure model for this species found that nest depredation risk began to increase starting at a nest age of about 40 d, and nests that are 80 or more days old have almost 100% chance of nest failure. Because nests for this species typically incubate for 42–80 d (Ernst and Lovich 2009), this pattern of nest depredation suggests that nest depredation risk is highest when nests are close to hatching. In addition, nests of Bog Turtles observed in this study often had eggs within clutches experiencing mixed fates; while nine of 36 nests produced surviving hatchlings, eight of these nine nests experienced 50–75% egg mortality due to depredation. The timing of depredation and mixed egg fates for some nests together suggest that olfactory and auditory cues given off by eggs that are close to hatching may attract predators. Although the exact identities of these predators are unknown, it could include voles, mice, and other small mammals (Zappalorti et al. 2017). Several depredated eggs in failed nests did not show any evidence of embryonic development, which may also suggest that rotting inviable eggs may provide olfactory

cues for predators to find nests. Regardless, because most of the techniques outlined in this paper require that nest survival be treated as a binary covariate, whereby a nest is considered to have survived the study period if it produces at least one offspring, partial depredation events cannot be readily incorporated into analyses using these techniques. For cases in which individual egg fates are known and individual eggs can be monitored, as is the case for Bog Turtles, individual egg fate could potentially be modeled using a hierarchical framework in which individual egg depredation probabilities covary within nests. Developing this model structure could potentially allow for more accurate characterization of the effects of depredation on reproductive success in both avian and reptilian systems.

Influence of weather on depredation.—Weather conditions may affect nest depredation by modulating predator behavior or the rate of decay for cues used by predators to find nests. Precipitation events in particular have been hypothesized to obscure visual and olfactory cues used by predators to find nests (Legler 1954), although tests of this hypothesis have found no consistent relationship between depredation and precipitation (Bowen et al. 2005). We found some evidence for an effect of weather conditions on nest survival for both species (minimum daily temperature in the case of Blanding's Turtles and maximum daily temperature in the case of Bog Turtles). Low nighttime temperatures tend to increase nest completion times for ovipositing Blanding's Turtles (Congdon et al. 1983), which could in turn extend the window over which potential predators would be able to find a turtle in the act of oviposition or a recently completed nest. Weather effects were relatively weak compared to temporal effects in models, however, and confidence intervals for predicted nest survival at the highest and lowest observed temperatures tended to overlap (Fig. 1, 2). More fine-grained temperature data and soil temperature data, as opposed to the daily temperature highs and lows used here, and more detailed data regarding nesting behavior could be useful in determining the importance of daily fluctuations in temperature on depredation risk.

Interspecific differences and study design.— Interspecific comparisons can be valuable for identifying both extrinsic factors that have similar impacts on nest survival across species and species-specific factors that can lead to differential nest depredation. Making these comparisons can be difficult in practice, however, as differences in nesting ecology among species means that one study design will rarely fit all species of interest. Other analytical methods than those described here have been used to test for interspecific differences in temporal survival patterns (e.g., Riley and Litzgus

2014), although these tests do not identify potential causes of these differences. An important advantage of the logistic exposure method applied to datasets for Bog Turtles and Blanding's Turtles here is that the framework is flexible enough to be applied to data collected from different studies. As with any inter-specific comparisons, it is important to note differences in study design that affect such comparisons. In the present study, for example, nest depredation rates early in the incubation period likely provide a good index of actual nest failure rates for Blanding's Turtles, despite cessation of nest checks after several weeks (Congdon et al. 1983) but must be interpreted with caution in the absence of data from across the entire incubation period. Because Bog Turtle nests were monitored for the entire incubation period, nest depredation rates estimated here likely reflect actual rates of nest depredation.

APPLICABILITY OF NEST SURVIVAL TOOLS FOR HERPETOFAUNA

Overall, we believe that the adoption of more advanced nest depredation and survival analysis techniques introduced in the avian literature will greatly facilitate current conservation research efforts for reptiles and amphibians, such as evaluating the efficacy of nest protection or habitat restoration efforts. At the same time, the wide range of techniques for estimating nest survival due to depredation now available for herpetological research means that we must carefully choose how we analyze nest success datasets. As reviewed above, apparent nest success, despite its frequent use by herpetologists, will often be a biased estimator of nest success (Mayfield 1961, 1975). By integrating these techniques for estimating daily nest survival (which have already been successfully applied and refined over many decades in the avian literature) into our current set of available analytical tools, herpetologists can answer more sophisticated questions about nest survival, offer more realistic conservation and management recommendations for turtles and other egg-laying species, and ultimately learn more about their focal study systems. Although we applied one of these more modern methods to turtles, we believe that these approaches should be evaluated for other nest-laying herpetological taxa, such as squamates and crocodilians, to determine the feasibility and applicability of these methods outside of chelonian and avian systems.

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