SNAKES AS PREDATORS OF BIRD NESTS: NOW AND IN A WARMING WORLD

BY

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DISSERTATION

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ABSTRACT

Exploring the causes and consequences of variation in species’ reproductive success is central to many research questions in ecology and evolutionary biology. For most species of birds, nest predation is the primary cause of nest failure and snakes have often been implicated as important nest predators. However, in other studies snakes are absent or infrequent predators. Here, I reviewed available nest camera studies from North America to better understand how the role of snakes as nest predators varies geographically and by snake species. I then conducted focal studies of two snake species (ratsnake [Elaphe obsoleta] and black racer [Coluber constrictor]) to better understand: 1) what factors influence nest predation rates by these two snakes, 2) which sensory mechanisms snakes use to locate prey, 3) how snake activity patterns vary with temperature, and finally, 4) how nest predation by snakes is predicted to change in a warming world.

To address my first research question I reviewed 53 North American nest camera studies to identify geographic and species-specific patterns in nest predation by snakes. Snakes accounted for 26% (range: 0-90%) of recorded predation events and the ratsnake was the most frequent predator accounting for 65% of all recorded nest predation by snakes. Overall, snakes were more frequent predators at lower latitudes and in open macrohabitats. At a local scale, a single site in South Carolina, I found ratsnakes were the dominant snake predator of bird nests (28% of recorded nest predation) followed by corn snakes (E. guttata: 15%), black racers (12%), and coachwhips (Masticophis flagellum: 3%). In addition to monitoring 206 bird nests with video cameras to determine their fates, I simultaneously tracked 33 ratsnakes and 16 black racers using radiotelemetry. An examination of snake habitat use and avian nest survival revealed that racers and coachwhips were frequent predators of nests located near powerlines, due to their use
of the shrubland habitat maintained below powerlines. Because racers and coachwhips were relatively infrequent predators of nests, however, daily nest survival rate was not influenced by distance to powerlines. Ratsnakes, the locally dominant nest predator, frequently preyed on nests near roads and distance to roads was the best predictor of daily nest survival of monitored nests. Radiotelemetry showed that ratsnakes were often near roads due to the associated forest edges, which ratsnakes are known to use for thermoregulatory purposes.

Relatively little is known regarding how snakes locate nests. Because many snakes are active both during the day and night, I investigated how ratsnakes and racers locate prey, how temperature affects their daily activity patterns, and if the foraging mode of each species constrains when they are active. Because studies in Texas have reported a high rate of ratsnakes capturing adult birds on nests at night, I was particularly interested in understanding why ratsnakes switch to nocturnal activity, how they locate prey in the dark, and why racers appear unable to switch to nocturnal activity. In laboratory trials, I found that ratsnakes were active when temperature was optimal, regardless of whether it was day or night, suggesting they have a genuinely plastic ability to switch between diurnal and nocturnal activity. Consistent with this flexibility, ratsnakes were successful at detecting prey in both low and high light using visual or chemical cues, and were most successful when visual and chemical cues were coupled. Racers were almost always active during the day and when temperatures were not optimal, they simply reduced their activity. Given that these results suggest an expansion of nocturnal ratsnake activity when temperatures are optimal, I next investigated how climate warming might alter ratsnake activity and patterns of songbird nest predation.

To test if climate warming will alter nest predation patterns by ratsnakes, I used a spatially-explicit agent-based model to evaluate how the timing (both daily and seasonal) of nest
predation would change with a warmer climate. Overall, daily nest predation by ratsnakes was predicted to increase 7% with a 2°C increase in temperature. Even modest increases in ambient temperature (0.5°C) caused nocturnal predation by ratsnakes to increase by 30%, particularly in the early spring (200% increase in nocturnal nest predation in March) when nocturnal snake activity is currently limited. Increased temperatures were also predicted to cause nest predation to increase substantially in forest and forest edge habitats due to the thermal heterogeneity of forests buffering snakes against potentially lethal environmental temperatures. If ratsnakes become more concentrated in small forest patches and edges, nest survival in these patches may fall below a sustainable level. Conversely, as temperatures increase, ratsnakes will be less likely to prey on nests in open habitats such as shrublands, which may provide refuges for some nesting birds.
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CHAPTER 1: GENERAL INTRODUCTION

Nest predation is the primary cause of nest failure for many bird species (Ricklefs 1969; Martin 1993) and thus, nest predation is expected to play a fundamental role in shaping avian life histories (Martin 1988; Martin 1993; Latif et al. 2012). Unraveling the effects of nest predation and the responses available to nesting birds requires an understanding of who the nest predators are. For example, options are likely to be quite different if visually-oriented avian predators account for most nest predation than if nocturnal, olfactory-foraging mammals do. Ironically, the ease of observing nests and adults that has made birds such attractive research subjects is matched by the difficulty in identifying their nest predators. Development of miniaturized video cameras that can unambiguously identify nest predators (Thompson et al. 1999) has finally changed that situation, and studies identifying predators and quantifying their importance have accumulated rapidly (Cox et al. 2012). Many of these studies have identified snakes as important predators, suggesting that ornithologists can better understand patterns of nest predation by studying snakes (Weatherhead and Blouin-Demers 2004). Here, I review the available nest camera studies from North America to better understand how the role of snakes as nest predators varies geographically and by snake species. I then follow the suggestion of Weatherhead and Blouin-Demers (2004) and conduct focal studies of two snake species (ratsnake [Elaphe obsoleta] and black racer [Coluber constrictor]) to better understand 1) what factors influence nest predation rates by these two snakes, 2) which sensory mechanisms snakes use to locate prey, 3) how snake activity patterns vary with temperature, and finally, 4) how nest predation by snakes is predicted to change in a warming world.
In addition to geographic variation in predator communities (Chapter 2), predator identity can vary at a single site, with the predators of nests in forest interior differing from those in shrubland habitat patches (Thompson et al. 2003). Nest predator identity can also be influenced by landscape features such as fragmentation and forest edge (Benson et al. 2010; Cox et al. 2012). Edge effects on nest predation rates vary between studies and are actively debated (Donovan et al. 1997; Lahti 2001). Edge effects are context dependent and likely driven by the local nest predator assemblage. A variety of nest predator species are associated with forest edges, including brown-headed cowbirds (*Molothrus ater*), mammalian mesopredators, and snakes (Gates and Evans 1998; Blouin-Demers and Weatherhead 2001; Chalfoun et al. 2002), suggesting that species-specific predator behaviors drive variation in nest predation rates associated with edges (Chalfoun et al. 2002). Thus, understanding how different nest predators are distributed across landscapes in relation to edges will influence predator identity and nest predation rates. However, relatively few studies have coupled autecological studies of nest predators and nest predator identification in relation to landscape features. In Chapter 3, I combine radiotelemetry of ratsnakes and black racers, visual encounter surveys of predatory birds, and miniature nest cameras to investigate predator distribution across a fragmented landscape in South Carolina and to calculate predator-specific nest predation rates in relation to landscape features such as forest edge, powerlines, and macrohabitat type.

Many species of snake, including ratsnakes, seasonally shift their diel activity patterns (Gibbons and Semlitsch 1987; Krysko 2002’ Sperry et al. 2010), presumably in response to seasonal temperature variability (Heckrotte 1975; Weatherhead et al. 2012). The timing of nest predation by snakes can have profound impacts on nesting birds. There is evidence that nocturnal predation by snakes is more successful because most birds cannot defend their nests at
night whereas they can during the day (Hensley and Smith 1986; Carter et al. 2007). Additionally, for at least one imperiled passerine species, the golden-cheeked warbler (*Dendroica chrysoparia*), nocturnal snake predation may result in predation of the incubating or brooding female in up to 75% of encounters, resulting in the annual loss of 14% of breeding females (Reidy et al. 2009). In contrast, the same study found that no incubating or brooding adults were preyed on during the day. Understanding the mechanisms behind why snakes shift to nocturnal behavior and how they locate prey during light and dark conditions can provide valuable insight into predator-prey interactions between snakes and birds. Despite the common occurrence of nocturnal nest predation by ratsnakes, relatively little is known concerning how non-viperid snakes locate prey. In Chapter 4, I artificially manipulated ambient temperature and light in the laboratory to investigate how ratsnakes and racers altered their activity patterns. I hypothesized that ratsnakes would shift their activity to take advantage of optimal temperatures whether they occur at night or day, whereas racers would be constrained to diurnal activity, regardless of temperature. I further hypothesized that the timing of activity is constrained by the sensory cues used for foraging. I test this hypothesis by presenting both species with a prey-location task under different light levels. The specific predictions I test are that ratsnakes will locate food using visual cues during the day and olfactory cues at night, whereas racers will rely on visual cues and thus be able to locate prey only during the day.

Recent studies examined snake activity across a latitudinal gradient, using thermal differences associated with latitude as a surrogate for climate change (Sperry et al. 2010; Weatherhead et al. 2012). That work predicted both an expansion of seasonal snake activity in response to warmer climates, with snakes becoming active earlier in the spring and continuing later in the fall, and a shift in diel patterns with increased nocturnal activity. For many birds,
nests initiated earlier in the season contribute more to population growth than those initiated later and in response birds often invest in more and larger eggs in early nests (Perrins; 1970; Daan et al. 1990; Borgmann et al. 2013). If climate warming results in an expansion of nocturnal or early-season snake activity, there could be consequences for bird populations. Alternatively, in response to increasing temperatures snakes may switch to cooler habitats and thereby encounter nests that were previously free from snake predation. In Chapter 5, I use spatially-explicit agent-based modeling (Railsback and Grimm 2011) to explore how climate warming may change ratsnake activity and habitat use and subsequently avian nest survival. I test the hypothesis that higher ambient temperatures will increase ratsnake predation on nests during cooler periods (night and early season). I also test the hypothesis that warming temperatures will cause snakes to occupy different habitats, thus altering habitat-specific nest predation rates. Specifically, I predict that warmer temperatures will cause snakes to use habitat with more moderate temperatures (forests), increasing nest predation rates in this habitat. Similarly, I predict that snakes will reduce their use of open and warmer habitat (shrublands) as that habitat becomes thermally inhospitable, resulting in less nest predation by snakes in these habitat patches. Further, I expect increasing temperatures will alter the intensity, timing, and location of ratsnake predation on bird nests. In addition to testing these hypotheses, my goal is to use this model to evaluate which of these changes are expected to be most pronounced and to interpret how these changes may affect avian ecology and conservation.
LITERATURE CITED


CHAPTER 2: SNAKE PREDATION ON NORTH AMERICAN BIRD NESTS: CULPRITS, PATTERNS, AND FUTURE DIRECTIONS

ABSTRACT

Predation is the leading cause of nest failure for most birds. Thus, for ornithologists interested in the causes and consequences of variation in nest success, knowing the identity and understanding the behavior of dominant nest predators is likely to be important. Video documentation of nests has shown that snakes are frequent predators. Here we reviewed 53 North American studies that used nest cameras and used these data to identify broad patterns in snake predation. Snakes accounted for 26% (range: 0 – 90%) of recorded predation events, with values exceeding 35% in a third of studies. Snakes were more frequent nest predators at lower latitudes and less frequent in forested habitat relative to other nest predators. Although 12 species of snakes have been identified as nest predators, ratsnakes (Elaphe obsoleta), corn snakes (E. guttata), and fox snakes (E. vulpina) were the most frequent, accounting for >70% of all recorded nest predation events by snakes and have been documented preying on nests in 30-65% of studies conducted within their geographic ranges. Endotherm-specialist snakes (Elaphe and Pituophis genera) were more likely to depredate nests in forests and the canopy relative to other snakes, due to their affinity for edge habitat. Predation by only ratsnakes and corn snakes was predominantly nocturnal and only ratsnakes were more likely to prey on nests during the nestling stage. Snakes were not identified to species in over 30% of predation events, underlining the need for more complete reporting of results. A review of research to date suggests the best approach to investigating factors that bring snakes and nests into contact involves combining nesting studies with radio tracking of locally important snake nest predators.

INTRODUCTION

Determining the causes and consequences of variation in reproductive success is central to many research questions in ornithology. Because predation accounts for approximately 80% of nest failure (Ricklefs 1969, Martin 1993), nest predation has a major influence on the ecology and evolution of avian life history traits as well as implications for avian conservation. It is therefore unsurprising that ornithologists have embraced the use of video cameras to unambiguously identify nest predators (Thompson et al. 1999) as a first step toward better understanding nest predation. Nest cameras are now readily available and studies identifying predators and quantifying their importance have been accumulating rapidly. When results from the first nest-camera studies became available, Weatherhead and Blouin-Demers (2004) drew attention to the fact that snakes were important predators and suggested that by studying snakes ornithologists could better understand nest predation. In the decade since, the number of nest camera studies has increased 10-fold (Cox et al. 2012), allowing evaluation of whether the study of snakes still seems likely to yield insights into nest predation, and if so, to refine suggestions for how that should be done. A recent review of camera studies illustrated the importance of snakes as nest predators in the southeastern United States (Thompson and Ribic 2012). However, because that review was based on only five studies, the scope of inference was limited and highlighted the need for identifying broad geographic patterns in snake predation. Here we review all available nest camera studies from the US and Canada to better illustrate how the importance of snakes as nest predators varies geographically.

In addition to geographic trends in snake predation, there are likely species-specific patterns in nest predation by snakes. Lima (2002) cautioned that predators should not be treated as “black boxes” acting in a generic and uniform manner and we suggest this principle be applied to snakes as a group. From the perspective of nest predation, not all snakes are equal and many could be research “dead ends” if they are not significant nest predators. Researchers interested in simultaneously studying snake behavior and avian nesting ecology are faced with the daunting (i.e., expensive, time-consuming) task of first identifying which snakes are major nest predators at a site and then coupling meaningful snake
research with nest monitoring. Many snakes may not be easily quantified using traditional survey or
capture techniques because they occur at low densities, have extremely secretive behaviors, or are
infrequently available to researchers (e.g., underground or inside structures; Dorcas and Willson 2009).
On the other hand, some snake species do occur at high densities or congregate seasonally and others
make suitable candidates for focal species studies (i.e., radiotelemetry). Here, we synthesize the available
information about snakes from nest camera studies to identify which snake species are frequent nest
predators and worthy of further research.

Ornithologists have used three approaches to explore the factors that bring snakes and nests into
contact: using radiotelemetry to study the behavior of a snake species in relation to nest predation risk,
conducting surveys to quantify variation in snake abundance within different habitats and then correlating
predation risk with snake abundance, and exploring nest site characteristics and how these characteristics
increase or decrease predation risk by snakes (Table 1.1). Radiotelemetry studies have elucidated
important links between snake activity patterns (Sperry et al. 2008, 2012, Weatherhead et al. 2010) or
snake habitat use (Sperry et al. 2010, Klug et al. 2010) and nest predation risk for songbirds. However,
attempts to correlate predation risk with snake abundance have not been as enlightening (Morrison and
association between snake abundance and nest predation risk may result from researchers focusing on the
wrong snake species or employing inappropriate field techniques. Here we identify avenues of research
that might lead to broader insights into the predator-prey relationship between snakes and birds, and
provide practical suggestions for pursuing those avenues.

METHODS

Data Sources

We conducted a literature search in Google Scholar using the following search terms individually
and in combination: “nest”, “predation”, “predator”, “camera”, “snake”, “video” and “videography”.
Further sources were located from the literature cited of the acquired articles and via personal contact
with other researchers. We used peer-reviewed published articles as well as unpublished theses and
dissertations. We also included two unpublished data sets from large-scale shrubland bird nest monitoring studies currently being conducted by the authors in Illinois and South Carolina. Because of biases associated with using artificial nests to infer predation on natural nests (Thompson and Burhans 2004), we excluded results based on artificial nests from our analyses. We used the most precise available geographic location for each study. In cases where a single study was conducted at multiple distinct sites (e.g., Thompson and Burhans 2003), we treated each site separately. In some studies (e.g., Carter et al. 2007, Conner et al. 2010, Ellis-Felege 2010) the number of predation events attributed to each snake species was not provided and we contacted the authors to solicit the required information. If we were unable to obtain these data we included these studies only in analyses not requiring those data. Finally, in cases where investigators have built up a large body of work within a single system, but results were presented in multiple publications (e.g., Stake and Cimprich 2003, Reidy et al. 2008, 2009, Reidy and Thompson 2012), we used the source or sources that presented the most complete dataset without double sampling. In some cases this required acquiring gray literature or dissertations (e.g., Cox 2011). In such cases, we often extracted data from multiple sources to acquire comprehensive information associated with each nest or predation event. However, we were always careful not to double count nests in these instances. We confined our search to the United States and Canada. We excluded studies conducted in Alaska and northern Canada outside of the range of any snake species (N = 6). Because snake taxonomy varies across sources we use the standard scientific and common names in Ernst and Ernst (2003).

Analyses

From each study we extracted the number of nests monitored with cameras and the number of nest predation events involving snakes or other identified predators. Because most snake species were infrequent nest predators, we placed snakes into ecologically meaningful groups to increase our sample sizes for analyses. Endotherm specialists [rattannakes (Elaphe obsoleta), corn snakes (E. guttata), fox snakes (E. vulpina), Great Plains ratsnakes (E. emoryi) and gopher snakes (Pituophis catenifer)] prey principally on endothermic prey such as mammals and birds and their eggs (Ernst and Ernst 2003).
Generalists [racers (*Coluber constrictor*), coachwhips (*Masticophis flagellum*), milk snakes (*Lampropeltis triangulum*), and common and prairie king snakes (*L. guttata* and *L. calligaster*)] opportunistically eat amphibians, insects, reptiles and their eggs, birds and their eggs, and mammals (Ernst and Ernst 2003). The third group was garter snakes, including common and plains garter snakes (*Thamnophis sirtalis* and *T. radix*), which are often semi-aquatic and primarily eat amphibians and earthworms. We assigned each recorded nest predation by snakes to one of these groups. Predation events attributed to other predator guilds were scored as a separate group. We also collected data on the timing (diurnal or nocturnal) and stage (eggs vs. nestlings) for each nest preyed on by snakes. To explore species-specific patterns of predation timing and nest-stage we used two-tailed Fisher’s exact tests.

To explore the factors that make a nest vulnerable to snakes as opposed to other nest predator groups, we used a generalized linear mixed model (GLMM) with binomial distribution and a logit link function. We categorized each nest with a known predator as either preyed on by a snake or preyed on by a predator other than a snake and used this binomial response (referred to as “fate” hereafter) as our response variable. Within this global model we evaluated the fixed factors of latitude and longitude (decimal degrees), elevation (m), nest height guild (ground, shrub, or canopy), habitat type, and egg size (breadth in mm) as possible predictors of predator identity. We included study (the source of the information) as a random effect. We categorized habitat as forest, shrubland, grassland, or other (beach, sand dune, urban environment). Latitude, longitude, and elevation were extracted directly from the primary source material or via Google Earth. When a study included multiple species that nest at different heights (N = 9 studies) we placed nests in the category for which the most commonly encountered nest within the study belonged unless the results were detailed enough to allow us to categorize each nest individually. Because snakes are gape-limited predators and some smaller-bodied species may be physically unable to ingest the eggs of larger bird species, we included egg size as a fixed factor. For egg size we used mean egg breadth for each nesting species based on the *Birds of North America* species...
accounts (Poole 2005). When multiple species were included within a study (N = 17 studies) we used the egg size of the most common species unless the data presented were nest-specific.

Next, we explored which of the above predictors influenced nest predation risk from each of the three snake groups (endotherm specialists, generalists, garter snakes). We again used a GLMM with a generalized logit link function but with a multinomial distribution to enable us to simultaneously examine the probability of predation by each snake group. Because predation events by endotherm specialists were most frequent, we used endotherm specialists as the reference group. Within this global model we evaluated the fixed factors of latitude, longitude, elevation, habitat, nest height, and egg size. We conducted all statistical analyses in SPSS 21.0 (IBM corp., New York, USA) and considered models significant at \( P < 0.05 \).

**RESULTS**

We found 53 sources that reported predator identity of North American bird nests (Appendix 1) obtained using continuous video cameras. Study locations ranged from central Florida to New Hampshire and southern California to Washington. Collectively, these studies filmed 4874 nests of which 45% (N = 2165) were fully or partially depredated, 48% (N = 2344) successfully fledged, and 7% (N = 365) failed due to other reasons (abandonment, storms etc.) or nest fate could not be ascertained due to equipment malfunction. In total, predator identity was known for 1819 predation events. Snakes accounted for 466 (26%) nest predation events for which predator identity was known. Snakes were reported as nest predators in 37 (68%) studies, accounting for between 3 and 90% (mean ± SD = 27 ± 22%) of reported predation within studies (Fig. 2.1). In a third of studies in which snakes were identified as predators, snakes accounted for greater than 35% of all predation events. Nest predation was attributed to 12 species of snakes in six genera: ratsnakes, corn snakes, fox snakes, Great Plains ratsnakes, racers, coachwhips, common kingsnakes, prairie kingsnakes, milk snakes, gopher snakes, common garter snakes, and plains gartersnakes. Among other taxa, mammals were the most frequent nest predators accounting for 709
events (39%), followed by avian predators (538 events: 30%), and then by insects (106 events: 5%) (Fig. 2.1).

Snake identity was either not ascertained or not reported for 142 (31%) of the 466 predation events attributed to snakes. When snake identity was known, ratsnakes were the most frequent predator, accounting for 186 of the 322 (58%) predation events (Fig. 2.2, 2.3). Racers were the next most frequent snake predator, accounting for 33 (10%) nest predation events. Many of these snake species co-occur, so the importance of ratsnakes as frequent nest predators is not due to patterns of occurrence but rather from differences in foraging ecology among snake species. For instance, in areas where the ratsnake occurs, it often overlaps with up to 10 other snakes that prey on nests (Fig. 2.2). As a group, the endotherm specialists (ratsnake, corn snake, fox snake, gopher snake, Great Plains ratsnake) accounted for 74% of all nest predation by identified snakes. Generalists (racers, coachwhips, common and prairie kingsnakes, and milk snakes) accounted for 18% and garter snakes (common and plains garter snakes) for only 8% of predation by snakes.

Some snake species occur over extensive geographic ranges (racers, garter snakes, milk snakes). Thus, even if they prey on nests infrequently they may account for a large proportion of total predation by snakes. To account for the limited distribution of certain species and biases in study site locations, we summarized data for each snake species within its geographic range. Thirty two nest predation studies have been conducted within the geographic range of the ratsnake, the numerically dominant snake predator, and in all but five studies (82%) ratsnakes were filmed depredating nests. Of the studies that did not document ratsnakes as predators, one study curiously documented no nest predation (Buler and Hamilton 2000), another had a limited sample size (N = 8 nests filmed) and no nest predation by any species of snake (Smith 2004), and the others were conducted in habitats (beach or grasslands) infrequently used by ratsnakes (Sabine et al. 2006, Klug et al. 2010, Lyons 2013). Ratsnakes accounted for 65% (range 0 – 100) of nest predation attributed to snakes and 17% of all nest predation within its geographic distribution. Despite the range of ratsnakes overlapping the ranges of 11 other snake species
documented to be nest predators, ratsnakes were the most frequently documented snake nest predator within their range. Although limited in geographic range, fox snakes and corn snakes were responsible for 66 and 30% of predation events attributed to snakes (Fig. 2.3) within their respective ranges (N = 5 and 9 studies), indicating that these two species are locally important nest predators. Although racers accounted for 10% of predation events by snakes, they were infrequent nest predators, accounting for only 11% of the predation by snakes within their geographic range and never surpassed 16% of predation events by snakes at a site.

Diel patterns of nest predation by snakes corresponded well with known patterns of snake activity (Fig. 2.4a). Ratsnakes and corn snakes, both seasonally nocturnal, primarily preyed on nests at night (P < 0.001) and the other species preyed on nests during the day (P < 0.002), although small sample sizes (N = 2) for the gopher snake precluded analysis. Ratsnakes were the only species more likely to prey on nestlings than eggs (Fig. 2.4b: P = 0.0001). No other snake species had a significant association with either nest stage (P > 0.22).

Only latitude had a significant effect on predator identity (GLMM: F₁,1756 = 7.19, P = 0.007), with odds of predation from a non-snake predators increasing at a rate of approximately 10% with each degree of latitude (111 km) (β = 0.095, 95% CI: 0.025-0.164, P = 0.007). Although the habitat variable was not well supported (GLMM: F₁,1756 = 0.737, P = 0.57), other predators were 2.6 times more likely than snakes to depredate nests in forested habitat (β = 0.97, 95% CI: -0.159-2.103, P = 0.092).

In the analysis of factors influencing nest predation by the three snake groups, only the variables latitude (F₂,298 = 5.38, P = 0.005) and habitat (F₂,298 = 5.76, P = 0.004) were significant. Odds of nest predation by garter snakes (relative to endotherm specialists) increased approximately 4% per 100 km increase in latitude (β = 1.44, 95% CI: 0.357-2.517, P = 0.009) and odds of nest predator by generalist snakes (relative to endotherm specialists) increased approximately 1% per 100km increase in latitude (β = 0.123, 95% CI: 0.182 – 2.228, P = 0.02, respectively). Generalists were less likely than endotherm
specialists to prey on nests in forests ($\beta = -1.04$, 95% CI: -1.740 - -0.329, $P = 0.004$). Finally, endotherm specialists were more likely to prey on nests in the canopy than were generalists or garter snakes ($\beta = 1.82$, 95% CI: 0.081 – 2.43, $P = 0.004$).

**DISCUSSION**

Beyond confirming the importance of snakes as nest predators (Weatherhead and Blouin-Demers 2004), our analyses provided insights into patterns of snake predation that can help guide future research. In particular, it is clear that the importance of snakes as nest predators varies both regionally and locally. From an analysis of five studies conducted in the southeastern and mid-western US, Thompson and Ribic (2012) found that snakes are more important nest predators in the south. Our results confirmed that snakes are more frequent nest predators in the eastern and central regions of the southern US compared to the north. Snakes may also be frequent nest predators in the desert southwest, but relatively few camera studies have been conducted in that region and until that gap is filled in we cannot fully evaluate the role of desert snakes as nest predators. The latitudinal shift in importance of snakes is likely a function of two factors. First, snake biodiversity decreases with latitude (Schall and Pianka 1978, Currie 1991), so the pool of snakes that are potential nest predators is larger in warmer climates. Second, snakes at lower latitudes benefit from an expansion of seasonal activity (Sperry et al. 2010, Weatherhead et al. 2012), and the risk of nest predation increases when snakes are more active (Sperry et al. 2008, Weatherhead et al. 2010) and temperatures are higher (Cox et al. 2013). Although snake density is likely to affect nest predation rates, we are unaware of any studies reporting snake density along a latitudinal gradient.

Weatherhead and Blouin-Demers (2004) suggested that birds might reduce nest predation risk by choosing nest sites that are thermally inhospitable to snakes. Whether this occurs remains unknown, but given the geographic patterns we have identified, we expect birds nesting in the southeastern US should be under stronger selection to adopt such strategies relative to birds at higher latitudes. Similarly, where snakes are major nest predators, birds may benefit from nesting outside the seasonal peak in snake
activity. Evidence that predation risk from snakes has shaped avian nesting behavior may be more apparent at southern latitudes where snakes are more frequent nest predators.

Our results also suggest an important caveat: although 12 species of snakes have been filmed preying on birds’ nests, only a subset of those species (i.e., ratsnakes, corn snakes, fox snakes) appeared to be major nest predators. Conducting avian nesting research where those species are abundant will be more likely to yield insights into the interaction between birds and snakes. Because none of these snake species is easily surveyed, determining their presence as local nest predators may require preliminary sampling using nest cameras. Focal species research directed at other snake species is unlikely to be as informative as studies on these three important snake species.

Patterns of predation risk follow those expected based on the ecology (habitat use and activity) of the major snake predators. Endotherm specialists have an affinity for forest edge habitat (Durner and Gates 1993, Keller and Heske 2000, Blouin-Demers and Weatherhead 2001, DeGregorio et al. 2011), so it is unsurprising that these snakes were most likely to prey on nests in forests. Generalists and garter snakes preferentially use grassland and shrubland (Plummer and Congdon 1994, Dodd and Barichivich 2007). Within grasslands, generalist snakes prefer shrubby patches (Klug et al. 2010) and in forested landscapes snakes are often concentrated in edges (Blouin-Demers and Weatherhead 2001). Bird species that are plastic in their nest site selection may benefit from avoiding patchy forests with a lot of edge (because of endotherm specialists) and shrubby patches in grasslands (due to generalists). Additionally, ratsnakes and corn snakes are facultatively nocturnal and thus able to prey on nests both during the day and night. Most of the generalist species are considered to be strictly diurnal, as is the timing of their predation on bird nests.

Sperry et al. (2009) proposed that ratsnakes may also use the upper edge of the tree canopy as “edge habitat”. If true, this may account for the trend of endotherm specialists preying more than other snakes on canopy nests. Because of the difficulties associated with filming nests in the canopy we likely
underappreciate the role of snakes as predators of canopy nests. Several studies have filmed canopy nests in the southern United States (Stake et al. 2004, Bader and Bednarz 2009, Chiavacci 2010) and each reported ratsnakes as the dominant predator. It remains unclear how nest predation risk from snakes may vary with height and how birds might alter nest site height to mitigate risk.

Although we were able to compile nearly 464 records of filmed snake nest predation events, snake identity was either not reported or could not be ascertained in 31% of cases. Accurately identifying nest predators to species improves our ability to detect patterns in predation probabilities (Benson et al. 2010), so we encourage authors to report the identity of predators to species when possible. Our analyses were also limited by gaps in the geographic coverage of nest camera studies, particularly the desert southwest, Great Plains, and northeast. Curiously, although garter snakes are widespread across North America, they have not been reported preying on nests south of Missouri (Thompson and Burhans 2003). However, no study in the southeast has filmed ground-nesting passerine nests, highlighting another bias in nest camera studies. As more bird nests are filmed, new culprits are likely to emerge and our understanding of important nest predators may change. Our results indicate that ratsnakes are the most frequent snake nest predator. Corn snakes and fox snakes each have limited geographic ranges and are frequent nest predators within those ranges. Thus, we suggest that ratsnakes, fox snakes and corn snakes are the most important snake predators of bird nests and warrant further research in relation to nest predation.

Research Recommendations

It makes inherent sense that if more predators are in an area, then local nest predation risk should be higher (Rosenzweig and MacArthur 1963). Thus, predation by snakes should be greatest where snakes are abundant. Unfortunately, estimating snake abundance is a significant challenge. Several ornithologists have attempted to make this link. Most researchers have used encounter rates, often while nest searching, to quantify snake abundance (Morrison and Bolger 2002, Cain et al. 2003, Patten and Bolger 2003).
However, encounter rates are poor indicators of true snake abundance (Rodda and Campbell 2002). Furthermore, many snakes are seasonally nocturnal, so diurnal surveys will be biased. Finally, snake behavior is context specific, with gravid or recently fed snakes most often encountered as they bask to increase their body temperatures (e.g., Charland and Gregory 1995). Thus, these individuals may be double-counted. Because relative abundance indices are biased and ineffective for measuring snake density, mark-recapture is the only reliable method for assessing snake abundance (Dorcas and Willson 2009). Snakes can easily and inexpensively be marked in the field using Passive Integrated Transponder (PIT) tags, scale clipping, or scale cauterization. Furthermore, some mark-recapture designs are can account for variation in capture probability due to demography, environmental variation, behavioral responses (trap-happiness or shyness), or temporary emigration (Dorcas and Willson 2009). Although mark-recapture methods are useful for estimating snake abundance, they are time-consuming and logistically challenging. Even studies with sound experimental designs that employ passive (coverboards and funnel traps) and active (visual searches) methods may suffer from low capture rates (e.g., Chalfoun et al. 2002, Klug et al. 2009), preventing accurate assessments of the abundance of secretive snakes (e.g., ratsnakes, corn snakes, fox snakes). Thus, in most cases, it may be preferable to focus instead on behavioral factors that put snakes in contact with nesting birds.

Radiotelemetry is the conventional approach to studying snake behavior in the field and, despite equipment costs, offers several benefits over other approaches. As discussed, radiotelemetry has yielded insights into links between snake ecology and nest predation (Table 1). Results are often immediately applicable to land management, such as placing brush piles away from nesting habitat (Sperry and Weatherhead 2010). Most snake nest predators are large enough for transmitters that last 24 mo, allowing researchers to track individuals across multiple nesting seasons. Although ratsnakes are well studied, links between fox snake and corn snake behavior and nest predation remain unexplored. Radiotelemetry projects should track multiple individuals (> 10) of different sexes and ages over multiple years to accurately describe variation in snake behavior. Advances such as automated telemetry appear likely to
make this approach even more effective (Ward et al. 2013). As with techniques for quantifying snake abundance, however, telemetry studies are neither quick nor cheap. Radiotelemetry offers an exciting approach in understanding how snakes encounter bird nests and may answer the important future questions including the role of temperature and weather variables in snake movement and predation risk (Cox et al. 2013), elucidating the mechanisms by which snakes locate nests, and the potential role of snakes as predators of fledgling birds.
### TABLES AND FIGURES

**Table 2.1.** Summary of studies that have use radiotelemetry, abundance estimation, or video monitoring to link snake ecology and nest predation.

<table>
<thead>
<tr>
<th>Radiotelemetry</th>
<th>Location</th>
<th>Focal Species</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sperry et al. 2008</td>
<td>Texas, USA</td>
<td>Ratsnakes (<em>Elaphe obsoleta</em>)</td>
<td>-Seasonal nest predation risk of black-capped vireos was greatest when snakes were most active</td>
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<td></td>
<td></td>
<td>Black-capped vireos (<em>Vireo atricapilla</em>)</td>
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<td></td>
<td>Golden-cheeked Warblers (<em>Dendroica chrysoparia</em>)</td>
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<tr>
<td>Sperry et al. 2009</td>
<td>Texas, USA</td>
<td>Ratsnakes (<em>Elaphe obsoleta</em>)</td>
<td>-Snakes preferentially used edge habitat although no relationship between snake habitat use and nest success was documented</td>
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<td>Black-capped vireos (<em>Vireo atricapilla</em>)</td>
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<td>Golden-cheeked Warblers (<em>Dendroica chrysoparia</em>)</td>
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<tr>
<td>Klug et al. 2010</td>
<td>Nebraska and Iowa, USA</td>
<td>Racer (<em>Coluber constrictor</em>)</td>
<td>-Snakes preferentially used shrubby patches in grasslands and nest predation rate was highest in shrubby patches</td>
</tr>
<tr>
<td>Weatherhead et al. 2010</td>
<td>Illinois, USA</td>
<td>Ratsnake (<em>Elaphe obsoleta</em>)</td>
<td>-Seasonal nest predation rates were highest when ratsnakes (but not racers) were most active. Snakes preferentially used edge but proximity to edge did not influence nest success</td>
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<tr>
<td></td>
<td></td>
<td>Racer (<em>Coluber constrictor</em>)</td>
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<td>Shrubland Birds</td>
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<tr>
<td>Sperry et al. 2012</td>
<td>Texas, USA</td>
<td>Ratsnake (<em>Elaphe obsoleta</em>)</td>
<td>-Seasonal predation rate of cardinal nests was greatest when ratsnakes were most active</td>
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<td></td>
<td></td>
<td>Northern Cardinal (<em>Cardinalis cardinalis</em>)</td>
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<table>
<thead>
<tr>
<th>Snake Abundance Studies</th>
<th>Location</th>
<th>Methods</th>
<th>No. Captures and Results</th>
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</thead>
<tbody>
<tr>
<td>Schaub et al. 1992</td>
<td>Florida, USA</td>
<td>Daily counts of snake tracks across a sandy firebreak</td>
<td>-Snake activity was mostly diurnal and was greatest in mid-late summer</td>
</tr>
<tr>
<td>Chalfoun et al. 2002</td>
<td>Missouri, USA</td>
<td>Mark-recapture</td>
<td>-37 snake captures</td>
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<td></td>
<td></td>
<td>Drift fence + funnel traps</td>
<td>Twice as many snakes captured in forest edge as forest interior</td>
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<td>Coverboards</td>
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(Table 2.1 Cont.)

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<thead>
<tr>
<th>Study</th>
<th>Location</th>
<th>Conclusions</th>
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<tbody>
<tr>
<td>Morrison and Bolger 2002</td>
<td>California, USA</td>
<td>Opportunistic snake (non-rattlesnake) encounters while nest-searching</td>
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<td></td>
<td></td>
<td>-0.011 and 0.016 snakes per hour encountered in shrubland interior and shrubland edge habitats. No difference in abundance between habitats</td>
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<tr>
<td>Patten and Bolger 2003</td>
<td>California, USA</td>
<td>Opportunistic snake (non-rattlesnake) encounters while nest-searching</td>
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<td></td>
<td></td>
<td>-104 snakes encountered (57 considered nest-eating species). Snake abundance was the best predictor of nest success for ground-nesting species</td>
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<tr>
<td>Cain et al. 2003</td>
<td>California, USA</td>
<td>Time-constrained visual searches</td>
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<tr>
<td></td>
<td></td>
<td>-Garter snakes detected at between 8-34% of surveys. No association with habitat variables. Garter snakes not documented preying on nests at the site</td>
</tr>
<tr>
<td>Klug et al. 2009</td>
<td>Nebraska and Iowa, USA</td>
<td>Coverboards</td>
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<tr>
<td></td>
<td></td>
<td>-Number of snakes captured not reported. Predator communities responded to variables at the patch and landscape scale</td>
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</tbody>
</table>

**Factors Influencing Nest Vulnerability Study**

<table>
<thead>
<tr>
<th>Study</th>
<th>Location</th>
<th>Conclusions</th>
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</thead>
<tbody>
<tr>
<td>Benson et al. 2010</td>
<td>Arkansas, USA</td>
<td>-Snakes more likely to prey on nestlings than eggs and more likely to find nests far from forest edge.</td>
</tr>
<tr>
<td>Conkling et al. 2012</td>
<td>Texas, USA</td>
<td>-Nest predation risk by snakes decreased with nest height</td>
</tr>
<tr>
<td>Cox et al. 2012a</td>
<td>Missouri &amp; Illinois, USA</td>
<td>-Snakes more frequently prey on indigo bunting than acadian flycatcher nests. Snakes more likely to prey nestlings than eggs and most likely to prey on nests mid-season.</td>
</tr>
<tr>
<td>Cox et al. 2012b</td>
<td>Missouri &amp; Illinois, USA</td>
<td>-Snakes more likely to prey on nests near forest edges.</td>
</tr>
<tr>
<td>Reference</td>
<td>Location</td>
<td>Findings</td>
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<tr>
<td>Cox et al. 2013</td>
<td>Missouri &amp; Illinois, USA</td>
<td>Nest predation risk from snakes increases with increasing mean daily temperatures.</td>
</tr>
<tr>
<td>DeGregorio et al. 2014</td>
<td>South Carolina, USA</td>
<td>Ratsnakes preferentially use edges associated with unpaved roads and nests near these roads are most likely to be depredated by ratsnakes. Racers often use shrub habitat associated with powerlines and are frequent predators of nests in these areas.</td>
</tr>
</tbody>
</table>
Figure 2.1. Location of camera studies, within North American and where snakes occur, and the composition of snake predators documented with nest cameras at each site. The size of each pie chart represents the sample size (number of nests filmed).
Figure 2.2. Location of camera studies and the composition of snake predators documented at each site. The size of each pie chart represents the proportion of overall nest predation events attributed to snakes: small chart = less than 10%, medium chart = 11 – 35%, and large charts = greater than 35% of all predation events were attributed to snakes. For ease of display, common and prairie king snakes are combined, and corn and Great Plains ratsnakes are combined. The shaded area of the map represents the geographic distribution of the ratsnake, the most frequent snake nest predator (adapted from Ernst and Ernst 2003). Circles with X’s indicate studies that did not record snakes as nest predators. Numbers beside pie charts indicate number of potential nest predator snake species (based on range maps) at each site.
Figure 2.3. Total number of avian nest predation events attributed to each snake species. Numbers above each bar represent the percent of nests depredated by each species within their geographic range relative to all snake species.
Figure 2.4. Diel patterns of snake predation of North American bird nests (A) and nesting stage most frequently preyed on by snakes (B).


Poole, A. 2005. The birds of North America online. Cornell Laboratory of Ornithology, Available via http://bna.birds.cornell.edu/BNA


CHAPTER 3: POWERLINES, ROADS AND AVIAN NEST SURVIVAL: EFFECTS ON PREDATOR IDENTITY AND PREDATION INTENSITY

ABSTRACT

Anthropogenic alteration of landscapes can affect avian nest success by influencing the abundance, distribution, and behavior of predators. Understanding avian nest predation risk necessitates understanding how landscapes affect predator distribution and behavior. From a sample of 463 nests of 17 songbird species we evaluated how landscape features (distance to forest edge, unpaved roads, and powerlines) influenced daily nest survival. We also used video cameras to identify nest predators at 137 nest predation events and evaluated how landscape features influenced predator identity. Finally, we determined the abundance and distribution of several of the principal predators using surveys and radiotelemetry. Distance to powerlines was the best predictor of predator identity: predation by brown-headed cowbirds (Molothrus ater), corvids (Corvus sp. and Cyanocitta cristata), racers (Coluber constrictor), and coachwhips (Masticophis flagellum) increased with proximity to powerlines, whereas predation by ratsnakes (Elaphe obsoleta) and raptors decreased. In some cases, predator density may reliably indicate nest predation risk because racers, corvids, and cowbirds frequently used powerline right-of-ways. Of five bird species with enough nests to analyze individually, daily nest survival of only indigo buntings (Passerina cyanea) decreased with proximity to powerlines, despite predation by most predators at our site being positively associated with powerlines. For all nesting species combined, distance to unpaved road was the model that most influenced daily nest survival. This pattern is likely a consequence of ratsnakes, the locally dominant nest predator (28% of predation events), rarely using powerlines and associated areas. Instead, ratsnakes were frequently associated with road edges, indicating that not all edges are functionally similar. Our

results suggest that interactions between predators and landscape features are likely to be specific to both the local predators and landscape. Thus, predicting how anthropogenic changes to landscapes affect nesting birds requires that we know more about how landscape changes affect the behavior of nest predators and which nest predators are locally important.

INTRODUCTION

Anthropogenic habitat alteration can have pervasive effects on wildlife beyond just loss of habitat. The quality of remaining habitat may decline due to an increase in edge habitat or the isolation of remaining patches (Andren 1994). These changes often cause shifts in wildlife species richness, density, or distribution within a landscape (Chalfoun et al. 2002). Installation of linear corridors such as roads and utility right-of-ways may result in relatively little habitat loss, but negatively affect wildlife by creating extensive edge habitat, by inserting early successional habitat into a forested matrix (Rich, Dobkin & Niles 1994), or by modifying the behavior of predators. Linear anthropogenic disruptions can act as travel corridors or barriers for wildlife that can change demographic processes (e.g., increased nest predation, decreased gene flow).

Creation of edge habitat associated with linear habitat features can have indirect effects on wildlife by increasing the frequency with which species interact (e.g., nest predation, brood parasitism), often to the detriment of one species (Murcia 1995). Here, we investigate the effect of landscape features (unpaved roads and powerline right-of-ways) on avian nest predation in a fragmented landscape and quantify the distribution of the principal nest predators relative to the two features.

The effects of edges on birds have been well studied (Gates and Gysel 1978) and many species have demonstrated sensitivity to factors related to edge at multiple spatial scales (Robinson et al. 1995; Flaspohler et al. 2001). Because nest survival is an important component
of songbird demography, edge effects on rates of nest predation for breeding songbirds have frequently been examined (Donovan and Thompson 2001; Manolis et al. 2002). At broad spatial scales nest predation may increase for forest songbirds as landscapes become more fragmented (Robinson et al. 1995). At finer scales, proximity to edge may negatively influence nest survival within a habitat patch (King and Byers 2002; Manolis et al. 2002) by increasing the risk of nest predation (Lloyd and Martin 2005). In some cases, however, no demonstrable edge effect on songbird nest predation has been found (e.g., Robinson and Wilcove 1994; Hanski et al. 1996), leading researchers to conclude that edge effects may be context specific (Donovan et al. 1997; Lahti 2001). In some cases, edge effects may be species or nesting guild-specific (Flaspohler et al. 2001). Additionally, not all edges may function in the same manner, with effects varying with edge age, orientation, structure, and the intervening habitat matrix (Murcia 1995). Nesting birds and their predators may therefore vary their response to different edge types. Lahti (2001) has suggested that exploring species-specific predator behaviors will be a more fruitful approach to understanding patterns in avian nest predation, given the possibility that different predator species respond to landscape features in different ways.

Increased rates of nest predation near edges has led to the study of predator autecology within edges or highly fragmented landscapes (Dijak and Thompson 2000; Chalfoun et al. 2002). Numerous nest predators including brown-headed cowbirds (Molothrus ater), mammalian mesopredators, and snakes preferentially occupy habitat edge over interior (Gates and Evans 1998; Blouin-Demers and Weatherhead 2001a; Chalfoun et al. 2002). The mechanisms underlying predator preference of edge vary by predator group. Ratsnakes (Elaphe obsoleta; Fig. 3.1), the dominant ectothermic nest predator in southeastern North America (DeGregorio et al. 2014), use edge habitat for its thermal qualities, which facilitate efficient digestion and
gestation (Blouin-Demers and Weatherhead 2001b, 2002; Carfagno and Weatherhead 2006). Mammalian mesopredators use edge habitats for foraging and travel corridors (Frey and Conover 2006). Avian predators such as raptors, corvids, and cowbirds use edge for the increased visibility provided by perching structures adjacent to open habitats or because of the high density of passerine nests (Evans and Gates 1997; Gates and Evans 1998). Edges associated with powerline right-of-ways may be especially preferred by these predator groups because edges are abrupt and well-defined, vegetation below powerlines is frequently managed, and the powerline structures provide hunting perches for avian predators (Knight and Kawashima 1993; Rich et al. 1994; Anderson and Burgin 2003). Because each predator group uses corridors and their edges for different purposes, it is not unreasonable to assume that these different landscape features may attract different nest predators. If nest predator communities vary with landscape features, then patterns of nest predation might also vary. Understanding how predator distribution across a landscape influences nest survival has been hampered by our inability to reliably identify nest predators, which until recently was not possible.

Miniature video cameras now allow researchers to identify nest predators unambiguously (Thompson et al. 1999; Reidy and Thompson 2012; Thompson and Ribic 2012). In some cases, the most visible or abundant potential predators at a site may not actually be important nest predators (Liebezeit and Zach 2008). Thus, predator abundance at a site or within a habitat may not be indicative of actual nest predation risk. Additionally, nest cameras can provide insight into how landscape-level factors influence predator assemblages. In one study, nest predation risk from raptors increased with proximity to agriculture edges (Benson et al. 2010) and in another, decreasing forest land cover increased predation risk from cowbirds and decreased predation risk from rodents (Cox et al. 2012). In Texas, predation by cowbirds increased with
urbanization and nest height, and also increased with more open land use in the landscape (Reidy and Thompson 2012). Our goal was to use nest cameras to evaluate edge-related effects, specifically those associated with powerlines and unpaved roads, on predation risk from different predators at songbird nests. We test the hypothesis that proximity to powerlines will decrease overall nest survival. If an increase in nest predation associated with powerlines is a consequence of powerlines creating edge habitat, then we expect an increase in predation with proximity to roads and forest edges. Similarly, the same suite of nest predators should be responsible for both patterns. Alternatively, if avian nest predators use powerline right-of-ways because of the hunting perches provided by the poles and lines, nest predation should be higher near powerlines than near roads because the former provide both edges and perches. Also, birds should be more frequent nest predators near powerlines than near roads and other forest edges.

METHODS

Study Site

We conducted research at the Ellenton Bay Set Aside Research Area on the U.S. Department of Energy Savannah River Site in Aiken County, South Carolina. Ellenton Bay is an 800 ha area that was once row-crop agriculture and pasture but has been reverting to forest since 1951 (Fig. 3.2). The habitat is now mature forest intermixed with areas of open shrubland. The site is bounded to the north by a creek and floodplain forest and to the south by a two-lane paved road with daily traffic by site employees. The site is bisected by four parallel corridors running East to West, two of which are powerline right-of-ways (45 m wide) and two of which are unpaved roads (30 m wide). The roads are used infrequently, primarily by field researchers. The powerline corridors are maintained by South Carolina Electric and Gas Co. and are mowed at least once a year in late summer. Shrubland patches within the right-of-ways are treated with
herbicides if they attain heights > 4m. Conversely, the roads are bordered by approximately 30 m of infrequently maintained shrubland habitat. Thus, edges along roads are more gradual than those along powerlines.

**Daily Nest Survival**

To assess daily songbird nest survival in relation to landscape features we located and monitored avian nests from 5-May to 15-August 2011 and 15-March to 1-August 2012 and 2013. We monitored the nests of a variety of shrub and low-canopy nesting bird species. We accumulated enough data to individually analyze daily survival rate of five species [northern cardinals (*Cardinalis cardinalis*), brown thrashers (*Toxostoma rufum*), blue grosbeaks (*Passerina caerulea*), indigo buntings (*P. cyanea*), and white-eyed vireos (*Vireo griseus*)]. The five focal species are abundant at our site and their nests could be located and monitored easily. Each of the focal species nests in all available macro-habitat types (see descriptions below) at our site. We located nests using systematic searching and behavioral cues. We filmed a subset of nests using 15 user-built miniature video systems (Cox et al. 2012). Although we preferentially filmed the nests of the focal species, we filmed the nests of other species when nests of the focal species were unavailable or camera systems were unused. We placed cameras 0.5-1 m from nests and camouflaged them with nearby vegetation to reduce the likelihood of the cameras attracting predators (Richardson et al. 2009). We put cameras only on nests that were incubating or brooding to reduce the risk of nest abandonment. We checked all nests (with and without cameras) every 48 hr following the protocol described by Martin and Geupel (1993). We considered a nest successful if it fledged at least one nestling or depredated if nestlings disappeared earlier than two days before average fledging dates for the species. At nests suspected to have fledged young we spent considerable time (up to 2 hr in 2 consecutive days) in
the area to confirm the presence of fledglings or parents carrying food to rule out predation late in the nestling period. If fate of the nest was still uncertain, we excluded the last monitoring interval. Following predation (full or partial) of a nest with a camera, we reviewed the video the same day to identify the predator. We considered multiple visits to a nest from the same predator species as one predation event, even if they occurred on different days, because we did not know whether this was more than one individual. Similarly, if multiple predators of the same species attended a nest simultaneously (e.g., five crows simultaneously took nestlings from a northern cardinal nest), we again considered this as only one predation event. If more than one predator species removed contents from the same nest we considered these independent events.

To assess the influence of landscape features on daily nest survival we used logistic exposure (Schaffer 2004) with Proc GENMOD in SAS 9.2 (SAS Institute, Cary, North Carolina). We developed models using macro-habitat type, distance to powerlines, distance to road, and distance to nearest forest edge. Distance to nearest forest edge was in some cases the same as distance to the edges of powerlines or roads, although the values were not strongly correlated (linear regression: $r^2 < 0.02$). Macro-habitat type was assessed for each nest in the field and was categorized as forest, shrubland, forest edge, pine plantation, or wetland. We defined forest edge consistent with definitions from the snake literature (e.g., Carfagno and Weatherhead 2006) and considered a nest to be in forest edge if it was less than 15 m in either direction of the interface between forest and any open habitat. The distance from each nest to the nearest road and powerline was measured in the field with a tape measure if the distance was < 100 m and was measured using ArcMap 10.0 (ESRI, Redlands, California) if the distance was > 100 m. We measured the distance from each nest to directly below the powerline and to the nearest tire rut of a road. Distance from each nest to the nearest edge was always measured in
the field because many edges were not discernible from aerial photographs. We used Akaike’s Information Criterion for small sample sizes (AICc) to rank models for each analysis. We assessed models for all nesting species combined and then for each of the five focal species independently.

To assess the influence of landscape features on nest predator identity we used a multinomial logistic regression model with Proc GLIMMIX in SAS 9.2. The data consisted of each 24 hr interval a nest was filmed and the “response” of each nest at the end of the interval. Responses were predation by ratsnake, corn snake (*Elaphe guttata*), racer (*Coluber constrictor*), coachwhip (*Masticophis flagellum*), raptor (*Buteo* spp, *Accipiter* spp, or *Elanoides forficatus*), corvid (*Corvus brachyrhynchos, C. ossifragus*, or *Cyanocitta cristata*), brown-headed cowbird, ant (*Solenopsis invicta, Chromatagaster sp*), mammal (*Procyon lotor* or *Lynx rufus*), other avian (non-predatory passerines or owls) or survived. Ideally, we would have assessed the response of each predator species independently. However, limited sample sizes for some predators (e.g., swallow-tailed kites [n = 2], blue jay [n = 3]) necessitated the creation of the generic groups “mammals”, “corvids”, and “raptors”, despite differences in their ecology and behavior. We excluded nests for which predator identity could not be ascertained due to camera failure and nests that failed for reasons unrelated to predation (e.g., storms). For this analysis we filmed nests of the five focal species as well as northern mockingbirds (*Mimus polyglottos*), mourning doves (*Zenaida macroura*), yellow-breasted chats (*Icteria virens*), painted buntings (*Passerina ciris*), and eastern towhees (*Pipilo erythrophthalmus*). We evaluated support for each of the following models: macro-habitat type, distance to nearest powerline, distance to nearest unpaved road, and distance to nearest forest edge. We used Akaike’s Information Criterion for small sample sizes to rank models.
**Predator Behavior**

In addition to monitoring songbird nests we used radiotelemetry to track the activity and macro-habitat use of ratsnakes and racers during the avian nesting seasons of 2011 – 2013. Both ratsnakes and racers are important nest predators in our study region (Thompson and Ribic 2012; DeGregorio et al. 2014), the activity and habitat use of which have been linked to nest predation risk (Sperry et al. 2008, 2010; Klug et al. 2010; Weatherhead et al. 2010). Snakes were captured opportunistically by hand throughout the nesting season. Snakes were captured as part of a larger study investigating their spatial ecology and respective roles as nest predators. Search activities were randomly distributed across the landscape with no particular emphasis placed on roadways, so snakes were not captured disproportionately along powerlines or unpaved roads. We transported snakes to a veterinarian who surgically implanted transmitters (model SI-2T 9g, 11g, or 13g, Holohil Systems Ltd, Ontario, Canada) following Blouin-Demers and Weatherhead’s (2001) modification of Reinert and Cundall’s (1982) technique. All transmitters weighed less than 3% of the snake’s total mass. Snakes were released at their capture location 3-5 days following surgery. Snakes were tracked at various times throughout the day and night at approximately 48 hr intervals and locations were recorded using GPS. At each snake location we recorded behavior and local habitat characteristics. We plotted each snake location on an aerial photograph of the study site and used ArcMap 10.0 to measure the distance from each snake point to the nearest powerline and road. We then used the buffer tool in ArcMap 10.0 to create 35 m buffers around each powerline right-of-way and unpaved road, which allowed us to quantify use (number of snake locations within each buffer) and availability (proportion of study site comprised of powerline or road buffers). We chose the 35 m buffer size to account for 15 m edges along either side of the corridor and an additional 5 m to span the width of the road or
We used Analysis of Variance to compare snake use of each habitat feature with 1000 random points distributed across the study site generated with ArcMap.

We also surveyed avian predators along both powerline right-of-way corridors (0.81 and 1.2 km long) and unpaved roads (0.93 and 0.91 km long). Twice per month during the nesting season in 2012 and 2013 (April – July) we walked the length of each road and powerline right-of-way and recorded all birds that were seen or heard. Although all birds were recorded, only potential nest predators were included in analyses. We recorded only birds that were within or on the edge of the corridor. Birds heard in the forests on either side of the survey transect were not recorded unless we determined that they were within 15 m of the forest edge. We performed all surveys in the early morning (between 0600 and 1000). We surveyed all four corridors on the same morning to standardize environmental conditions and we varied the order in which the corridors were surveyed between days to avoid time-of-day effects. Only one author (B.A.D.) conducted surveys to eliminate inter-observer variability.

We grouped birds detected as crows, raptors, cowbirds, or jays for analyses. We estimated relative density of each group for each survey (number of each predator detected / length of corridor surveyed). We then used Multivariate Analysis of Variance with a Tukey’s post hoc test to compare the mean density of predator groups between and within the two corridor types.

**RESULTS**

*Daily Nest Survival*

We located and monitored 463 nests of 17 species, 415 of which belonged to the five focal bird species, for a total of 5680 exposure days (focal species = 5259 exposure days). We monitored 257 northern cardinal nests (3306 exposure days), 53 brown thrasher nests (637 exposure days), 42 blue grosbeak nests (559 exposure days), 42 indigo bunting nests (448 exposure days), and 27 indigo bunting nests (328 exposure days).
exposure days), and 18 white-eyed vireo nests (309 exposure days). For all species combined, the top ranked model from our set of six candidate models influencing daily nest survival rate was the distance to nearest unpaved road (Table 3.1). This model accounted for 78% of the total weight of evidence and no other model was within 3.8 delta AICc units. The effect size for this model was negative and relatively mild (Fig. 3.3) and the next top ranked model was constant survival accounting for 11% of the weight of evidence. When analyzed individually, distance to nearest road was not a top ranked model for any of our five focal species. For indigo buntings, the top ranked model from our set of five candidate models influencing daily nest survival was the distance to nearest powerline (Table 3.1). This model accounted for 81% of the total weight of evidence and no other model was within 4.9 delta AICc units. However, models for nearest powerline were poorly supported for all other focal species. For cardinals, brown thrashers, and white-eyed vireos the top ranked model was constant survival (Table 3.1) indicating that landscape factors had little influence on species-specific daily nest survival at our site, although limited sample sizes for individual species may have influenced this result. The top ranked model for blue grosbeaks was distance to the nearest forest edge. This model accounted for 39% of the total weight of evidence but was only 1.1 delta AICc units above the next model, which was constant survival. Distance to unpaved roads was not a top-ranked model for any of our five focal species and both distance to road and distance to powerlines had relatively minor effects of daily nest survival (Fig. 3.3).

**Predator Identification**

We deployed nest cameras at 206 nests and confirmed predator identity for 137 predation events (Table 3.2). This includes 10 occasions in which more than one predator preyed on the same nest. Twelve nests failed due to non-predation events or were abandoned and 67 nests
successfully fledged at least one bird without any documented predation of eggs or nestlings. Snakes collectively were the most frequent nest predators, accounting for 80 predation events. Ratsnakes were the most frequently documented snake species (38 events), followed by corn snakes (20 events), black racers (17 events), and coachwhips (5 events). Avian predators were the next most frequent group, with 40 predation events attributed to at least nine species. Of the avian predators, crows (American and fish) and blue jays were responsible for 14 predation events and brown-headed cowbirds for 11 events. Ants and mammals were responsible for 8 and 9 predation events, respectively. We attributed predation at six nests to avian predators that did not fit into the previous avian predator groups (owls or non-cowbird passerines).

Distance to powerlines was the best predictor of predator identity. This model accounted for 96% of the weight of evidence and all other models were at ≥ 8 delta AICc units below it (Table 3.3). Daily predation risk from coachwhips was most influenced by distance to powerlines, with the odds of a nest being preyed on by coachwhips relative to surviving decreasing by 1.4% for each 10 m increase in distance from powerlines ($\beta = -0.032$; 85% CI: -0.036, -0.028). The odds of predation by black racers ($\beta = -0.0046$; 85% CI: -0.0051, -0.0041), corn snakes ($\beta = -0.0057$; 85% CI: -0.0062, -0.0052), brown headed cowbirds ($\beta = -0.0042$; 85% CI: -0.0048, -0.0037), and corvids ($\beta = -0.0021$; 85% CI: -0.0026, -0.0016) each decreased by approximately 1% for each 10 m moved away from powerlines (Fig. 3.4). Predation risk from ants ($\beta = -0.00047$; 85% CI: -0.00096, -0.0002) and mammals ($\beta = -0.0006$; 85% CI: -0.00059, 0.00046) also increased with proximity to powerlines, but these effects were weak and had confidence intervals that encompassed zero, indicating uncertainty. Contrary to our predictions, predation by ratsnakes ($\beta = 0.0016$; 85% CI: 0.0014, 0.0019) and raptors ($\beta = 0.00059$; 85% CI: 0.0008, 0.0010) decreased by approximately 1% with each 10 m nearer to powerlines. Although
the models received little support, predation by ratsnakes was positively associated with distance to nearest forest edge ($\beta = -0.0016; 85% \text{ CI: } -0.0024, -0.0008$) and even more strongly with nearest unpaved road ($\beta = -0.0028; 85\% \text{ CI: } -0.0034, -0.0022$). Predation by raptors was also positively associated with distance to nearest road ($\beta = -0.0043; 85\% \text{ CI: } -0.0056, -0.0031$) but negatively associated with distance to nearest forest edge ($\beta = 0.0050; 85\% \text{ CI: } 0.0038, 0.0062$).

**Predator Behavior**

From May – August 2011 and March – August 2012 and 2013 we used radio-telemetry to track 33 ratsnakes and 16 black racers accumulating 1387 and 755 locations, respectively. Powerlines and unpaved roads comprised 5% and 7% of the study site respectively. Snake use of powerlines was non-random and also differed by species: racers were found near powerlines at 17% of relocations and ratsnakes only 2% of relocations ($F = 10.85, P = 0.01$). Use of roads by both species exceeded that expected by chance, with racers using roads at 19% of relocations and ratsnakes at 10% of relocations ($F = 14.48, P = 0.008$). Thus, both snake species were positively associated with roads but exhibited opposite responses to powerlines.

We surveyed each unpaved road and each powerline 13 times during the 2012 and 2013 breeding seasons. We detected a total of 102 brown-headed cowbirds, 78 crows (American and fish), 37 blue jays, and 14 raptors (red-tailed hawks [*Buteo jamaicensis*], American kestrels [*Falco sparverius*], and Mississippi kites [*Ictinia mississippiensis*]). Overall predator density differed between powerlines and unpaved roads ($F_{4,47} = 11.01, P = 0.001$). Brown-headed cowbirds ($F = 35.35, P = 0.001$), crows ($F = 14.73, P = 0.001$) and raptors ($F = 7.80, P = 0.007$) were more dense along powerlines than roads (Fig. 3.5). There was some evidence that blue jays were also more abundant along powerlines ($F = 5.74, P = 0.057$). There were differences in density between the two surveyed powerlines with more cowbirds, crows, and jays detected at
powerline right-of-way 1 relative to 2 ($P > 0.01$). However, powerline 2 still had greater
densities of cowbirds compared to either of the unpaved roads 1 ($P < 0.03$). Powerline 1 had
greater densities of blue jays than powerline 2 ($P = 0.01$) or than either of the unpaved roads ($P <
0.03$). There was no difference in raptor density between the two powerlines surveyed ($P =
0.02$). No significant differences in predator density were detected between the two unpaved
roads ($P > 0.98$).

**DISCUSSION**

Three general patterns emerged from our results. First, distance to nearest powerline
strongly influenced nest predator identity at our site. Predators that used powerlines and poles as
perching structures (crows and cowbirds) or that used the frequently maintained shrub habitat
under powerlines (coachwhips and racers) frequently preyed on nests near powerlines. Second,
distance to powerlines had relatively little impact on daily nest survival for 4 of the 5 focal
songbird species. Only indigo bunting daily nest survival was strongly influenced by distance to
nearest powerline (Fig. 3.3). We interpret this as a consequence of the relative importance of
each predator to overall nest predation. Similar with results from other studies of nest predators
(Thompson et al. 1999; Weatherhead et al. 2010), ratsnakes were more important nest predators
than racers. In fact, ratsnakes were the locally dominant nest predator at our site, accounting for
28% (38 of 137 predation events) of all filmed predation. Although proximity to powerlines was
a strong predictor of nest vulnerability to some predators, the opposite was true for ratsnakes and
raptors. Third, different predators used landscape features differently. Radiotelemetry revealed
that ratsnakes rarely used powerline right-of-ways but were often associated with unpaved road
edges. Raptors, corvids, and cowbirds were more frequently encountered along powerline right-
of-ways than along unpaved road corridors. In some cases, these distribution patterns were reliable predictors of nest predator identity, but in others (raptors) they were misleading.

Ratsnakes were disproportionately located with radiotelemetry near unpaved roads. The association of ratsnakes with unpaved roads was actually an association with the adjacent edge habitat (only once was a ratsnake encountered on a road). Edge use by ratsnakes has been well documented (e.g., Blouin-Demers and Weatherhead 2001a,b; Carfagno and Weatherhead 2006). Contrary to our predictions, ratsnakes rarely used the edges associated with powerlines, suggesting that not all edges are the same from a snake’s perspective. We suggest that because edges associated with powerlines are abrupt they do not provide the thermal heterogeneity for which ratsnakes use edges. In the only study to date that reported snake use of different edge types, Blouin-Demers and Weatherhead (2001a) found that ratsnakes used both natural and artificial edges equally. Artificial edges in that case were predominantly the interface between field and forest habitats, which may be less abrupt than edges associated with powerlines. Alternatively, that study took place in Ontario where ratsnakes are more thermally challenged (Blouin-Demers and Weatherhead 2001c) than those in South Carolina, potentially increasing the reliance of snakes on edges regardless of structure. Edges along unpaved roads at our site were gradual and may have been more attractive to ratsnakes seeking thermally heterogeneous habitat. Unlike ratsnakes, racers at our site often used powerline right-of-ways. We suggest that racers, a grassland and shrubland species (Plummer and Congdon 1994; Keller and Heske 2000), were using powerlines for the early-successional habitat associated with powerlines due to their frequent mowing. Ratsnakes also might avoid powerline right-of-ways because they can be preyed on by the raptors which use the poles as perches. However, it is unclear why ratsnakes would avoid predation associated with these landscape features whereas racers, coachwhips, and
corn snakes were often located near powerlines and preyed on nests under powerlines. Future investigations of edge use by snakes should quantify the properties and use of different types of edges, but our results make it clear that even at the same site, different types of edges can have different ecological effects.

Proximity to unpaved roads was the best supported model for influencing daily nest survival rate. The effect of distance to nearest unpaved road on daily survival rate was negative but mild. Although ratsnakes were the most frequently documented nest predator at our site, we also filmed at least 16 additional species of nest predators. Unpaved roads affected nest survival when all nesting species were combined for analyses, yet when nesting species were analyzed separately, distance to unpaved roads was never included in the top models. We suggest that this is a consequence of small sample sizes for individual species.

We predicted that potential avian nest predators would be denser near powerlines because they use the associated perching structures and therefore, that predation of nests near powerlines would more often be attributed to avian predators. We did find that raptors, crows, and cowbirds occurred in higher densities near powerlines relative to unpaved road corridors and that greater abundance of cowbirds and corvids near powerlines and more use of powerlines by racers did increase predation risk from these predators at our site. However, greater predator abundance in an area does not necessarily translate to higher nest predation from that predator (Liebezeit and Zach 2008), which was the case for raptors. Although raptors were positively associated with powerlines, they were more likely to prey on nests away from powerlines. This discrepancy is due to species-specific responses. Although we often observed red-tailed hawks using powerlines, they were not as frequently observed as nest predators as Accipiters, a forest interior-associated group of raptors. Red-tailed hawks, while abundant near powerlines, may be using
perches to hunt for mammalian prey rather than avian nests. Without nest cameras we may have erroneously concluded that raptors were more frequent predators of nests near powerlines. Responses of predators to landscape features will be species-specific and grouping predators in broad taxonomic groups (e.g., “raptors”) might mask trends. Examining species-specific patterns in predation will require large sample sizes of predation events, which can be logistically infeasible to acquire for infrequent nest predators. Additionally, density of potential avian nest predators may vary between powerlines. For instance, only one of the powerline right-of-ways we surveyed had higher densities of blue jays than unpaved roads. Also, density of crows and cowbirds was greater at one powerline than the other. However, even the powerline with lower predator density still had higher densities of crows and cowbirds than either of the unpaved roads.

Our results indicate that landscape features can affect daily nest survival because of their influence on nest predator distribution and behavior. Predator response to landscape features is likely to be species-specific and influenced by geographic location and the surrounding habitat matrix, confounding our ability to make broad generalizations. Whereas both unpaved roads and powerline right-of-ways fragment forests and create linear edge habitat, they are used differently by predators. Numerous predators at our site were associated with powerline right-of-ways (e.g., racers, cowbirds, raptors), but their relative importance as nest predators at this site was minor relative to ratsnakes. For many shrubland-nesting species in the Northeastern United States, powerline right-of-ways provide refuges of shrub habitat (King et al. 2009; Kubel and Yahner 2009). The importance of nest predators varies geographically (Thompson and Ribic 2012). In areas where shrubland habitat is restricted to powerline right-of-ways, these habitats could act as ecological traps by increasing encounters between powerline-associated nest predators and
imperiled bird species. Our results suggest that nest predator identity can be influenced by landscape features, although this may not necessarily drive trends in nest survival. Broad generalizations about the influence of landscape features such as unpaved roads and powerlines, will be region-specific and driven by the behavior and identity of local nest predators. Further work investigating the geographic trends in importance of nest predators (Thompson and Ribic 2012; DeGregorio et al. 2014) and the behavior of these nest predators in relation to landscape features will be necessary to understand the mechanisms influencing avian nest survival in relation to landscape features.
### TABLES AND FIGURES

Table 3.1. Factors influencing daily nest survival rate of 463 nests (5680 exposure days) of shrubland nesting birds at the Savannah River Site in South Carolina, USA during the 2011, 2012, and 2013 breeding seasons.

<table>
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<th>ΔAICc</th>
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Table 3.2. Nest predators identified using miniature video cameras at 206 songbird nests at the Savannah River Site in South Carolina, USA from 2011-2013. We recorded a total of 137 nest predation events, in 10 instances multiple predators preyed on the same nest.

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Table 3.3. Influence of landscape features on nest predator identity for 198 bird nests filmed from 2011 – 2013 at the Ellenton Bay Set Aside Research Area.

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<td>1650.08</td>
<td>24.31</td>
<td>&lt;0.01</td>
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</table>
Figure 3.1. A ratsnake (*Elaphe obsoleta*), the dominant avian nest predator at our study site, has just preyed on a mourning dove (*Zenaida macroura*) nestling and is returning to the empty nest.
Figure 3.2. Ellenton Bay Set Aside Research Area, in Aiken County, South Carolina, is approximately 800 ha in size and is comprised of highly fragmented forest habitat. The two unpaved roads that were surveyed for predators are marked with solid black lines and the two powerline right-of-ways that were surveyed are marked with dotted black lines.
Figure 3.3. Modeled daily nest survival rates (± 95% confidence intervals) for five focal songbird species as a function of distance to unpaved roads (left column) and distance to powerlines (right column).
Figure 3.4. Daily nest predation rate (± 85% confidence intervals) by different nest predators as a function of their distance from powerlines.
Figure 3.5. Mean density (± S.E.) of avian nest predators detected along two powerline right-of-way corridors and two unpaved road corridors at the Savannah River Site, South Carolina, USA. Each corridor was surveyed 13 times during the avian nesting seasons of 2012 and 2013.


CHAPTER 4: FACULTATIVE NOCTURNAL BEHAVIOR IN SNAKES: EXPERIMENTAL EXAMINATION OF WHY AND HOW WITH RATSNAKES AND RACERS

ABSTRACT

Diel activity patterns are often fixed within species such that most animals can be classified as diurnal, crepuscular, or nocturnal, and have sensory abilities that reflect when they are active. However, many snake species appear capable of switching between diurnal and nocturnal activity. Here, we evaluate the hypothesis that some species are constrained in their activity by the sensory cues used for foraging. We experimentally assessed differences between two sympatric snake species in their ability to alter diel activity patterns, to address why those snakes that switch do so (do thermal constraints force them to be active in otherwise non-preferred conditions?), and to explore how sensory abilities to locate prey facilitate or constrain this shift. Ratsnakes, *Elaphe obsoleta* (Say in James, 1823), were active when temperature was optimal, regardless of light level, suggesting their activity pattern is genuinely plastic. Consistent with our predictions, ratsnakes successfully detected prey in low and high light using visual or chemical cues, and were most successful when cues were coupled. Racers, *Coluber constrictor* (L., 1758), were almost exclusively diurnal, regardless of temperature, and became less active when daytime temperatures were suboptimal. The ability of ratsnakes to shift activity may confer a foraging advantage and should buffer ratsnakes and similarly flexible

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3 This chapter has been published in the Canadian Journal of Zoology. Full citation: DeGregorio, B.A., J.H. Sperry, D.P. Valente, and P.J. Weatherhead. 2014. Facultative nocturnal behavior in snakes: experimental examination of why and how with ratsnakes and racers. Canadian Journal of Zoology 93: 229-237. Throughout this chapter of my dissertation I have retained the plural form and British spelling to remain consistent with the published version.
species from climate change, whereas climate change may pose a more serious threat to inflexible species such as racers.

**INTRODUCTION**

Diel activity patterns are often fixed within species such that most animals can be classified as diurnal, crepuscular, or nocturnal (Metcalf et al. 1998). The sensory systems and hormonal cycles of most species constrain their activity to times when they perform best (Snyder and Weathers 1976; Thorpe and Morgan 1978; Lutterschmidt et al. 2002, 2010). Deviations from these patterns have been viewed as minor, such as modest shifts between diurnal and crepuscular activity rather than overall shifts between diurnal and nocturnal activity (Ashby 1972; Metcalfe et al. 1998). For certain taxa, such as snakes, this behavior appears to be more plastic (Gibbons and Semlitsch 1987; Oishi et al. 2004). Here, we use experiments to investigate the differences between two sympatric snake species in their ability to alter their diel activity patterns, examine why those snakes that switch do so (do thermal constraints force them to be active in otherwise non-preferred conditions?) and explore how sensory abilities to locate prey facilitate or constrain this shift.

Facultatively nocturnal species may shift their activity in response to a number of mechanisms including predation risk (Fraser et al. 2004), competition (Cloudsley-Thompson 1970), body condition, (Metcalf et al. 1998), habitat (Fox et al. 2011), age (Krysko 2002) or season (Abom et al. 2012). For instance, black bears, *Ursus americanus* (Pallus, 1780) may shift from diurnal to nocturnal activity to avoid grizzly bears, *U. arctos horribilis* (L., 1758), or humans (Schwartz et al. 2010). Changes in activity may not only reduce predation risk but may also confer advantages to flexible predators. Black bears foraging at night may be more successful because their salmonid prey is less evasive (Reimchen 1998). Ratsnakes, *Elaphe*
obsoleta (Say in James, 1823), that prey on bird nests at night are more likely to consume both
the nest contents and the attending female, the latter being rarely captured by diurnally foraging
snakes (Reidy et al. 2009).

The relatively common occurrence of diel activity shifts among snakes (Gibbons and
Semlitsch 1987; Krysko 2002; Oishi et al. 2004; Sperry et al. 2010) is often assumed to be
associated with ectothermy, such that snakes shift activity in response to temperature variability,
although only a few studies have explored this phenomenon systematically (e.g., Heckrotte 1975;
Weatherhead et al. 2012). Our interest here is in two general questions about plasticity in timing
of activity in snakes. First, why do shifts occur? For example, do snakes capable of being active
under either light or dark conditions prefer to be active under one of those conditions but shift
activity to the other only when environmental temperatures favor doing so? Second, given that
being active both day and night requires detection and acquisition of prey in very different light
conditions, how do the snakes’ sensory abilities allow them to hunt in both light and dark
conditions? To date, no study has investigated which sensory cues snakes use to detect prey in
both high and low light and whether plasticity in which sensory cues are used is associated with
plasticity in timing of activity.

Information on the sensory cues that non-viperid snake species use to find prey is available
primarily for garter snakes (Thamnophis sp.) and water snakes (Nerodia sp.). Chemical cues
(Gove and Burghardt 1975; Saviola et al. 2012), visual cues (Drummond 1985; Mullin and
Cooper 1998), or a combination of both (Heinin 1995; Shivik 1998) have been documented. All
of these studies tested snakes under only one light condition (either day or night), however, and
only Shivik (1998) studied snakes at night. To understand how snakes can forage in both light
and dark, it is necessary to study the same snakes under both conditions. Furthermore, many of
these studies presented snakes with a prey cue (a scented cotton swab or a skewered chunk of earthworm) to record tongue flicking rates, rather than studying actual foraging behavior. Within the confines of laboratory experiments, more realistic foraging situations and prey cues would be more informative.

In this study we evaluate the hypothesis that facultative nocturnal activity of ectotherms is constrained by the sensory cues used for foraging and not temperature. To test this hypothesis we determine experimentally whether the timing of activity of two sympatric snake species is a function of preference for particular light conditions, ambient temperatures, or both, and how sensory ability allows effective foraging both diurnally and nocturnally. Ratsnakes are active year round in parts of their range, with individuals seasonally switching between diurnal and nocturnal behavior (Weatherhead et al. 2012). Racers, *Coluber constrictor* (L. 1758), are sympatric with ratsnakes across much of the eastern United States and are considered strictly diurnal (Ernst and Ernst 2003). Thus, we first predicted that ratsnakes would shift their activity to take advantage of optimal temperatures whether they occur at night or day, whereas racers would be constrained to diurnal activity, regardless of temperature. Associated with being active both diurnally and nocturnally, ratsnakes have been documented capturing avian prey during the day and at night (Thompson and Burhans 2003; Reidy et al. 2009). Conversely, racers appear to be exclusively diurnal hunters. To test the hypothesis that timing of activity is constrained by the sensory cues used for foraging we presented both species with a prey-location task under different light levels. The specific predictions we test are that ratsnakes will locate food using visual cues during the day and olfactory cues at night, whereas racers will rely on visual cues and thus be able to locate prey only during the day.
METHODS

Study Animals

Ratsnakes and racers were captured opportunistically by hand in Aiken and Barnwell Cos., South Carolina, USA. We probed the cloaca of each individual to determine its sex, assessed the reproductive condition of females by palpation. We excluded gravid females because they may be less vagile and less food-motivated than their non-gravid counterparts. We held any snake with a visible food bolus until the item was digested and excreted. All other snakes were held for between 2 and 5 days for activity trials and for one week prior to foraging trials. Only adults (> 70 cm) were used in trials. Captured animals were housed individually at the Savannah River Ecology Laboratory animal care facility in either 38 or 75 liter aquaria. Each aquarium had a substrate of aspen shavings, a water bowl, and an overturned bowl under which a snake could hide. A 60 watt bulb at the end of each aquarium created a thermal gradient within the enclosure. All animals were kept on a 12:12 light:dark cycle at a constant ambient temperature of 30°C. Different snakes were used for each experiment to minimize time in captivity and were subsequently released at their capture locations. All snakes were collected under South Carolina Department of Natural Resources permits # G-11-03 and 23-2012A and all procedures conformed to permits approved by the University of Illinois (IACUC #11054) and University of Georgia (AUP #A2011 04-007-Y2-A0).

Snake Activity

To assess the influence of temperature on snake activity we filmed snakes under three temperature treatments in a wooden frame enclosure (2.25m L X 1.5m W X 0.46m H) with nylon screen walls. The enclosure had aspen bedding and was otherwise empty except for a waterbowl. At one end of the enclosure we installed a camera with infrared diodes to film snake
activity continuously. Video was recorded at 6 frames per second and downloaded every 24 hr. The enclosure was in a room that allowed control of temperature and light. Snakes were placed individually in the enclosure and exposed to each of following three treatments in a randomly determined order: 1) optimal day (30° C: Blouin-Demers and Weatherhead 2001) and night temperatures (30° C), 2) optimal day (30° C), and suboptimal night (22° C) temperature, and 3) suboptimal day (22° C) and optimal night (30° C), temperature. Each of the three treatments lasted 24 hr and was conducted under a 12:12 light:dark cycle. All trials took place between 01-May and 25- July 2012 and 2013.

Movement on video recordings can best be quantified by detecting pixel changes (Radke et al. 2005). Similar to pixel-difference methods presented in Valente et al. (2007), we created software to detect and quantify snake activity. Because the camera was static and the snake was the only moving object, simple pixel-difference measures could reasonably approximate snake motion, including postural changes. By summing the number of frames for which pixel differences were greater than the background level we could calculate the amount of time a snake was moving (Fig. 4.1). We wrote the software in Python using the OpenCV library.

To ensure the accuracy of this method we randomly selected 30 min segments of video and manually determined the amount time a snake was actively moving. We then used linear regression to compare the amount of activity detected by our software and by observation. Additionally, when watching video we categorized each snake movement as either slight or substantial and either under or above substrate, or stationary other than the head moving. We used these categories to test for differences between the species in particular behaviors (i.e., movement under substrate) that might bias results from our software. We assigned each
behavior a nominal score and compared the amount of time each species was engaged in each behavior using a t-test.

To analyze differences in snake activity relative to the three temperature treatments we quantified the amount of time each snake was moving during each 12 hr period of each treatment. We log transformed the data to better meet the assumptions of normality. We analyzed data using a repeated measures generalized linear mixed model. We evaluated the influence of the fixed factors (species and treatment) and their interaction on snake activity, using individual as a random factor. If we found either fixed factor to be significant at $\alpha < 0.05$, we analyzed the trials separately by species and treatment using pair-wise t-tests.

Prey Detection

To assess how ratsnakes and racers locate prey in different light conditions we presented snakes with a discrimination task that required them to locate prey using a visual stimulus, a chemical stimulus, or both stimuli together, in both light and dark conditions. Within their first two days in captivity, each snake was offered a dead mouse (*Mus musculus*; purchased frozen but thawed in warm water prior to presentation) weighing less than 2% of their body mass. All snakes accepted the mouse, establishing the sight and smell of dead mice as desirable food. After consumption of the mouse we held snakes for a minimum of 7 days (range 7 – 14: mean $8.3 \pm 2.8$ SD) before trials to ensure a strong appetitive response.

We performed all trials in a room with a constant temperature of $30^\circ$C and one of two light levels: high light provided by overhead fluorescent lighting or low light (1 lux) to approximate light conditions on a cloudy night. We placed snakes individually in a plastic holding container ($33.8\text{cm} \times 21.6\text{cm} \times 11.9\text{cm}$) with three clear tubes ($10.2\text{cm}$ diameter x
120cm long) radiating out (one on each of 3 sides; Fig. 4.2). At the end of each tube was a compartment, one of which was baited with prey during each trial. The snake was initially prevented from entering any of the tubes by clear screen gates (aluminum window screen) placed between the holding container and the tube entrances. In each trial, both a dead, thawed mouse and a life-like toy mouse on a string were placed together at the end of one tube, either behind opaque screen made from 6 layers of charcoal fiberglass window screen (chemical stimulus only), a clear plastic barrier (visual stimulus only), or a clear barrier made from aluminum window screen (visual and chemical stimuli). The barriers used in each of these treatments also prevented snakes that chose the baited tube from accessing the prey. Snakes were allowed access to all three tubes in each trial, but only one tube (randomly determined) contained prey. Thus, in each trial there was one baited tube and two non-baited tubes. After allowing the snake 30 min to acclimate (to cease escape behavior and to react to the prey) we removed the gates, providing the snake simultaneous access to all three tubes. We interpreted the snake entering one of the tubes as having reacted to the prey (or lack thereof) in that tube. A trial ended when a snake had entered a tube or after 30 min, whichever came first. After each trial we cleaned tubes thoroughly with paper towels and an odorless disinfectant and then rearranged them in a randomly determined order.

We recorded a snake’s response as a multinomial variable, with snakes entering the baited tube designated as having “reacted to prey”, snakes entering one of the un-baited tubes as “failed to react to prey”, and snakes that remained in the holding container for the entire 30 min as “failed to respond”. One of the authors (B.A.D.) watching from behind a blind (and making the mouse on a string move in a life-like fashion) determined that a snake had “selected” a tube when its head was 25 cm from the holding container (marked by a piece of black tape around
each tube). Note that under low light conditions during trials it was still (just) possible to detect the dark snakes in the clear plastic tubes. We also recorded the time from removal of the barriers to when a snake’s head was 25 cm from the container (defined as latency). We tested snakes either three (night trials only) or six times (day and night trials) with the stimulus treatments presented in random order. All tests for a given snake were conducted on the same day and we used “trial order” as a variable in our analyses to control for a snake’s ability to learn between trials. All trials took place between 1-June and 15- August 2011 or 1-May and 5-June 2012 between 0900 to 1400 h. Only one author (B.A.D) performed trials to eliminate inter-observer variability.

We compared the number of snakes that detected prey to that expected by chance (33.3%) using Chi-square analysis. Because reaction to prey was recorded as a multinomial variable (reacted to prey vs. failed to react to prey vs. no choice), we then used a generalized linear mixed model with multinomial logistic regression to compare the effect of stimulus type on reaction to prey. We used species (rat snake vs. racer), stimulus type (visual, chemical, or both), light level (day or night), an interaction effect between stimulus type and light, time since last meal, and trial order as fixed factors, with snake identity as a random factor. We analyzed latency to reaction using a univariate generalized linear model with the fixed factors of stimulus type, light level, an interaction effect between stimulus type and light, time since last meal and trial order, with snake identity as a random factor. We used a Tukey’s post hoc test to assess differences in latency between stimulus types.
RESULTS

Snake Activity

We tested 14 ratsnakes and 10 racers for a total of 69 trials and accumulated 1656 hours of video. We scored 37 30-min video segments manually and using our automated scoring software. The two methods agreed reasonably well ($r^2 = 0.68$, $P = 0.01$) although the software underestimated activity by an average of 30%. This was primarily due to the program missing movement when the snake was under the substrate or making slight movements at the far end of the arena. We detected no difference in these behaviors between the two snake species ($t = 0.44$, $P = 0.33$). All subsequent results are based on data obtained using the automated software.

Racers were generally more active than ratsnakes and nearly all racer activity was diurnal. Treatment and the interaction between treatment and species had significant effects on activity ($F = 3.65$, df = 3,65, $P = 0.002$; Fig. 4.3). When temperatures were optimal for a full 24 hr period, racers were active almost exclusively during the day (84% of movement: $t = 3.05$, $P = 0.007$). Ratsnakes were active both day and night, with a tendency to be more active during the day (67% of movement: $t = 1.65$, $P = 0.06$). When daytime temperature was decreased to 22° C, racers halved their mean diurnal activity compared to when temperatures were optimal, but still moved only during the day (94% of movement: $t = 3.54$, $P = 0.003$). Ratsnakes also substantially decreased their diurnal activity when daytime temperatures were suboptimal (51% of movement), while maintaining high nocturnal activity ($t = 0.34$, $P = 0.37$). The largest discrepancy in movement between day and night for both species occurred when day temperatures were optimal and night temperatures were suboptimal. Both species showed high levels of diurnal activity and little or no nocturnal activity (79% diurnal movement for ratsnakes: $t = 3.36$, $P = 0.003$; 87% diurnal movements for racers: $t = 6.08$, $P = 0.001$). Although racers
were expected to be exclusively diurnal, we did detect some nocturnal activity. This activity primarily occurred soon after the lights were dimmed (32% of movement within 60 min of light change).

**Prey Detection**

We tested 16 ratsnakes for a total of 48 night trials and 33 day trials, and 9 racers for a total of 24 night and 24 day trials. Ratsnakes successfully reacted to prey at greater than chance (i.e., 33%) rates in day ($\chi^2 = 12.3$, df = 10, $P = 0.02$) and night trials ($\chi^2 = 8.9$, df = 15, $P < 0.01$; Fig. 4.3a). Racers reacted to prey at rates expected by chance in both light and dark conditions ($\chi^2 = 2.60$, df = 11, $P = 0.99$; Fig. 4.3b). Ratsnakes were more successful than racers at reacting to prey ($F = 6.94$, df = 1.68, $P = 0.001$). Because species had such a strong effect, we analyzed species separately.

For ratsnakes, stimulus type had a significant effect on successfully reacting to prey ($F = 3.07$, df = 2.69, $P = 0.05$). Success was highest in both light treatments when chemical and visual stimuli were coupled (> 70% success). Success was lowest in both light levels when only a visual stimulus was presented (50% night, 30% day). Although ratsnakes were slightly more successful at night (60% vs. 57%), the effect of light was not significant ($P = 0.50$). The interaction of stimulus type and light, time since last meal, and trial order were all non-significant ($P = 0.21$). Ratsnakes did not leave the holding container in seven trials, four during night and three during day. Four of the “no choice” results occurred when only a visual stimulus was presented and the other three when visual and chemical cues were presented together. When only a chemical stimulus was presented, ratsnakes always made a choice. For racers, none of the variables had a significant effect on an animal’s ability to react to prey ($P = 0.50$). Additionally,
racers did not leave the holding container in 40% of day trials and always left the container in night trials.

For ratsnakes, stimulus type also had the greatest impact on latency to react to prey ($F = 3.76, \text{df} = 2, P = 0.03$). When presented with only a chemical stimulus, ratsnakes reacted to and approached prey more quickly than when a visual stimulus ($P = 0.03$) or both stimuli ($P = 0.07$) were present (Fig. 4.3a). Light treatment, the interaction effect of light and stimulus type, trial order, and time since last meal were all non-significant ($P = 0.60$). Racers tended to react to prey more quickly during the day ($P = 0.08$; Fig 4.4). Stimulus type, the interaction between stimulus type and light, time since last meal and trial order all had non-significant effects on latency to react to prey for racers ($P = 0.25$).

**DISCUSSION**

Ratsnakes were more active when temperature was optimal, regardless of whether it was light or dark, suggesting their ability to switch between diurnal and nocturnal activity is genuinely plastic. Interestingly, ratsnakes appeared capable of altering activity patterns in response to short-term proximate cues (temperature and light). Ratsnakes in the wild shift from diurnal to nocturnal behavior gradually over periods of weeks or months (Sperry et al. 2013). Although relatively little is known about reptilian circadian rhythms (Oishi et al. 2004), many species appear to have internal, entrained clocks that operate in the absence of light or temperature cues (Klein et al. 2006; Ellis et al. 2009). The rapid shifts in timing of activity by ratsnakes indicate that whatever circadian rhythms they possess do not prevent these snakes from responding to short-term changes in environmental factors. Consistent with this flexibility, ratsnakes successfully reacted to prey in both low and high light. Contrary to our prediction that they would switch sensory modalities, regardless of light conditions ratsnakes were most
successful reacting to prey when both visual and chemical cues were provided, but also reacted to prey when either cue was available alone. Racers were almost exclusively diurnal, regardless of temperature. When daytime temperatures were suboptimal, racers simply became less active. Unfortunately the foraging experiments were not informative regarding whether racers are exclusively diurnal due to an inability to forage at night. Under both light conditions racers “located” prey at chance levels, although their behavior suggested they were primarily motivated to either hide or to escape from the apparatus. Thus, we restrict most of the discussion to the implications of our results for ratsnakes.

Ratsnakes are major avian nest predators (Weatherhead and Blouin-Demers 2004) and prey on nests during the day and at night (Thompson and Burhans 2003), with potentially severe consequences for birds whose nests are located at night. Reidy et al. (2009) reported that in 75% of cases when ratsnakes find nests at night the attending female is eaten by the snake with the contents of the nest. Despite their importance as nest predators, however, we know little about how ratsnakes find nests. We hypothesized that ratsnakes would be visually oriented hunters during the day and olfactory hunters at night. Mullin and Cooper (1998) showed that ratsnakes in captivity used the visual cue of an animated bird on a string to locate a nest cavity more quickly. Although those results indicate that ratsnakes can use vision, the experiment was conducted only in daylight and used only visual cues. Our results indicate that ratsnakes do not change sensory modalities between day and night, but rather use coupled stimuli during both periods. Synergy between visual and olfactory cues has been identified as an important foraging stimulus for other snake species (Heinen 1995; Shivik et al. 2000). Complicating our understanding of ratsnake foraging strategies are observations suggesting that snakes may
sometimes locate nests during the day and wait until nightfall to prey on them (Stake et al. 2005), although confirmation that this actually occurs, and if so, how frequently, has not been obtained.

Many snake species switch from diurnal to nocturnal behavior seasonally (Gibbons and Semlitsch 1987). Presumably, this shift occurs in response to changing temperatures. However, other factors influence the seasonal rhythms of snakes including light-dark cycles (Ellis et al. 2009) and hormones (Lutterschmidt et al. 2002, 2010). Ratsnakes display some nocturnal activity even near the northern extent of their geographic range (Sperry et al. 2013). At northern latitudes it is unlikely that extreme temperatures force snakes to switch to nocturnal activity, but rather releases them from strict diurnal activity. If nocturnal activity confers foraging benefits to flexible predators (e.g., the capture of adult birds), plasticity in timing of activity could provide substantial advantages. This raises the question of why some snake species (e.g., racers) have not evolved the ability to switch between diurnal and nocturnal activity. Despite the perspective that snakes are generally quite flexible in when they are active (Gibbons and Semlitsch 1987), little is known about the activity patterns of most snake species and even less about their foraging ecology. Further investigations into interactions between snakes and their prey are needed. Additionally, studies are needed on more snake species relating sensory modalities to foraging ecology. Very little is known regarding the visual acuity of most snake species and how this may vary between species. Limited evidence indicates North American colubrids have keen eyesight (Baker et al. 2008), but we do not know how visual acuity varies with light levels and among species.

In addition to temperature, light-dark cycles and hormones influence reptile circadian rhythms (Oishi et al. 2004; Klein et al. 2006; Ellis et al. 2009). Performance of diurnal or nocturnal species may be adversely affected if tested during times when they are not typically
active (Llewelyn et al. 2006). Because we conducted all of our foraging tests during the day, racers should not have been at a performance disadvantage relative to ratsnakes, so constraints associated with underlying circadian rhythms cannot explain the inability of racers to locate prey. Additionally, ratsnakes should not have been at a disadvantage because they never entirely abandon diurnal activity for strict nocturnality even at the southern portions of their range (Sperry et al. 2013).

As climates change, many animals adjust their phenology (e.g., Visser and Both 2005), including diel and seasonal changes in activity (Parmesan 2007). Animals with more plastic traits may survive better in a changing world. Ectotherms may need to mediate the effects of climate warming behaviorally by shifting their activity and spending more time inactive or in retreats (Huey et al. 2009; Kearney et al. 2009). Rising temperatures throughout the geographic range of both ratsnakes and racers (IPCC 2007) will result in more frequent inhospitable daytime temperatures. Our results indicate that ratsnakes should be able to respond to such temperatures by increasing nocturnal activity, supporting Weatherhead et al.’s (2012) suggestion that shifts in diel activity rather than seasonal activity should be sufficient for ratsnakes to respond successfully to warmer climates. The less flexible racer may not be able to respond to climate change behaviorally (Huey and Tewksbury 2009; Sears and Angilleta 2011) and may face the same deleterious consequences of warming currently facing diurnal lizards (Sinervo et al. 2010). Again, the dearth of detailed studies of snake activity and sensory ecology limit our ability to generalize how climate warming will affect most snakes.
Figure 4.1. Example of output from our custom software. The Y-axis indicates the sum of squared pixel differences from one frame to the next (in arbitrary units) as the snake moved. The flat line above the X-axis indicates no movement, with each spike indicating that pixels are changing and the snake is moving. We summed the number of frames for which pixel differences were above baseline to calculate the amount of time a snake was moving. In this example, the ratsnake (*Elaphe obsoleta*) moved in 2580 frames or 7 min and 10 sec in the 30-min period.
Figure 4.2. A schematic of the experimental apparatus. A snake was held in the container for 30 min., after which it was given simultaneous access to all the three tubes, two of which were unbaited controls in any given trial, with the third leading to a dead mouse (odour cue) and a lifelike mouse on a string (visual cue). By varying which tube had the mouse stimuli (both were always presented together), each trial consisted of one of three treatments: visual cues only, chemical cues only, or both cues together.
Figure 4.3. Differences in time ratsnakes (*Elaphe obsoleta*) and racers (*Coluber constrictor*) moved (mean ± SE) in a laboratory enclosure under three temperature treatments: optimal day and night temperatures (30° C), suboptimal night (22° C) and optimal day temperatures, and optimal night/suboptimal day temperatures.
Figure 4.4. Proportion of ratsnakes (*Elaphe obsoleta*) and racers (*Coluber constrictor*) that reacted to prey in either high or low light conditions.
Figure 4.5: Mean (+/- S.D.) latency of ratsnakes (*Elaphe obsoleta*) and racers (*Coluber constrictor*) to react to prey in either day or night conditions. Trials for which snakes did not leave the holding container in the 30-min period are excluded.
LITERATURE CITED

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CHAPTER 5: INDIRECT EFFECT OF CLIMATE CHANGE: SHIFTS IN RATSNAKE BEHAVIOR ALTER INTENSITY AND TIMING OF AVIAN NEST PREDATION

ABSTRACT

Understanding how climate change will affect the abundance, distribution, and behavior of wildlife has garnered substantial attention, but predicting how climate change may alter interspecific relationships is more challenging and has received less attention. Here, we use agent-based modeling to explore how climate warming may alter activity patterns and habitat use of ratsnakes and how this will change their interactions with nesting birds. Overall nest predation by ratsnakes increased with warming environmental temperatures, with a 7% increase in daily nest predation as temperatures warmed by 2°C. Modest increases in ambient temperature (0.5°C) caused nocturnal predation by ratsnakes to increase by 30%, particularly in the early spring (200% increase in nocturnal nest predation in March) when nocturnal snake activity is normally limited. Increased nocturnal nest predation can have important demographic consequences beyond nest failure when adult birds on the nest are vulnerable to snakes. Increased temperatures also caused nest predation to increase substantially in forest and forest edge habitats. In a warming world, ratsnakes use forested habitats more because the thermal heterogeneity of forests buffers snakes against potentially lethal environmental temperatures. If ratsnakes become more concentrated in small forest patches and edges, nest survival in these patches may fall below a sustainable level. Conversely, as temperatures increase, ratsnakes will be less likely to prey on nests in open habitats such as shrublands, which may provide refuges for some nesting birds. Species conservation in a warming world requires understanding how the behavior of both the focal species and its predators are affected.

INTRODUCTION

The potential consequences of global climate change on the abundance, distribution, and behavior of wildlife are a growing concern (Thomas et al. 2004; Malcolm et al. 2006; Robinson et al. 2009). To date, most research on animals has focused on species-specific responses to climate change, with relatively little consideration of alterations to community level interactions and the underlying mechanisms. Although more difficult to predict, climate-mediated changes to interspecific relationships could have profound ecological effects. For example, shifts in the onset of avian migration in response to climate change (Parmesan 2007; Robinson et al. 2009) potentially decouples the timing of breeding by birds and the availability of their insect prey, thereby lowering nestling survival (Visser and Both 2005). Similarly, because nest predation is the primary cause of nest failure in temperate songbirds (Ricklefs 1969; Martin 1988), climate-mediated changes in predator abundance, distribution or behavior could profoundly affect bird reproductive success, although this hypothesis has yet to be tested. Here, we use ecological modeling to test the hypothesis that changes in snake behavior due to warming temperatures will affect the timing and intensity of predation by ratsnakes (*Elaphe* spp.; formerly *Elaphe obsoleta*) on songbird nests.

A growing body of evidence has identified snakes as primary predator of many birds’ nests (Weatherhead and Blouin-Demers 2004; Carter et al. 2007; Reidy and Thompson 2012; DeGregorio et al. 2014a). As ectotherms, it is likely that snakes will be strongly affected by climate warming (Deutsch et al. 2008; Kearney et al. 2009; Sinervo et al. 2010). Recent studies examined snake activity across a latitudinal gradient, using thermal differences associated with latitude as a surrogate for climate change (Sperry et al. 2010; Weatherhead et al. 2012). This work predicts both an expansion of seasonal snake activity in response to warmer climates, with
snakes becoming active earlier in the spring and continuing later in the fall, and a shift in diel patterns, with snakes in warmer climates switching from diurnal to nocturnal activity at the warmest time of the year. Because snake activity and behavior can be directly linked to songbird nest predation risk (Sperry et al. 2008; Klug et al. 2010; Weatherhead et al. 2010; Cox et al. 2013; DeGregorio et al. 2014b), this shift in seasonal and nocturnal activity is likely to alter the predator-prey interactions between snakes and birds, most likely to the detriment of bird populations.

Nest survival rates often vary seasonally, with nests initiated earlier in the season contributing more to population growth than those initiated later (Borgmann et al. 2013). Nests initiated early in the nesting season often contain more and larger eggs than later nests, indicating that birds invest more in early-season nests (Perrins 1970; Daan et al. 1990; Nager and Nordwijk 1995). In areas where snakes are primary nest predators, nest survival rates can vary with snake activity, with high nest survival early in the season before snakes are active and declining as snakes become active during the hotter months (Sperry et al. 2008; Weatherhead et al. 2010). If climate warming allows snakes to become active earlier in the nesting season, nests initiated early in the season may no longer be safe and overall reproductive output for birds may decline.

Nocturnal snake predation on avian nests has been extensively documented across a wide range of ecosystems (e.g., Thompson et al. 1999; Thompson and Burhans 2003; Reidy et al. 2009; Reidy and Thompson 2012) and has been implicated as a conservation concern for several imperiled bird species (Carter et al. 2007; Reidy et al. 2009). There is evidence that nocturnal predation by snakes is more successful because most birds cannot defend their nests at night whereas they might during the day (Hensley and Smith 1986; Carter et al. 2007). Additionally, for at least one imperiled passerine species, the golden-cheeked warbler (Dendroica
Chrysoparia), nocturnal snake predation may result in the predation of the incubating or brooding female in up to 75% of encounters, resulting in the loss of 14% of breeding females (Reidy et al. 2009). In contrast, the same study found that no incubating or brooding adults were preyed on during the day. If this phenomenon occurs generally for birds, an expansion of nocturnal snake behavior could have severe detrimental impacts on nesting birds, including reduced nest survival, increased adult mortality, and skewed sex ratios resulting from a disproportionate loss of breeding females. A deeper exploration of the link between snake activity patterns (diel and seasonal), temperature, and nest predation is needed to better understand the potential implications of increased nocturnal snake predation on nesting birds.

Snakes preferentially occupy particular habitat patches to facilitate efficient thermoregulation (e.g., Shine 1987; Charland and Gregory 1995; Blouin-Demers and Weatherhead 2001a; Harvey and Weatherhead 2010). In response to warming temperatures, snakes may not only change the time of day they are active, but also alter the habitats they occupy. Nesting birds may select thermally inhospitable nest sites to minimize predation risk by snakes (Weatherhead and Blouin-Demers 2004). If climate change results in snakes altering their habitat use, however, nest sites that were once thermally protected from predation by snakes may become vulnerable. Using spatially explicit agent-based modeling (Railsback and Grimm 2011), we explore how different climate warming scenarios will affect ratsnake activity and habitat use and subsequently avian nest survival. We test the hypothesis that higher ambient temperatures will increase ratsnake predation on nests during cooler periods (night and early season). We also test the hypothesis that warming temperature will cause snakes to occupy different habitats, thus altering habitat-specific nest predation rates. Specifically, we predict that warmer temperatures will cause snakes to use habitat with more moderate temperatures (mature
forests), increasing nest predation rates in this habitat. Similarly, we predict that snakes will reduce their use of open and warmer habitat (shrublands or clear cuts) as they become thermally inhospitable, resulting in less nest predation by snakes in these habitat patches. Further, we expect increasing temperatures will alter the intensity, timing, and location of rat snake predation on bird nests. In addition to testing our hypotheses, our goal is to use the model to evaluate which of these changes are expected to be most pronounced and to interpret how these changes may affect avian ecology and conservation.

METHODS

Study Site

Data for our model were collected at and around the Ellenton Bay Set Aside Research Area on the Department of Energy’s Savannah River Site, South Carolina (http://srel.uga.edu/set-asides/area1.html). Our model focused on an approximately 450 ha area at the center of the set aside area. For the model, this irregularly shaped area was gridded into 5m resolution cells and enclosed in a minimal bounding box of 760 ha (609 cells east-to-west and 497 cells north-to-south). Snakes were bound within the closed study area such that they were not allowed to leave or enter. The study area contained a mix of habitat types from mature, closed-canopy forests to younger open forests, and shrublands and clear-cuts. The area was once used for row-crop agriculture and pasture, but since 1951 has been allowed to regenerate naturally. The site is primarily wooded, with mixed forests of laurel oak (Quercus laurifolia), loblolly pine (Pinus taeda) and slash pine (P. elliottii) interspersed with open shrubland areas of Chicasaw plum (Prunus angustifolia) and blackberry (Rubus sp). Areas of the site have been clear-cut. In some areas, long-leap pine seedlings are present (P. palustrus) and in others shrubby laurel oaks are sprouting from stumps. All clear cut habitats are hot, dry, devoid of
canopy cover and have piles of woody debris present. The site also has four utility right-of-ways bisecting the site from East to West. These corridors are maintained by the state utility company and are surrounded by shrubland. Since May 2011, predator-prey interactions between Eastern Ratsnakes and shrubland bird nests have been studied via nest monitoring, nest cameras, and radiotelemetry of snakes (DeGregorio et al. 2014b).

Model Description and Entities

We incorporated three types of individual-based entities in our model: ratsnakes (predators), bird nests (prey), and dynamic thermally-variable habitat patches. The model was designed to represent a generic songbird species based on the nesting patterns of the most common local nesting bird (Northern Cardinal [*Cardinalis cardinalis*]) and predation by the ratsnake, the locally dominant nest predator (DeGregorio et al., 2014b). Cardinals are ideal “generic” birds for this study because they nest in a broad range of habitats. We used open-source, agent-based simulation modeling software (NetLogo 5.0: Wilensky 1999) to investigate how thermal heterogeneity of a patchy landscape and different climate change scenarios will influence the predator-prey interactions between ratsnakes and bird nests. We followed the overview, design concepts, details, and protocol for describing individual-based models suggested by Grimm et al. (2006, 2010). We have attached the model code, which includes model discussion following a complete ODD protocol, as supplementary material (Appendix A). Several previous agent-based models have simulated predator “agents” to explore foraging behavior according to various behavioral rules (e.g., Fronhofer et al. 2012; Ringelman 2014). Our model differs from previous studies in that snake behavioral decisions are based on the dynamically changing thermal qualities of the environment and nest predation is a byproduct of snake activity and habitat use. Additionally, we use the model to explore plausible climate-
warming scenarios for the study region to predict snake behavior and nest predation. The inherent assumptions of our model make it likely that increased ambient temperature will alter the intensity, timing, and location (habitat shifts) of nest predation by ratsnakes. Thus, our goals with this model are to quantify how extensive these changes may be, which changes are likely to be most pronounced, and to evaluate the ramifications of the observed changes.

**Thermal Landscape and Inputs**

Using aerial photographs and extensive ground truthing, we used GIS software (ArcMap 10.0: ESRI Inc, Redlands, CA, USA) to delineate boundaries of the six major habitat types available at the site: deciduous forest, mixed forest, clear cuts, shrublands, forest edge, and wetland. Deciduous forests had a continuous tree canopy greater than 25 m in height and were dominated by laurel oak, live oak (*Q. virginiana*), and in wetter areas, sweet gum (*Liquidambar styraciflua*). Conversely, mixed forests were drier habitats, lacked a continuous canopy composed of laurel oak and pine, and often had a dense understory of herbaceous vegetation, shrubs, and vines in all areas where sunlight reached the forest floor. Mixed forests were more structurally complex and thermally heterogeneous relative to deciduous forests. Clear cuts were areas that had been logged and were being regenerated by planted long-leaf pine seedlings or laurel oaks sprouting from stumps. All clear cuts were devoid of canopy and often had large amounts of fine and coarse woody debris on the ground. We considered any habitat lacking an overstory canopy (continuous or scattered) and with primarily shrubby or grassy vegetation as shrubland. It should be noted that shrublands often contained scattered, mature laurel oaks that provided cooler micro-sites that were often used by snakes and nesting birds. Finally, we considered forest edge as the 30 m strip of habitat occurring where one of the two forest types abutted any of the other habitat types. Thus, forest edge extended 15 m into the forest and 15 m
out from the forest. We chose 30 m as the definition of edge to be consistent with studies of snake habitat use (e.g., Carfagno et al. 2006). Although wetlands occurred at our study site, they were not used by ratsnakes and were excluded from analyses. However, the forest edges at the wetland – forest interfaces were included in analyses. The resulting vector ESRI shapefile map, which delineates the six habitat types and forest edges, provided input to the NetLogo model to establish a habitat type for each 5 m resolution grid cells over the entire study site.

Each macrohabitat type has unique thermal qualities based on its vegetative composition and structure. Our goal was to measure the full range of body temperatures snakes could experience in each habitat (hereafter “operative environmental temperatures”: Hertz et al. 1993). To measure operative environmental temperatures we used biophysical models that had the same thermal characteristics as ratsnakes. Each model consisted of a 40 cm length of 1.5 cm diameter copper pipe, filled them with water, and painted glossy black and gray to approximate the reflectance of ratsnakes. We suspended a thermocouple in each model and capped the ends with rubber caps and silicone. The thermocouples were attached to miniature temperature loggers (HOBO Temp, ONSET Computer Corp., Pocasset, MA, USA). We programmed temperature loggers to record at 10 min intervals. Similar models have been calibrated with the carcasses of ratsnakes by Blouin-Demers and Weatherhead (2001c) and were found to accurately reflect the internal body temperatures experienced by snakes under a wide range of temperatures, humidity, wind, precipitation, and solar radiation conditions.

We placed models in each of the major macrohabitat types at the site and situated models in locations representing the microsites used by ratsnakes (e.g., brushpiles, hollow logs, vine tangles). We placed models to establish the general thermal properties of each habitat type. We left models in place for 2-3 weeks at a time (48 total sites) before retrieving their recorded data.
We acquired meteorological data recorded during the same time period at a nearby (~ 7 km) weather station (courtesy of Savannah River National Laboratory). Using backwards step-wise linear regression we derived a regression equation for each habitat type that related air temperature, relative humidity, solar radiation, rainfall, and wind speed to temperatures recorded by the biophysical models (Table 5.1). Thus, using local weather station data we were able to calculate operative environmental temperatures for each of the habitat types for each weather record (at 15 min intervals) throughout the bird nesting seasons of 2011 – 2013. We used these data in our model to calculate a temperature at each patch at each 15-minute time step using the regression equations in Table 5.1 to generate a dynamic thermal landscape, to which the snakes responded.

*Ratsnake Movement*

Ratsnakes are often associated with forest and forest edge habitat (Weatherhead and Charland 1985, Durner and Gates 1993) and appear to use different habitat patches for their thermal properties (Blouin-Demers and Weatherhead 2001a,b). Ratsnakes placed in thermal gradient chambers preferentially maintain body temperatures of 28° C (Blouin-Demers and Weatherhead 2001c). In our dynamic thermal model, ratsnakes are motivated to find and occupy grid cells with a temperature of 28° C. Similarly, ratsnakes are most likely to move when their body temperature is at 28° C (J. H. Sperry, Unpubl. Data). Based on snake movement data collected through radio-telemetry in Texas (J.H. Sperry, Unpubl. Data) and South Carolina (B.A. DeGregorio, Unpubl. Data), modeled snake movement increases linearly with temperature, starting at 0 m per hour at 11° C to a maximum of 52 m per hour at 28° C and decreases linearly from that maximum to 0 m per hour at 34° C. Accordingly, for each 15-min time-step, the distance each snake travels is established. To ensure that a snake would not “jump” over a cell,
the total movement was divided into 5-m movement steps. Before each of those steps, each snake would inspect all of the grid cells within 15 m and ± 45 degrees of the direction it was currently facing and then face the grid cell that would provide the temperature closest to the preferred body temperature. To reflect the notion that not all movement decisions in nature are optimal, a degree of randomness was added by having the snake turn a random amount to the right between 0 and 10 degrees, and then back to the left 0 to 10 degrees, a movement often called a “wiggle”. Finally a check was made to ensure that a movement ahead was onto a space with an appropriate vegetation type. If this were not true, the snake would repeat the above random turn until true, and finally move forward. Steps were repeated until the required distance was achieved. Snakes could occupy any location within a cell; they were not constrained to the “center” of a cell. Because ratsnakes maintain home ranges, snakes in our model would not move more than 1000 m from their hibernation location, which were typically located in the center of their home ranges at our site (DeGregorio, Unpubl. Data). The probability of turning toward the home range center increased with distance from that center, such that at 1000 m the probability of turning toward the center of their home range was 100%. Once per day, at noon, snakes made the choice whether to turn back towards center or remain going the way they were going. The probability of turning towards the home-range center increased linearly from 0 to 100% as the snake reached the 1000 m limit. Because our study site was relatively small (460 ha), a 1000 m home range ensured that any individual snake was able to reach and explore a large percentage of the study area comprised of a mix of habitat patch types. Consistent with the reported range of ratsnake densities (Fitch 1963; Stickel et al. 1980), for our model we assumed there were 100 ratsnakes at the site. All snake movements were independent of other snakes on the landscape.
We used empirically derived data from our field sites (DeGregorio et al. 2014 and unpublished data) to estimate timing and placement of nests in our model. Cardinals begin nesting at our site in early March, peak in May, and taper off in July and early August. Therefore we limited our model to 1-March to 1-August. Consistent with observed nesting intensity, we placed 15% of the nests on the landscape in March, 75% in April, and 100% in May. Beginning in June, the number of nests was allowed to decrease to 75% as nests fledged or were destroyed by a snake, and to 45% beginning in July. Nests were initiated on 1 March. When a nest was preyed on or fledged, a 3-day wait period occurred before a nest could be regenerated, which happened if the total number of active nests was below the current monthly number needed. We placed 38% of model nests in shrublands, 10% in open forest, 8% in mature forest, 17% in clear cut, and 27% in forest edge. Each nest existed for a maximum of 22 days (the mean time required for a cardinal clutch to hatch and fledge; Poole et al. 2005) unless a snake moved into the same grid cell, in which case there was a probability of the snake detecting and preying on the nest, which caused the nest to be removed. Evidence suggests that ratsnakes are more likely to find nests during the nestling stage when more adult activity occurs around the nest and nestlings are presumed to provide odor cues. Thus, if a snake moved into a grid with a nest older than 12 days (presumed to have nestlings), the probability of the snake finding and eating the nest contents was set at 0.8. Nests younger than 12 days (incubation stage) were presumed to be found and eaten by snakes at a probability of 0.2, because much less adult activity occurs around incubating nests providing fewer clues for predators. Similarly, because adult birds are less likely to actively defend their nest at night (Hensley and Smith 1986) we assumed that nests located at night were preyed on with a probability of 1.0 relative to nests encountered by snakes.
during the day being preyed on at a probability of 0.75. Thus, nests > 12 days of age encountered during the day had a probability of being preyed on of 0.6 (0.8 * 0.75), nests encountered during the night with contents < 12 days of age were preyed on with a probability of 0.5 (1.0 * 0.2), etc. Although these values are not available in the literature, based on our understanding of ratsnake behavior and foraging, we believe these values are realistic. If a nest was not encountered by a snake in 22 days, it was considered successful. The habitat the nest was in, the time the snake encountered the nest, and the number of days the nest had survived until being located by the snake (observation days) were recorded. After a nest had been “preyed on” it was removed from the landscape and a new nest was regenerated at the same location 72 hr later, simulating a re-nesting attempt to maintain a constant source of nests available to foraging snakes. Our data suggest that cardinals at this site will attempt to nest in excess of six times per season, often initiating a new nest only days after a nest has failed or fledged.

**Analyses**

We conducted 36 simulations of five climate-warming scenarios in which ambient temperatures (based on weather data recorded in 2011, 2012, and 2013) were elevated 0, 0.5, 1, 1.5, and 2°C for a total of 180 simulations. All ambient temperatures from the weather station were then adapted for each habitat patch based on the regression equations derived from biophysical models. To initiate a simulation we placed ratsnakes on the landscape at randomly determined locations in mature forest (75% of snakes) and open forest (25% of snakes), reflecting the observed distribution and habitats in which this species overwinters at our site based on four years of radio tracking more than 45 individual ratsnakes (DeGregorio, Unpubl. Data). Ratsnakes were randomly initiated within 200 m of the forest edge to represent hibernation locations observed in the field. During the simulation all snakes were able to leave
hibernation patches and reach all other available habitat types. For each climate scenario, habitat type, and each month of the active season (March – July) we calculated daily nest predation rates (Mayfield 1961), defined as:

“(The number of failed nests / Total number of nest observation days)”

We qualitatively compared results from model simulations of contemporary conditions (0°C increase) to field-collected seasonal nest predation patterns. Additionally, we compared habitat-specific predation-rates generated by the model to those documented in the field. To examine the influence of climate change scenarios on overall nest predation rate we used a univariate general linear model with temperate change scenario as our fixed factor and daily predation rate as our response variable. If differences were detected, we used least significant difference (LSD) post hoc tests to examine differences between the temperature scenarios.

We used a two-way general linear model to examine the influence of month and habitat type on daily predation rate. We used month and habitat as fixed factors and daily predation rate as our response variable. We then used LSD post hoc tests to explore differences between the groups.

To explore how increasing temperatures might alter the timing of predation by snakes on bird nests, we summarized the proportion of predation events occurring during the day (>0600 and < 2030 hours) relative to during the night. We first examined whether temperature warming scenarios would alter overall timing of nest predation using a general linear model with temperature scenario as a fixed factor and proportion of nests preyed on at night as our response variable. We then used LSD post hoc tests to explore differences between the five temperature change scenarios. To explore how nocturnal nest predation varied by month and temperature
scenario, we used a two-way general linear model with temperature scenario and month as fixed factors and LSD post hoc tests to examine differences between groups.

**RESULTS**

*Model Validation*

Model and field results were strongly aligned. Overall intensity of daily nest predation rate was similar between the model (0.056) and field results (0.05). Seasonal patterns of predation in the model varied significantly by month ($F = 444.728$, df = 4, $P < 0.001$) and conformed to the pattern observed in the field, with daily predation rate being lowest in March, moderate in April and May and highest in June with a decline in July. These trends align well with reported trends in seasonal ratsnake movement, with ratsnakes moving less later in the summer as temperatures exceed preferred snake body temperatures (e.g., Sperry et al. 2008, 2010). At our field site, daily predation risk from ratsnakes is greatest in forest edge and forested habitats and lowest in open habitats (shrubland and clear cuts). Under contemporary conditions, the model predicted an identical trend, with daily predation rate highest in forest edge followed by deciduous forest then mixed forest and lowest in shrubland and clear cut. Similar trends between field and model predation intensity, seasonality, and habitat-specific rates provide confidence in the model’s future projections.

*Seasonal and Habitat-specific Nest Predation*

Overall, daily nest predation rate was significantly influenced by increasing ambient temperature ($F = 3.874$, df = 4, $P = 0.004$: Fig. 5.1). In general, daily nest predation rate increased in a stepwise manner as temperatures increased, with daily predation rate at the 2$^\circ$ C increase scenario being higher than in all other scenarios ($P < 0.050$) except 1$^\circ$ increase ($P =$
0.292). When ambient temperatures were elevated by 2° C, overall mean daily nest predation rate increase by 7% relative to contemporary conditions.

Increasing temperatures did not alter the observed seasonal trend in daily nest predation rate reported earlier. However, increases in nest predation rate corresponding to warming temperatures were not equal throughout the nesting season, with daily predation rate during the spring months (March and April) increasing most dramatically while nest predation in July actually decreased (Fig. 5.2). A temperature increase of 2° C caused nest predation in March to increase by 43% relative to contemporary conditions ($P < 0.001$). Similarly, daily nest predation rate in April increased by 10% as temperature warmed by 2° C ($P = 0.019$). Very little change was detected in daily predation rate in May and June as temperatures increased ($P > 0.093$ and $P > 0.079$, respectively). A temperature increase of 2° C also resulted in significant rises in nest predation rate relative to contemporary conditions in May and June ($P = 0.036$ and $P = 0.001$, respectively). In July, daily nest predation rate decreased by 16% with 1.5 and 2° C temperature increases relative to contemporary conditions ($P = 0.005$ and $P = 0.008$, respectively).

Daily nest predation rate also varied among habitats ($F = 552.079$, $df = 4$, $P < 0.001$), with the greatest predation rate occurring in forest edge and forest and the lowest rates in open habitats such as shrublands and clear cuts (Fig. 5.3). There was also evidence that habitat-specific predation rates would be affected by warming temperatures ($F = 2.738$, $df = 4$, $P = 0.001$). Relative to contemporary conditions, a 2° C increase in temperature resulted in 8%, 13%, and 15% increases in predation in deciduous forest, mixed forest, and forest edge ($P = 0.004$, 0.011, 0.003, respectively). Daily predation rate was higher in forest edge for all temperature treatments relative to contemporary temperature conditions ($P < 0.018$).

Anecdotally, snakes were observed to use forest edge habitats to a very high degree during
model runs. Increased predation in deciduous forest was only significant when temperature increased by 2° C ($P = 0.004$). Daily nest predation rate in mixed forest was significantly higher when temperature was increased by 1, 1.5 or 2° C. Increasing temperatures had no effect on predation rates in shrubland ($P > 0.251$) or clear cut habitat ($P > 0.459$).

*Nocturnal Nest Predation by Ratsnakes*

The proportion of nests preyed on at night varied by both temperature change scenario ($F = 48.718, \ df = 4, \ P < 0.001$) and month ($F = 2236.441, \ df = 4, \ P < 0.001$). The proportion of nests preyed on at night increased from 30% at current conditions to 40% in the 2° C increase scenario (Fig 5.4). Even at modest temperature increases (0.5°), nocturnal predation increased by 7% relative to contemporary conditions. Nocturnal predation increased by 30% with a 2° C increase in temperature relative to contemporary conditions ($P < 0.001$). In general, nocturnal predation was infrequent in March (3%), and increased throughout the summer, with the most nocturnal predation occurring in July (> 52% for all temperature scenarios; Fig 5.5). Under contemporary conditions, nocturnal predation was less frequent in March relative to all other months ($P < 0.001$). Nocturnal predation in April was also less frequent than in May ($P < 0.001$), June ($P < 0.001$), and July ($P < 0.001$). A 2° C increase in temperature caused the proportion of nocturnal nest predation in March to increase by nearly 200% ($P < 0.001$). Similar increases were seen in April (51%), May (35%), and June (19%; $P < 0.02$).

**DISCUSSION**

Species conservation in a warming world will rely upon understanding how not only the behavior of the focal species is influenced by climate change, but by how their predators and prey are affected. Using agent-based modeling, we predicted that warming temperatures would
cause ratsnakes, a major ectothermic predator of bird nests (Thompson et al. 1999, DeGregorio et al. 2014a), to shift activity patterns and habitat use, thereby altering patterns of nest predation risk. Our model predicts that a 2°C increase in ambient temperature will increase overall predation risk by up to 7% and that temporal (seasonal and diel) and spatial patterns of predation risk will also change, and in some instances the predicted change is substantial. Thus, if we assume that 310 cardinal nests are laid annually at our site, under contemporary conditions we should expect 87 to successfully fledge but with a 2°C increase in temperature only 79 are expected to fledge.

Increasing temperatures led to a shift in seasonal snake activity such that snakes were active earlier in the spring and became less active in late-summer when it became too warm. This is similar to what would be predicted based on latitudinal comparisons of snake seasonal activity patterns (Sperry et al. 2010). Under current temperature conditions, both empirically derived nest data from our site (Unpubl. Data) and our model indicate that nest survival is highest in the spring and then declines later in the nesting season, a pattern reported for many bird species (Borgmann et al. 2013). Ectothermic nest predators are relatively inactive when temperatures are suboptimal, but as temperatures increase so does their activity and thus the possibility of interaction with nests (Sperry et al. 2008; Cox et al. 2013). Avian population viability may rely on the production of offspring in the early part of the season when predation rates are lowest and clutch sizes are largest (Perrins 1970; Daan et al. 1990; Nager and Nordwijk 1995). If climate warming causes predation by snakes to increase in the early part of the season, as predicted by our model, this may counteract the benefit to birds of having larger clutches early in the season (Borgmann et al. 2013). However, our model does not take into account climate-induced shifts in avian breeding phenology. As climate change allows ratsnakes to become more
active in the spring, birds may be able to nest earlier in response (Crick et al. 1997). Initiation of avian breeding can be dependent on a wide variety of factors (e.g. migration, leaf phenology, insect emergence), so earlier nesting in response to warming temperatures may not always occur. Given the importance of temperature for snake activity, however, warming temperatures seem likely to cause snakes to become active earlier in the spring. Conversely, as snake activity is constrained during the hotter months, birds may be able to invest more heavily in these nests to offset early losses.

In addition to shifts in seasonal activity, our model predicted interesting patterns of diel activity shifts with increasing temperatures. Ratsnakes, like many snake species, are facultatively nocturnal (Gibbons and Semlitsch 1989; Abom et al. 2010). Ratsnakes alter their activity patterns to take advantage of optimal environmental temperatures (DeGregorio et al. 2014c). Our model indicated that even modest temperature increases (0.5°C) were enough to cause substantial increases (7%) in the amount of nocturnal nest predation by ratsnakes and that substantial temperature elevations (2°C) increased nocturnal predation by 30%. Increased nocturnal predation was especially prevalent during the early spring (200% increase in nocturnal predation in March), which, under contemporary conditions, is a time when ratsnakes are primarily diurnal (Sperry et al. 2013; Ward et al. 2013). Increased nocturnal predation is a cause for concern because snake predators are more successful due to the inability of most birds to defend their nests at night (Hensley and Smith 1986; Carter et al. 2007). Additionally, nocturnal snake predation may result in the predation of the incubating or brooding adult (Reidy et al. 2009). Although we have not documented ratsnakes capturing incubating or brooding adults at night at our site (Unpubl. data), more research is needed to identify which bird species or nesting
characteristics (e.g., nest height, diameter of supporting tree limb) make nesting birds vulnerable to snakes at night.

Nest predation by ratsnakes varied by habitat and model results of contemporary temperature conditions produced a pattern similar to that observed in the field. Ratsnakes are generally associated with forests and forest edges and accordingly, predation by ratsnakes in both the model and field were highest in these habitats relative to open, canopy-free habitats. We predicted that as temperatures increased, open habitats such as shrubland and clear cuts would become unsuitable for ratsnakes, causing nest predation in these patches to decrease. Conversely, as temperatures increased, ratsnakes would use cooler, more forested habitats causing nest predation in these patches to increase. Results from the model support our hypotheses, with marked increases in predation rates within forest and forest edges (Fig 5.3). Ratsnakes are an edge-associated species (Durner and Gates 1993; Blouin-Demers and Weatherhead 2001a,b; Carfagno et al. 2006) and appear to use edges for the thermoregulatory heterogeneity that they provide (Blouin-Demers and Weatherhead 2001b, Carfagno et al. 2006). As climate warms, edges may continue to provide thermal refugia for ratsnakes. Edge effects on avian nesting survival have been debated in the literature for decades and appear to be context and species-specific (Gates and Gysel 1978; Hanski et al. 1996; Flaspohler et al. 2001). Studies documenting edge effects attribute them to increased predation rates from edge-associated predators such as brown-headed cowbirds (*Molothrus ater*), snakes, and mammalian mesopredators such as raccoons (*Procyon lotor*). Although our model results indicate that nest predation in edges by ratsnakes will increase as temperatures warm, predicting how overall nest predation in edges will change requires knowing how edge use by other nest predators will change in warmer climates. However, increased nest predation by ratsnakes alone in forest
edges under warming temperatures could cause these habitats to become sinks for many nesting
birds (Gates and Gysel 1978; Battin 2004).

Our results provide an important step in exploring how climate change may affect
behavior of a predator species and thereby affect survival of one of its prey species. Our
research indicates that although the overall intensity of nest predation is expected to increase, the
most pronounced effect of climate change on predation may be changes in when and where nest
predation occurs, such as increases in early-season and nocturnal predation or increases in
specific habitats. Understanding how a predator is likely to respond to a changing climate
provides an important platform to begin to explore the scope that the prey species has for
countering these effects, such as shifts in nesting phenology or nesting habitats.
Table 5.1: Regression equations for calculating the body temperature of a resting snake where: 
T = temperature (degrees C), R = solar radiation (W/m²), Rh = relative humidity (%), and W = wind speed (m/s).

<table>
<thead>
<tr>
<th>Macrohabitat Type</th>
<th>Regression Equation for Calculating the Body Temperature of a Resting Snake</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrubland</td>
<td>0.11 + 0.889 * T + 0.008 * R + 0.02 * Rh</td>
</tr>
<tr>
<td>Mature Forest</td>
<td>0.699 + 0.947 * T - 0.002 * R + 0.008 * Rh + 0.166 * W</td>
</tr>
<tr>
<td>Clear Cut</td>
<td>-1.45 + 0.477 * T + 0.019 * R + 0.151 * Rh + 0.203 * Rain</td>
</tr>
<tr>
<td>Open Forest</td>
<td>-4.964 + 0.855 * T + 0.007 * R + 0.104 * Rh - 0.381 * W</td>
</tr>
<tr>
<td>Forest Edge</td>
<td>-10.694 + 0.949 * T + 0.011 * R + 0.153 * Rh</td>
</tr>
</tbody>
</table>
Figure 5.1: Daily nest predation rate (± SE) of songbird nests by ratsnakes (*Elaphe obsoleta*) as a function of five temperature increase scenarios (0 – 2° C increments) derived from 180 simulations of an agent-based model.
**Figure 5.2:** Monthly mean daily nest predation rates during contemporary temperature conditions and 1 and 2° temperature increase scenarios derived from an agent-based model.
Figure 5.3: Habitat-specific daily nest predation rates under contemporary climate conditions and ambient temperature increases of 1 and 2° C derived from an agent-based model.
Figure 5.4: Proportion of songbird nests (± SE) preyed on at night by ratsnakes (*Elaphe obsoleta*) under five climate warming scenarios derived from an agent-based model.
Figure 5.5: Proportion of nests preyed on at night as a function of month and ambient temperature increase derived from an agent-based model.
LITERATURE CITED

Formatted for the Journal Ecological Modeling


Harvey, D.S., Weatherhead, P.J., 2010. Habitat selection as the mechanism for thermoregulation in a northern population of massasauga rattlesnakes (Sistrurus catenatus). Ecoscience 17, 411-419.


CHAPTER 6: SUMMARY

The general goal of my dissertation was to examine predator-prey relationships between snakes and nesting birds and to investigate how these interactions are likely to change due to climate warming. My first specific goal was to understand the general importance of snakes as predators of bird nests on a broad-scale. The recent proliferation of studies using cameras to identify nest predators presented an opportunity to synthesize the findings from 53 recent North American studies. I found that snakes accounted for 26% (range: 0-90%) of recorded predation events and the ratsnake (*Elaphe obsoleta*) was by far the most frequent predator, accounting for 65% of all recorded nest predation by snakes. Overall, snakes were more frequent predators at lower latitudes and in open macrohabitats. Only the ratsnake was reported to be an important snake predator of nests in forested habitats.

My second specific goal was to investigate snake-bird interactions on a local scale to better understand the factors that influence nest vulnerability to different snake species. At a fragmented site in South Carolina I located and monitored 463 bird nests and monitored 206 of them with miniature infrared nest cameras to identify predators. I combined nest monitoring with simultaneous radiotracking of 33 ratsnakes and 16 black racers (*Coluber constrictor*) to examine their habitat use at the site. I found that ratsnakes, the locally dominant nest predator (28% of observed nest predation), frequently preyed on nests near roads and distance to roads was the best supported model influencing daily nest survival at this site. Radiotelemetry showed that ratsnakes were often near roads due to the associated forest edges, which ratsnakes are known to use for thermoregulatory purposes. Racers and coachwhips were more likely to prey on nests located near powerlines, presumably due to their use of the shrubland habitat maintained below powerlines. Because racers and coachwhips were relatively infrequent predators of nests
(12 and 5%, respectively), however, daily nest survival rate was not influenced by distance to powerlines.

Ratsnakes are capable of diurnal and nocturnal activity and some studies have reported that nocturnal nest predation by ratsnakes often results in the capture of brooding or incubating birds in addition to their nestlings/eggs, something that rarely happens during the day. Given these reports, in Chapter 4 I explored why ratsnakes switched to nocturnal activity, how they located prey in the dark, and why racers appeared unable to switch to nocturnal activity. By altering ambient temperatures in the laboratory and filming snake activity, I found that ratsnakes were active when temperature was optimal, regardless of whether it was day or night, suggesting they have a genuinely plastic ability to switch between diurnal and nocturnal activity. Consistent with this flexibility, ratsnakes were successful at detecting prey in both low and high light using visual or chemical cues, and were most successful when visual and chemical cues were coupled. Racers were almost always active during the day and when temperatures were not optimal, they simply reduced their activity.

The ultimate goal of my dissertation was to draw from Chapters 2-4 to investigate how climate warming is likely to alter predator-prey relationships between ratsnakes and nesting birds. Based on our understanding of the consequences of nocturnal nest predation (potential capture of adult birds) and predation of early-season nests (higher investment by birds), expansion of nocturnal or early season activity by snakes could have profound impacts on bird population. A spatially-explicit agent-based model parameterized with my field data predicted nest predation by ratsnakes will increase 7% with a 2° C increase in temperature. Modest increases in ambient temperature (0.5° C) caused nocturnal predation by ratsnakes to increase by 30%, particularly in the early spring (200% increase in nocturnal nest predation in March) when
nocturnal snake activity is normally limited. Increased temperatures were also predicted to cause
nest predation to increase substantially in forest and forest edge habitats due to the thermal
heterogeneity of forests buffering snakes against potentially lethal environmental temperatures.
If ratsnakes become more concentrated in small forest patches and edges, nest survival in these
patches may fall below a sustainable level. Conversely, as temperatures increase, ratsnakes will
be less likely to prey on nests in open habitats such as shrublands, which may provide refuges for
some nesting birds.

Researchers investigating patterns in nest predation are ultimately interested in
understanding the options available to nesting birds to reduce their risk of predation, or in the
case of imperiled species, actions that land managers could take to reduce nest predation. My
research has provided insight into the factors that influence nest predation risk from snakes on
continental and local scales. These results can assist researchers to predict if snakes are likely to
be important predators in a region prior to study initiation and can inform land managers how
landscape alteration (powerlines, roads, forest fragmentation) may affect nest predator identity
and nest survival. Chapter 4 provides novel information regarding how ratsnakes locate prey
during day and night and how temperature influences daily activity patterns. These data were
necessary for parameterizing a model to explore multi-trophic predator-prey interactions in
response to climate change. Results from the model predict substantial increases in early-season
and nocturnal activity by snakes. Future research should explore how birds may respond to these
changing pressures in a warming world to maintain viable populations in the face of increased
predation risk by snakes.