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Snake predation on North American bird nests: culprits, patterns and future directions

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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.

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 and Burhans 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). Radiotelemetry studies have elucidated important links between snake activity patterns (Sperry et al. 2008, 2012, Weatherhead et al. 2010) or snake habitat use (Klug et al. 2010, Sperry 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 Bolger 2002, Cain et al. 2003, Patten and Bolger 2003, Klug et al. 2009). The lack of meaningful 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 (Thompson and Burhans 2003), we treated each site separately. In some studies (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 (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 (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 (ratsnakes *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. gotula* 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

Table 1. Summary of studies that have use radiotelemetry, abundance estimation or video monitoring to link snake ecology and nest predation.

Study	Location	Focal species	Results
		Radiotelemetry	
Sperry et al. 2008	Texas, USA	ratsnakes *Elaphe obsoleta* black-capped vireos *Vireo atricapilla* golden-cheeked warblers *Dendroica chrysoparia*	–seasonal nest predation risk of black-capped vireos was greatest when snakes were most active
Sperry et al. 2009	Texas, USA	ratsnakes *Elaphe obsoleta* black-capped vireos *Vireo atricapilla* golden-cheeked warblers *Dendroica chrysoparia*	–snakes preferentially used edge habitat although no relationship between snake habitat use and nest success was documented
Klug et al. 2010	Nebraska and Iowa, USA	racer *Coluber constrictor* Great Plains ratsnake *Elaphe emoryi* grassland birds	–snakes preferentially used shrubby patches in grasslands and nest predation rate was highest in shrubby patches
Weatherhead et al. 2010	Illinois, USA	ratsnake *Elaphe obsoleta* racer *Coluber constrictor* shrubland birds	–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
Sperry et al. 2012	Texas, USA	ratsnake *Elaphe obsoleta* northern cardinal *Cardinalis cardinalis*	–seasonal predation rate of cardinal nests was greatest when ratsnakes were most active

Snake abundance studies	Location	Methods	No. captures and results
Schaub et al. 1992	Florida, USA	daily counts of snake tracks across a sandy firebreak	–snake activity was mostly diurnal and was greatest in mid-late summer
Chalfoun et al. 2002	Missouri, USA	mark–recapture drift fence + funnel traps coverboards opportunistic captures	–37 snake captures Twice as many snakes captured in forest edge as forest interior
Morrison and Bolger 2002	California, USA	opportunistic snake (non-rattlesnake) encounters while nest-searching	–0.011 and 0.016 snakes per hour encountered in shrubland interior and shrubland edge habitats. No difference in abundance between habitats
Patten and Bolger 2003	California, USA	opportunistic snake (non-rattlesnake) encounters while nest-searching	–104 snakes encountered (57 considered nest-eating species). Snake abundance was the best predictor of nest success for ground-nesting species
Cain et al. 2003	California, USA	time-constrained visual searches	–garter snakes detected at between 8–34% of surveys. No association with habitat variables. Garter snakes not documented preying on nests at the site
Klug et al. 2009	Nebraska and Iowa, USA	coverboards	–number of snakes captured not reported. Predator communities responded to variables at the patch and landscape scale

Study	Location	Conclusions
		Factors influencing nest vulnerability
Benson et al. 2010	Arkansas, USA	–snakes more likely to prey on nestlings than eggs and more likely to find nests far from forest edge.
Conkling et al. 2012	Texas, USA	–nest predation risk by snakes decreased with nest height
Cox et al. 2012a	Missouri and Illinois, USA	–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.
Cox et al. 2012b	Missouri and Illinois, USA	–snakes more likely to prey on nests near forest edges.
Cox et al. 2013	Missouri and Illinois, USA	–nest predation risk from snakes increases with increasing mean daily temperatures.
DeGregorio unpubl.	South Carolina, USA	–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.

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 and considered models significant at $p < 0.05$.

Results

We found 53 sources that reported predator identity of North American bird nests (Supplementary material 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. 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. 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, 3). Racers were the next most frequent snake predator, accounting for 33 (10%) nest predation events. It should be noted that 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). As a group, the endotherm specialists (ratsnake, corn snake, fox snake, gopher snake, Great Plains rat snake) 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.

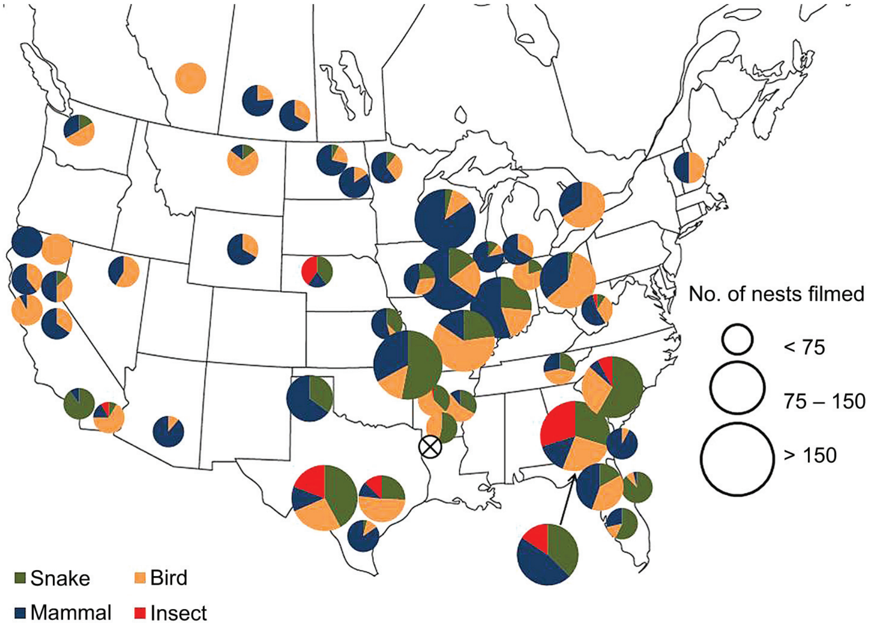

Figure 1. Location of camera studies, within North American and where snakes occur, and the composition of snake predators documented with nest cameras at each site. The size of each pie chart represents the sample size (number of nests filmed).

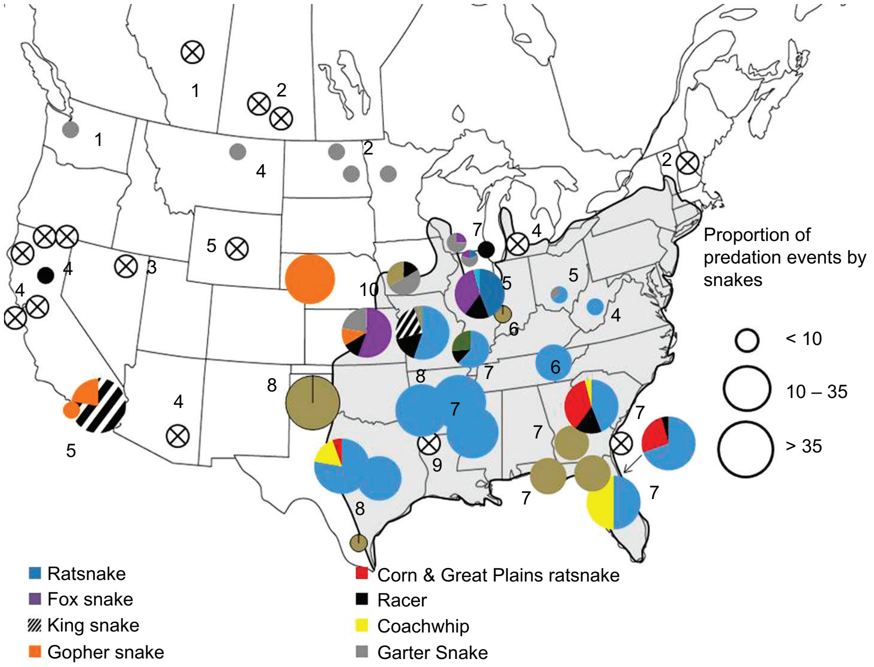

Figure 2. Location of camera studies and the composition of snake predators documented at each site. The size of each pie chart represents the proportion of overall nest predation events attributed to snakes: small chart = less than 10%, medium chart = 11–35%, and large charts = greater than 35% of all 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.

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. 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.

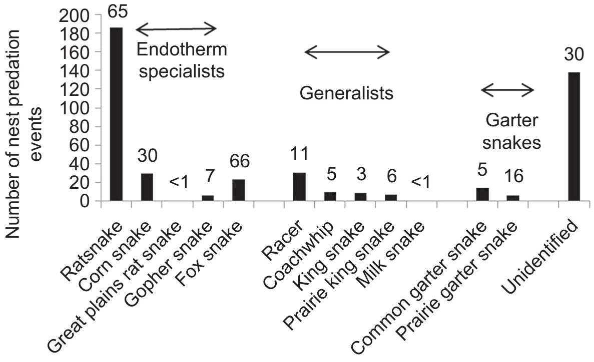

Figure 3. Total number of avian nest predation events attributed to each snake species. Numbers above each bar represent the percent of nests depredated by each species within their geographic range relative to all snake species.

Diel patterns of nest predation by snakes corresponded well with known patterns of snake activity (Fig. 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. 4b: $p = 0.0001$). No other snake species had a significant association with either nest stage ($p > 0.22$).

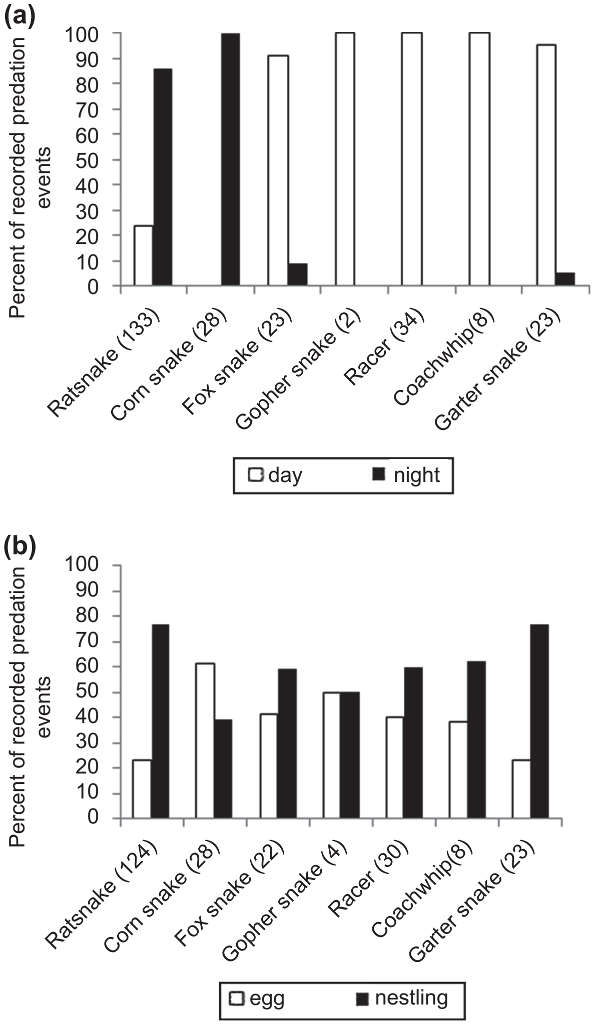

Figure 4. Diel patterns of snake predation of North American bird nests (a) and nesting stage (b) most frequently preyed on by snakes.

Only latitude had a significant effect on predator identity (GLMM: $F_{1,1756} = 7.19$, $p = 0.007$), with odds of predation from a non-snake predators increasing at a rate of approximately 10% with each degree of latitude (111 km) ($\beta = 0.095$, 95% CI: 0.025–0.164, $p = 0.007$). Although the habitat variable was not well supported (GLMM: $F_{1,1756} = 0.737$, $p = 0.57$), other predators were 2.6 times more likely than snakes to depredate nests in forested habitat ($\beta = 0.97$, 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 ($F_{2,298} = 5.38$, $p = 0.005$) and habitat ($F_{2,298} = 5.76$, $p = 0.004$) were significant. Odds of nest predation by garter snakes (relative to endotherm specialists) increased approximately 4% per 100 km increase in latitude ($\beta = 1.44$, 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 ($\beta = 0.123$, 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 censused, 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 have been shown to 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 (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 (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 months, 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.

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Supplementary material (Appendix JAV-00364 at <www.avianbiology.org/readers/appendix>). Appendix 1.