

REVIEW

Reviews provide an opportunity to summarize existing knowledge within ornithological research, especially in areas where rapid and significant advances are occurring. Reviews should be concise and should cite all key references. An abstract is required.

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Understanding avian nest predation: why ornithologists should study snakes

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Despite the overriding importance of nest predation for most birds, our understanding of the relationship between birds and their nest predators has been developed largely without reliable information on the identity of the predators. Miniature video cameras placed at nests are changing that situation and in six of eight recent studies of New World passerine birds, snakes were the most important nest predators. Several areas of research stand to gain important insights from understanding more about the snakes that prey on birds' nests. Birds nesting in fragmented habitats often experience increased nest predation. Snakes could be attracted to habitat edges because they are thermally superior habitats, coincidentally increasing predation, or snakes could be attracted directly by greater prey abundance in edges. Birds might reduce predation risk from snakes by nesting in locations inaccessible to snakes or in locations that are thermally inhospitable to snakes, although potentially at some cost to themselves or their young. Nesting birds should also modify their behavior to reduce exposure to visually orienting snakes. Ornithologists incorporating snakes into their ecological or conservation research need to be aware of practical considerations, including sampling difficulties and logistical challenges associated with quantifying snake habitat use.

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Birds have long been among the favored research subjects of ecologists and evolutionary biologists. The relative ease of observing adults and their nests presumably accounts for birds being particularly well represented in field studies of breeding biology. Those studies have revealed that predators are responsible for most nest failures (Ricklefs 1969, Martin 1993), making it likely that nest predation as a selective agent has shaped everything from nest site selection, to life histories, to community structure of birds (Martin 1988, 1995, Martin and Clobert 1996, Marini 1997). Not surprisingly, therefore, ornithologists have studied nest predation extensively, documenting both the factors that are correlated with variation in the

occurrence of predation, as well as the consequences of predation for the birds. By contrast, however, the predators themselves, and the factors that account for how they affect nesting birds, have largely remained a black box. There is growing recognition that full understanding of predator-prey interactions is unlikely to be achieved without studying the predators in addition to the prey (Schmidt 1999, Lima 2002, Chalfoun et al. 2002a, Larivière 2003, Stephens et al. 2003). Recent evidence suggests that for many ornithologists, this might require that they study snakes.

The ornithological literature abounds with anecdotal reports of particular animals preying on birds' nests, but

quantitative attribution of predation to individual species is generally lacking. Predation usually occurs quickly and often under circumstances that make observation of the event difficult, even if the researcher is present. Moreover, the unpredictability of when predation will occur and in which nest makes it virtually impossible for researchers to be present when predation takes place, other than by happenstance. Traditional approaches of attributing predation to at least a class of predator (e.g., birds, mammals) based on the state of the nest after the fact has been shown to be unreliable. Overlap among, and inconsistency within classes of predators in the state of nests following predation (confirmed photographically) produce far too many ambiguous cases for this approach to be effective (Hernandez et al. 1997, Larivière 1999, Pietz and Granfors 2000, Thompson and Burhams 2003). Similarly, using marks left by predators on artificial eggs placed in artificial nests is proving to be unreliable because artificial eggs and nests do not attract the same suite of predators as real eggs and nests (Pärt and Wretenberg 2002).

A technological solution to this problem appears to be at hand. Miniaturized video cameras now allow researchers to photograph nests continuously, capturing video records of predation whenever it occurs (Thompson et al. 1999). Nocturnal predation can be detected using illumination from infrared light-emitting diodes in the camera housing. The 950-nm light is not visible to vertebrates (Thompson and Burhams 2003), although it could potentially attract snakes that are capable of detecting infrared radiation (Viperidae and Boidae). However, none of the studies that have used this technology to date have reported predation by snake species from either of these families. In six of eight studies that have used this technology, snakes have been documented as the most important group of nest predators (relative to groups such as mammals or birds), accounting for up to 90% of all nest predation (Table 1). Furthermore, in the study by Stake et al. (2003), three of the cases of nest predation by snakes also included predation of the incubating females. All eight studies involved New World, open-nesting passerine birds, so in this respect the studies cannot be considered representative. However, the studies were scattered geographically, including one tropical location, they included a variety of habitats, and collectively involved a variety of species of both birds and snakes. Heretofore recognition of the importance of snakes as avian nest predators was restricted to a few well-documented cases, such as that involving the introduced brown treesnake *Boiga irregularis* in Guam (Fritts and Rodda 1998) and ratsnake *Elaphe obsoleta* predation on nests of the endangered red-cockaded woodpecker *Picoides borealis* (Neal et al. 1993). Results of the recent video camera studies, however, suggest that snake predation on nests is widespread and important to many species of birds.

Research directions

More studies using video cameras are required to determine just how widespread and important predation by snakes is for nesting birds. Results to date, however, suggest that it is not premature to begin exploring the implications of bird-snake interactions. The areas of investigation discussed below are not mutually exclusive, and all are likely to be most informative if birds and snakes are studied simultaneously.

Landscape ecology

No area of current ecological research seems likely to benefit more from a better understanding of avian nest predation than the study of habitat fragmentation, the ecological and conservation consequences of which has received enormous attention. Studies of breeding birds have been prominent in that body of work, with many studies providing evidence of increased nest predation associated with habitat fragmentation and edges (Heske et al. 2001). Rates of predation are sufficient in some fragmented habitats that the productivity of nesting birds is well below that necessary to sustain populations (Robinson et al. 1995). Despite the general association between nest predation and habitat fragmentation, however, the pattern is far from consistent among studies (Lahti 2001), producing a consensus regarding the need to study the predators that are responsible for nest predation (Chalfoun et al. 2002a, Stephens et al. 2003).

How might habitat fragmentation affect snakes, and why might that vary among locations? Edges provide snakes the thermal properties of both adjoining habitats, allowing greater flexibility for thermoregulation (Blouin-Demers and Weatherhead 2002). At the northern extreme of their distribution, black ratsnakes *Elaphe obsoleta* preferentially use habitat edges, particularly when their need to thermoregulate is greatest (Blouin-Demers and Weatherhead 2001a, b). Interestingly, black ratsnakes also prefer edges in Maryland, the central portion of their range (Durner and Gates 1993). At more thermally benign latitudes, edges may be less important for thermoregulation, although there will always be times when temperature (either hot or cold) constrains snake activity. For nocturnally active snakes, the thermal quality of retreat sites used during the day can affect habitat selection (Pringle et al. 2003), so higher thermal heterogeneity may still make edges preferred habitat. Even in the tropics, snakes may preferentially use edges (Henderson and Winstel 1995), although the reasons for the preference remain to be determined. Using different survey techniques, Chalfoun et al. (2002b) found that snakes were almost twice as abundant in forest edges vs. interiors in Missouri, whereas

Table 1. The importance of snakes as nest predators in studies that have used video cameras to record nest predation.

Location	Habitat	Bird species	Sample size ^a	% Snakes	Snake species ^b	Source
Missouri	Old field	<i>Spizella pusilla</i> , <i>Passerina cyanea</i>	25	64	<i>Elaphe obsoleta</i> , <i>Lampropeltis calligaster</i> , (<i>Coluber constrictor</i> , <i>Thamnophis</i> sp.)	Thompson et al. 1999
North Dakota	Grassland	10 passerine species	29	0		Pietz and Granfors 2000
California	Sage scrub	<i>Aimophila ruficeps</i>	10	90	<i>Lampropeltis getula</i> , <i>Pituophis melanoleucus</i>	Morrison and Bolger 2002a
Missouri	Old field	<i>Spizella pusilla</i> , <i>Passerina cyanea</i>	46	72	<i>Elaphe obsoleta</i> , <i>Lampropeltis calligaster</i> , <i>Coluber constrictor</i> , (<i>Lampropeltis getulus</i> , <i>Thamnophis</i> sp.)	Thompson and Burhans 2003
	Forest	<i>Passerina cyanea</i> , <i>Oporornis formosus</i> , <i>Helmitheros vermivorus</i> , <i>Seiurus aurocapillus</i> , <i>Hylocichla mustelina</i> , <i>Empidonax vireescens</i> , <i>Seiurus motacilla</i>	15	33	<i>Elaphe obsoleta</i> , <i>Lampropeltis calligaster</i>	
Wisconsin	Grazed pastures	<i>Passerculus sandwichensis</i> , <i>Ammodramus savannarum</i> , <i>Dolichonyx oryzivorus</i> , <i>Melospiza melodia</i> , <i>Sturnella</i> spp.	24	12.5	<i>Elaphe vulpina</i> , <i>Thamnophis sirtalis</i>	Renfrew and Ribic 2003
Texas	Scrub oak forest	<i>Vireo atricapillus</i>	48	38	<i>Elaphe obsoleta</i> , (<i>Masticophis flagellum</i>)	Stake and Cimprich 2003
Texas	Oak-juniper forest	<i>Dendroica chrysoparia</i>	25	48	<i>Elaphe obsoleta</i> , (<i>Masticophis flagellum</i>)	Stake et al. 2003
Panama	Forest	4 species of antbirds (Formicariidae)	10	80	<i>Pseustes poecilonotus</i>	Robinson et al. 2003

^a Number of predation events recorded.

^b Species in parentheses accounted for fewer than 15% of cases of snake predation, or were only seen in nests after predation had occurred.

Morrison and Bolger (2002a) found no edge sensitivity of snakes (or edge effects on nest predation) in southern California.

The assumption underlying the thermal ecology hypothesis for increased snake predation in habitat edges is that predation is a result rather than the cause of snakes using edges. The alternative is also possible. Higher densities of breeding birds in habitat edges (Gates and Gysel 1978) could attract more snakes because the snakes cue directly on bird abundance. Another possibility is that alternative prey of the snakes such as small mammals may occur at higher densities in edges, attracting more snakes, which then prey opportunistically on birds' nests. Evidence that edges influence small mammal abundance is mixed, with some studies reporting a positive association and others no significant pattern (Chalfoun et al. 2002a). Devising field tests of these hypotheses will be challenging, particularly when multiple trophic levels are involved and patterns of habitat association may be temporally dynamic.

Nest-site selection

If snakes are the principal nest predators for many birds, and nest predation is the principal cause of nest failure, then we should expect birds to have evolved nesting behaviors that reduce that predation risk. This might occur in several ways. First, birds might choose nest locations that are inaccessible to snakes. For example, Acadian flycatchers *Empidonax vireescens* preferentially nest in Nuttall oaks *Quercus nuttallii* and nests in those trees suffer less predation (Wilson and Cooper 1998, Schmidt and Whelan 1999). These patterns appear to be a consequence of ratsnakes being unable to climb the smooth bark of Nuttall oaks (Mullin and Cooper 2002). There is also at least one example of birds modifying nest sites to make them inaccessible to snakes. Red-cockaded woodpeckers remove loose bark below their nests to make trunks more difficult for ratsnakes to climb, and excavate resin wells that create a physical barrier to snakes (Rudolph et al. 1990).

Birds might also exploit the fact that snakes are ectotherms and preferentially nest in locations that are thermally inhospitable to snakes. Morrison and Bolger (2002b) speculated that high nest success of rufous-crowned sparrows *Aimophila ruficeps* during a cool, rainy El Niño year could have been a consequence of reduced activity of snakes (the birds' major nest predator). Also consistent with the possibility that birds might find thermal refuge from snakes are the two cases of low snake predation in Table 1. Both studies were conducted in grazed or grassland habitat. Where cover is lacking, snakes would risk overheating on sunny days,

although greater exposure of snakes to predators could also cause them to avoid areas without cover.

If birds do preferentially nest in microclimates that snakes avoid, they may incur some cost in doing so. Thermal conditions in the nest are affected by the local microclimate and can affect rates of incubation and nestling growth, incubation costs of parents, and ultimately reproductive success (Walsberg 1985, Webb 1987, Conway and Martin 2000). Microclimates inhospitable to snakes may also be suboptimal for birds, requiring tradeoffs between predator avoidance and offspring and parental health (Amat and Masero 2004).

Parental behavior

More than 50 years ago Skutch (1949) proposed that parental activity around the nest could increase exposure of the nest to predation, an idea that has received recent support (Martin et al. 2000a, b). This may be particularly relevant to nest predation by snakes, because the limited evidence available suggests that snakes may locate nests visually, particularly when parents are active (Eichholz and Koenig 1992, Lillywhite and Henderson 1993, Mullin and Cooper 1998). Indirect support for the importance of parental activity for snake predation comes from studies that have used artificial nests to identify predators. In contrast to evidence from real nests (Table 1), snakes appear to be under-represented as predators of artificial nests (Davison and Bollinger 2000). If snakes are predictable in how they search for nests (e.g., temporal or thermal correlates of searching), then it should be possible to look for avian adaptations to reduce detectability and to assess the consequences of those adaptations.

A valuable approach to assessing how snake predation has influenced the evolution of specific aspects of avian nesting behavior would be to compare birds breeding in areas where snake predation is important with birds in areas where snakes are rare. For example, Martin and Clobert (1996) found that nest predation was lower for European than for North American birds, which was correlated with changes in life history (e.g., fecundity). Martin and Clobert (1996) attributed the difference in predation to continental differences in human impact on nest predators. Given the general human antipathy toward snakes, snakes are likely to be less abundant in areas with prolonged human presence and extensive habitat modification. Oceanic islands, or high latitude (or altitude) sites where snakes do not occur would also provide opportunities to study avian behavior in the absence of snakes. Comparative analyses could be used to determine whether birds behave differently with and without the risk of snake predation.

Conservation

Snake predation will be a general conservation concern when habitat fragmentation increases the importance of snakes as nest predators. In more specific situations, snake predation might have serious negative effects on bird species of conservation concern. For example, both Texas studies in Table 1 involved birds that are listed as endangered in the United States, respectively black-capped vireos *Vireo atricapillus* and golden-cheeked warblers *Dendroica chrysoparia*. In both cases, the same species of ratsnake *Elaphe obsoleta* was the most important predator. Finding ways to reduce ratsnake predation is thus important for efforts to protect these birds. Potential management approaches could include active removal of ratsnakes or modification of the habitat in ways that make it unattractive to ratsnakes without substantially reducing its quality for the birds. Management in this, or similar, situations is most likely to succeed if plans are informed by knowledge of the snakes' natural history, and particularly the factors that bring the snakes and birds into contact.

Practical considerations

If ornithologists heed the advice herein and consider incorporating snake research into their studies, two general practical points should be noted. First, although a variety of well-established techniques exist for studying snakes in the field (Fitch 1987), one must be aware of their shortcomings. Different capture methods target different species of snakes, so the survey method employed will dictate to some extent the snakes that are observed (e.g. Chalfoun et al. 2002b). Even within species, captures can be biased by size (Prior et al. 2001) and observations can be biased by habitat (Weatherhead and Charland 1985). Second, reliable information on habitat use and thermal ecology of snakes is best obtained using temperature-sensitive radio-telemetry. This approach requires intensive fieldwork from which the return is greatest when effort is restricted to a relatively small area. By contrast, avian nesting studies such as those assessing the effect of habitat patch size on predation are usually extensive, and results can be sensitive to the scale of the study (Stephens et al. 2003). To obtain adequate replication, sampling is conducted at multiple sites over a relatively wide area. The cost of overlaying a snake telemetry study on such an experimental design would be prohibitive. For practical reasons, therefore, it may be necessary to design snake studies in ways that allow results to be extrapolated to the associated bird studies, rather than attempting to study birds and snakes in all the same places.

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