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Nest Defense- Grassland Bird Responses To Snakes

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Nest Defense

GRASSLAND BIRD RESPONSES TO SNAKES

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Abstract. Predation is the primary source of nest mortality for most passerines; thus, behaviors to reduce the impacts of predation are frequently quantified to study learning, adaptation, and coevolution among predator and prey species. Video surveillance of nests has made it possible to examine real-time parental nest defense. During 1999–2009, we used video camera systems to monitor 518 nests of grassland birds. We reviewed video of 48 visits by snakes to 34 nests; 37 of these visits resulted in predation of active nests. When adult birds encountered snakes at the nest (n = 33 visits), 76% of the encounters resulted in a form of nest defense (nonaggressive or aggressive); in 47% of the encounters, birds physically struck snakes. When defending nests, most birds pecked at the snakes; Eastern Meadowlarks (*Sturnella magna*) and Bobolinks (*Dolichonyx oryzivorus*) pecked most frequently in any one encounter. Also, two Eastern Meadowlarks ran around snakes, frequently with wings spread, and three Bobolinks struck at snakes from the air. Nest defense rarely appeared to alter snake behavior; the contents of seven nests defended aggressively and two nests defended nonaggressively were partially depredated, whereas the contents of six nests defended each way were consumed completely. One fledgling was produced at each of three nests that had been aggressively defended. During aggressive defense, one snake appeared to be driven away and one was wounded. Our findings should be a useful starting point for further research. For example, future researchers may be able to determine whether the behavioral variation we observed in nest defense reflects species differences, anatomic or phylogenetic constraints, or individual differences related to a bird's prior experience. There appears to be much potential for studying nest defense behavior using video recording of both real and simulated encounters.

Key Words: grassland birds, nest defense, nest predation, snakes.

Variation in avian responses to predation, with adaptive responses in nest placement, clutch size, sociality/coloniality, and feeding behavior, across both species and broader taxonomic units, demonstrates that nest predation is an important force in avian evolution (e.g., Ricklefs 1969, Martin 1995, Hansell 2000). Parental nest defense often entails dramatic behaviors that have captured the interest of behaviorists and the general public. The distraction display of a Killdeer

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(*Charadrius vociferous*; Brunton 1986), the hiss of a titmouse (*Baeolophus* spp.) or chickadee (*Poecile* spp.) (Grubb 1998), and the heightened aggression of Red-winged Blackbirds (*Agelaius phoenicus*; Knight and Temple 1988) and Northern Mockingbirds (*Mimus polyglottos*; Breitwisch 1988) in the presence of potential predators all likely reflect selection for behaviors to reduce reproductive losses to predators. Early researchers sought to study nest defense by eliciting behaviors with simulated predators (e.g., taxidermic mounts, recorded calls, rubber snakes, etc.), live predators [e.g., American Crow (*Corvus brachyrhynchos*), Knight and Temple 1986; and mink (*Mustela lutreola*), Hakkarainen et al. 1998], and humans (assuming humans and predators would elicit similar responses; see review by Knight and Temple 1986).

Predation pressure can lead to development of innate displays and to learned responses. A growing body of work suggests that the risk of predation can influence aspects of behavioral and reproductive decision making within the lifetime of individual breeding birds, also known as "ecological time" (reviewed in Lima 2009). For instance, decision pathways for sequential steps leading to encounters can be created (Fig. 12.1) and used to design studies through which video analysis of avian responses to real and perceived threats can now be assessed. Such results can be used to analyze the balance between the effectiveness (reward) and individual risk (and with individually marked birds, the cost beyond the current reproductive attempt) of nest defense behavior. However, lack of information about interactions between birds and their nest predators has limited researchers' ability to evaluate these behaviors.

The application of video cameras to monitor nests has the potential to change the study of avian nest defense (Thompson et al. 1999; Pietz and Granfors 2000, 2005; Tewksbury et al. 2002); now the theoretical aims of a whole body of research are testable because adequate samples of interactions between birds and their nest predators can be recorded and studied in detail. Here, we describe the responses of grassland passerines to several species of snakes, a predator group that is becoming a focus of study (Weatherhead and Blouin-Demers 2004) and has been found to depredate grassland bird nests in several geographic areas (Pietz et al., chapter 1, this volume). We characterize the behaviors of birds and snakes and assess the degree of variation in avian behavioral responses to encounters. We then test simple hypotheses regarding the probability of nest defense relative to predator size and to timing of attempted predation.

METHODS

Study Area

The data used herein were taken from several studies in southwestern Wisconsin conducted in three different grassland habitats: continuously grazed pastures, Conservation Reserve Program (CRP) fields, and remnant prairie. The topography in southwestern Wisconsin is a series of ridges and valleys running south from the Military Ridge, an east–west ridge that extends from west of Madison (near Mount Horeb) west to the confluence of the Wisconsin and Mississippi Rivers. Historically, ridge tops in this landscape were dry and dry-mesic prairie, whereas the draws and valleys were mesic and wet prairie and oak savanna (Curtis 1959, Cochrane and Iltis 2000). Modern land use is primarily agricultural, with a large portion of the land in pasture, hay, and small grains and relatively few acres in row crops [corn (*Zea mays*) and soybeans (*Glycine max*)] compared to many other agricultural areas of Wisconsin.

Pastures used by Renfrew and Ribic (2003) and Ribic et al. (chapter 10, this volume) ($n = 13$; range = 1.5–169.0 ha) were dominated by nonnative cool-season grasses such as Kentucky bluegrass (*Poa pratensis*) and brome (*Bromus* spp.); on a sample of the sites, average stocking rate was 2.1 Animal Units/ha (SD = 1.0, $n = 9$; range = 0.80–4.31). CRP fields used by Ribic et al. (chapter 10, this volume) and this study ($n = 15$; 10.7–75.6 ha) had been enrolled continuously for 15 or more years at the time of the studies; vegetation consisted of cool-season grasses, primarily smooth brome (*Bromus inermis*) and Kentucky bluegrass, and a wide variety of forbs. The remnant prairie/native warm-season grass CRP fields ($n = 16$; range = 6.6–21.9 ha) used by Ribic et al. (chapter 10, this volume) and this study were dominated by little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), needle (porcupine) grass (*Stipa spartea*), Indian grass (*Sorghastrum nutans*), side-oats grama (*Bouteloua curtipendula*), and panic grass (*Panicum* spp.). At all of the sites, relatively little woody vegetation was present.

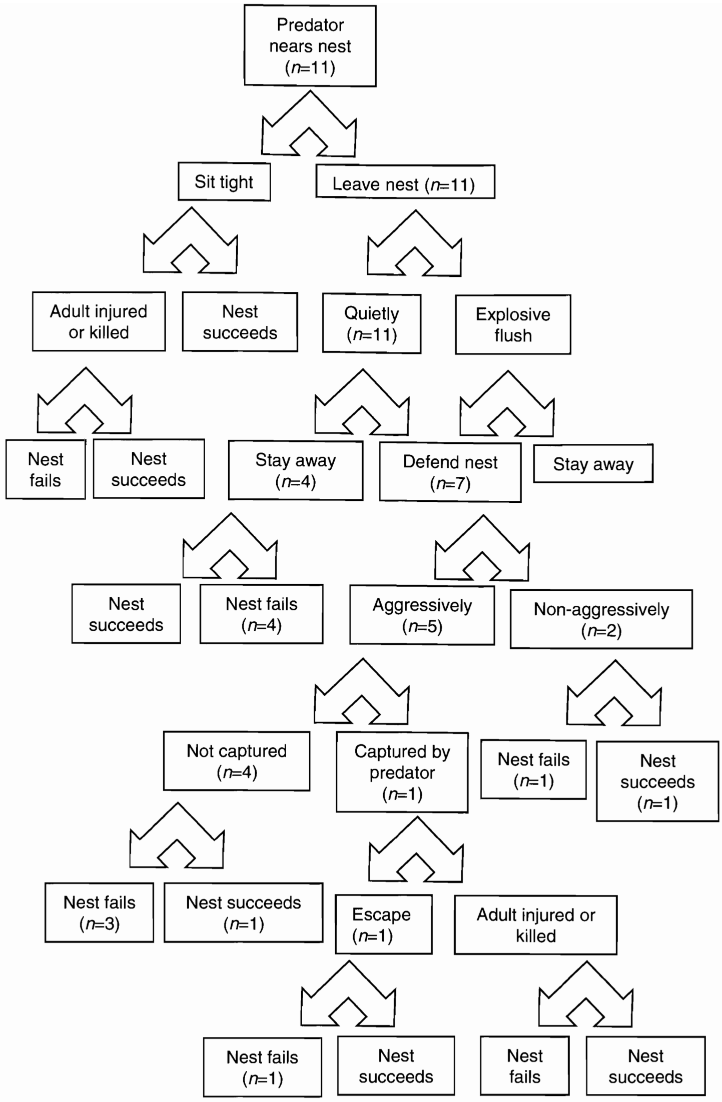

Figure 12.1. Theoretical decision model for an incubating or brooding bird, after Edmunds (1974) in Caro (2005). Parts of the model were simplified for illustrative purposes (e.g., some other potential scenarios were excluded from the "sit tight" path). Nest success was defined as the fledging of one or more young. Data are from Eastern Meadowlark (*Sturnella magna*) nests in southwest Wisconsin (1999–2009). Sample sizes listed are for cases where meadowlarks encountered snake predators within the field of view of our cameras. Boxes without sample sizes indicate that $n = 0$.

Nest Searching and Monitoring

All studies used the same basic techniques for finding and monitoring nests. We located and monitored nests from late April until the completion of nesting, approximately 10 August, in 1999–2009. We searched each site every 1–2 weeks, for a total of 4–10 searches per year (variation due to number of sites per study). Search effort was limited on larger sites to approximate the effort expended on smaller sites. We searched 7–38-ha portions of grassland primarily in areas 0 to 225 m from any edges. We located most nests by walking (4–10 people spaced 2 m apart) systematically through fields (06:00–10:00 CST) and flushing adults from nests. We also located nests through behavioral observation of nesting activity and flushing adults by dragging 10–20-m ropes. For the walking and rope-dragging methods, we used flagging to keep track of searched areas and to minimize overlap.

We marked nests for relocation with a 0.5-m tall wire flag (6-cm^2 vinyl) (in CRP fields, remnant prairie) or a 30-cm diameter paint spot (in pastures, because cows ate flags) located 4 m north or south of the nest (a random direction was chosen for each nest). This system allowed us to check nests without approaching them closely (see Camera Deployment below). Nests were monitored continuously with video, and contents were checked via a monitor every 1–3 days when batteries or VHS tapes were replaced.

Camera Deployment

We deployed video systems that included miniature cameras with infrared light-emitting diodes (LEDs) (Renfrew and Ribic 2003) at randomly selected grassland bird nests to determine nest fates and to identify sources of nest failure. We followed many of the recommendations of Richardson et al. (2009) when deploying cameras. We distributed cameras among fields to ensure that no clustering of cameras occurred. We set up cameras at nests during or soon after the egg-laying stage ended to lower the chance of abandonment (Thompson et al. 1999, Renfrew and Ribic 2003). We deployed cameras on nests that had already hatched only when nests with eggs were not available.

We used two types of camera systems. In the earlier studies, 1999–2005 (Renfrew and Ribic 2003, Ribic et al., chapter 10, this volume), we used analog videotape recorders (VHS at 2–6 frames/sec), whereas during 2006–2009 we used digital video recorders (Archos AV500 at 30 frames/sec). Both recording systems were attached to cameras with 25-m cables (following the protocol established by Renfrew and Ribic 2003). Each camera was mounted on a wooden dowel 3–38 cm above the ground. Cameras were 64 cm^3 and placed 12–25 cm from a selected nest, depending on the nest structure and surrounding vegetation. The field of view at these distances ranged from 414 to 1,320 cm^2. Cameras were typically placed at or below the height of surrounding vegetation to avoid creating a visual cue for potential predators. We buried the cable beneath grass litter and camouflaged cameras with nearby grass; this process typically took 10–15 min. For VHS recorders, tapes were replaced and nest contents viewed on a monitor every 24 hr; batteries were replaced every 24–48 hr. For digital video recorders, batteries and recorders were replaced and nest contents viewed on the recorder every 48 hr.

Review of Video Footage

For this paper, we only analyzed video footage of snake visits to nests. Snakes were the only taxon with which birds frequently interacted within camera view during attempts at nest predation. We recorded 25 interactions with snakes (during 37 cases of predation), versus two interactions with mammals (in 103 cases of predation), and none with birds (in 5 cases of predation). We acknowledge that this in part reflects the size of the potential predators; defensive birds might fly at parts of a large predator that are not within the camera's field of view. We recorded the time of day, nest age, and date when the snake visit occurred.

To avoid missing attempts at predation that may have been thwarted by nest defense, we watched a minimum of three days of video at the nests where visits by snakes occurred; we also documented any multiple snake visits. In addition, we watched video from 98 nests that were primarily reviewed for other purposes: predation by other taxa (Renfrew and Ribic 2003, Ribic et al., chapter 10, this volume), a study of nestling care by Henslow's Sparrows (*Ammodramus henslowii*) (Guzy et al. 2002), and a study of avian sleep (T. C. Roth, unpubl.). However, given the limited view from our cameras, successful nest defense still could have occurred outside the field of view.

We indexed snake size by estimating the distance between the eyes of each snake on a monitor screen. To obtain an estimate of inter-eye distance (in millimeters), we compared published measurements of eggs or the mandible length of the adult female bird (Wheelwright and Rising 1993, Lanyon 1995, Martin and Gavin 1995, Arcese et al. 2002) and measurements from our video to generate scaling factors. These measurements were used when determining whether multiple visits to the same nest were made by different individuals. For analyses, we also classified the snakes as small, medium, and large based on the snake's head width relative to the width of the camera's field of view. After ingesting an individual egg or nestling, snakes often straightened their bodies, sometimes out of the field of view for up to a few minutes; to accommodate these brief absences, we only counted visits separated by more than 15 min as additional visits by the same snake to the same nest.

We interpreted the departure of an adult bird coincidental to the appearance of a predator at the nest or an adult bird's arrival during the predator's presence as indicating that the bird had encountered the predator. We interpreted any presence of an adult bird beyond the initial entry of the potential predator into the field of view as an attempt at nonaggressive defense (*sensu* Larsen et al. 1996). Nonaggressive defense includes alarm calling and scolding behaviors from distances where the bird is unlikely to be harmed. Aggressive defense refers to more overt acts such as diving and pecking in close proximity to potential predators, during which the bird could be injured or killed.

We defined a successful nest predation attempt as the consumption of at least one egg or nestling. An unsuccessful attempt was one where a predator attempted to remove an egg or nestling but failed to do so. We defined nest defense, whether aggressive or nonaggressive, as successful when a predator left the nest without consuming all of the eggs or young. Thus, in cases of partial predation with nest defense, the predator and the defending adult were both classified as successful. We considered scavenging to be a special form of predation defined by the consumption of dead nestlings or of eggs at an abandoned nest. The existence of these items generally indicated an unsuccessful nesting attempt; however, if a bird drove a potential predator away from an unsuccessful nest, we still considered it successful nest defense.

Analyses

The occurrence of nest defense (0 = no defense, 1 = defense) was analyzed relative to snake size, nest age, date, bird species mass, and snake species using logistic regression; analyses were conducted using Program R (ver. 2.9.0, R Foundation for Statistical Computing, Vienna, Austria). (R Development Core Team 2007). We also tested whether the defense rate during day or night was different from chance (i.e., 50%); the null hypothesis was that birds would defend during half of the snake visits, regardless of time of day. To avoid reliance on asymptotic results, we used a Monte Carlo simulation to test this null hypothesis on our small sample (Rugg 2003).

RESULTS

We recorded 48 visits by snakes to 34 nests. Western foxsnake (*Mintonius vulpinus*) visited nests more than any other species (65% of visits), followed by the milksnake (*Lampropeltis triangulum*) (27% of visits), and common gartersnake (*Thamnophis sirtalis*) (8%). Seven visits to nests by snakes resulted in no predation and 14 visits resulted in partial predation.

The majority of individual snakes we recorded ($n = 36$) were in the small (28%) and medium size classes (53%); those classified as large (19%) were all foxsnakes. Seven nests received multiple snake visits; two of these involved multiple visits by what appeared to be the same individuals (Table 12.1). The number of snakes visiting a single nest varied from 1 to 3 and the time intervals between visits varied from about 30 min to 3 days (median time was 1 hr 48 min; Table 12.1). Scavenging occurred at four nests; a milksnake and a foxsnake each scavenged eggs at separate nests and both a foxsnake and a milksnake ate a dead nestling at separate nests. The scavenged nestlings had died shortly (11 and 3 hr) before they were consumed. There were two unsuccessful predation attempts, likely due to the small size of the snakes (one nest was defended nonaggressively and no encounter occurred at the other); in each case, foxsnakes attempted to grasp eggs but apparently their gapes were too small and they left the nest contents unchanged.

During 15 visits to nests by snakes, no adult birds were seen in the field of view; for these snake visits, we assumed that no encounter with an adult bird had taken place and that the nest was undefended. When birds encountered snakes at the nest ($n = 33$), 76% of the encounters resulted in nest defense. In 25 cases, an adult bird was present at the nest when a snake arrived, whereas in 8 cases a returning adult encountered a snake at the nest. During 11 of the cases where an adult was present prior to a snake's arrival, the adult bird initially flushed but then returned and defended the nest. No incubating or brooding adults were killed by snakes. An Eastern Meadowlark (*Sturnella magna*) was caught by the leg during aggressive defense (Fig. 12.2) against a western foxsnake, but it escaped and resumed defending the nest.

For our relatively small sample, we did not find evidence that the occurrence of nest defense was related to snake size, nest age, date within the breeding season, bird species mass, or snake species ($P > 0.10$, all variables). However, birds were more likely to defend nests, aggressively or nonaggressively, during the day (84% of 25 encounters) than at night (57% of 7 encounters) ($G = 11.7$, $P < 0.005$).

TABLE 12.1

Description of multiple visits to grassland bird nests by snakes in southwestern Wisconsin, 1999–2009.

Types of multiple snake visits to nests	Intervals between visits (hr:min)	Species and number of snakes
Snake leaves nest contents intact; another consumes them	71:49	Two western foxsnakes (*Mintonius vulpinus*)
Snake eats all nest contents; two subsequent snakes visit	1:48, 0:41	Two western foxsnakes, then common gartersnake (*Thamnophis sirtalis*)
Snake eats part of nest contents; second snake finishes them	0:32	Milksnake (*Lampropeltis triangulum*) then common gartersnake
	24:40, 4:45, 1:28	Two western foxsnakes, second makes three visits
	2:48	Western foxsnake then milksnake
Snake eats part of nest contents; second snake finishes them; third snake visits	10:02, 1:02	Three milksnakes
Single snake eats all contents on two different days	44:26	One western foxsnake

NOTES: Snakes are listed in order of visitation at each nest. Common and scientific names are from Crother (2008).

Nest defense varied in frequency and form both among and within species (Table 12.2). Eastern Meadowlarks, for example, responded to snake visits with aggressive defense more often than nonaggressive defense, but also showed no defense (on camera) during a high proportion of encounters. In our sample, Grasshopper Sparrows (*Ammodramus savannarum*, $n = 2$) and a Savannah Sparrow (*Passerculus sandwichensis*) exhibited nonaggressive nest defense, appearing to be scolding within 0.5–1 m of the snakes. The most common form of aggressive nest defense was pecking, with Eastern Meadowlarks and Bobolinks (*Dolichonyx oryzivorus*) pecking most frequently in any one encounter (Table 12.3). In addition, two Eastern Meadowlarks and three

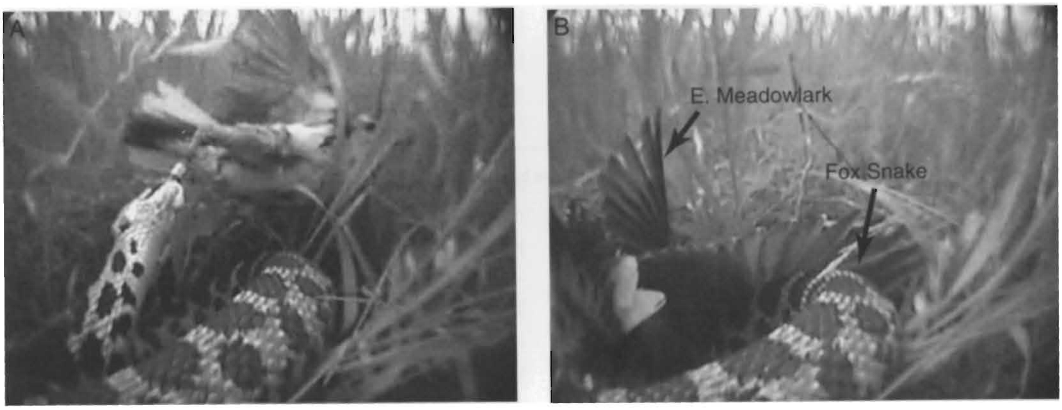

Figure 12.2. Risks encountered during aggressive nest defense: When a color-banded Eastern Meadowlark attacked a western foxsnake (*Mintonius vulpinus*), (a) the snake caught the meadowlark by the leg, and (b) held the bird for 43 sec. Subsequently, the meadowlark escaped, returned after 8 sec, and resumed attacking the snake. In total, the bird struck the snake 198 times with its bill during a 15-min period.

TABLE 12.2

Numbers of snake encounters at nests and types of nest defense aimed at snakes by grassland passerines in southwestern Wisconsin, 1999–2009.

			Encounters with defense		
Bird species	Snake encounters	Nests	Aggressive	Non-aggressive	No defense
Eastern Meadowlark (*Sturnella magna*)	11	10	5	2	4
Bobolink (*Dolichonyx oryzivorus*)	10	8	6	2	2
Song Sparrow (*Melospiza melodia*)	4	2	2	1	1
Grasshopper Sparrow (*Ammodramus savannarum*)	3	3	0	2	1
Henslow's Sparrow (*A. henslowii*)	3	2	1	2	0
Field Sparrow (*Spizella pusilla*)	1	1	1	0	0
Savannah Sparrow (*Passerculus sandwichensis*)	1	1	0	1	0
Total	33	27	15	10	8

NOTE: No Defense = no defense was recorded within the camera field of view.

TABLE 12.3

Characteristics and outcomes of aggressive nest defense against snakes by grassland passerines in southwestern Wisconsin, 1999–2009.

Bird species	Peck count mean, r (n)	Nest contents depredated		
		None	Partial	All
Eastern Meadowlark	45, 1–198 (5)	0	2	3
Bobolink	2, 3–53 (6)	0	3	1
Song Sparrow	11, 2–20 (2)	0	1	1
Henslow's Sparrow	1, n/a (1)	0	1	0
Field Sparrow	5, n/a (1)	0	0	1

NOTES: n = number of snake visits where aggressive nest defense by pecking occurred. At two Bobolink nests, adults defended dead nestlings while a snake scavenged them.

Bobolinks exhibited species-specific behavior in separate cases of aggressive nest defense. Eastern Meadowlarks ran around the nest, frequently with wings spread, while pecking at snakes. Bobolinks struck at snakes from the air, swooping and hitting them with their bills. In contrast, our small samples for the Henslow's Sparrow (*A. henslowii*, 1), Song Sparrow (*Melospiza melodia*, 2), and Field Sparrow (*Spizella pusilla*, 1) did not include any running or flying at snakes; instead, these birds stood on the ground when they pecked the snakes.

We recorded 13 cases of successful nest defense by our liberal definition (e.g., including cases with partially depredated or unsuccessful nests). Four of these cases involved six visits by small foxsnakes, a different snake at each of two nests. We did not find any missed cases of successful nest defense in our review of 3,148 hr of additional video footage. This total included 2,272 hr of control video to assess whether any successful cases of nest defense had gone undetected because the nest contents had not changed.

During 15 snake visits that involved aggressive nest defense, only once did nest defense appear to clearly alter snake behavior. In this case, a gartersnake consumed a hatchling Eastern Meadowlark when the adult was absent, but when the adult returned, it pecked at the snake once and the snake left. The snake was small in relation to the bird and the strike was an extremely vigorous one. Of 15 nests that were aggressively defended, snakes partially depredated contents of seven nests (ultimately, three fledged young and four failed), consumed all the contents of six nests, and scavenged a dead nestling from each of two nests (Table 12.3). Similarly, nonaggressive nest defense (n = 10) did not clearly alter snake behavior; the contents of six nests were consumed completely, two nests were partially depredated, one nest was empty (it was defended after the young had fledged), and one snake left without eating eggs that appeared to be too large for it to ingest.

We documented one case where a snake was injured after a successful predation attempt during which all young were consumed. A large western foxsnake was struck 198 times by a color-banded Eastern Meadowlark over the course of the encounter (Fig. 12.2). The snake recoiled from each strike the bird landed. The following day, a western foxsnake was found within 100 m of the nest. The snake was similar in size to the snake recorded in our footage. The snake had 5–10 visible puncture wounds, about 1–3 mm in size.

DISCUSSION

We found that nest defense by grassland songbirds appears to be common, with defense occurring almost 75% of the time when the birds encountered snakes. However, the effects of nest defense against snakes were difficult to assess. There was only one case where snake behavior was clearly altered by defense. In two cases, snakes left without consuming any nest contents after encountering a defending adult bird, but causality was uncertain (e.g., the snake might have left because the eggs were too large for it to ingest). For the several cases of partial predation, we could not discern whether partial predation occurred due to snake satiation or harassment from birds.

Although the immediate benefits of nest defense may be difficult to ascertain, we assume there are some rewards for these efforts. In our study, three of 15 nests that were aggressively defended against snakes eventually fledged young. Similarly, Pietz and Granfors (2005) reported 5–7 of 21 nests that were aggressively defended against various types of predators eventually fledged young. Relative to the risks we documented for adult birds (Fig. 12.1), the potential rewards of successful nest defense make even minimal levels of defense, particularly to distract a predator from young capable of fleeing, a profitable strategy. Another direct benefit may result if defensive attacks cause injury to the predator, as we recorded for one snake. Indirect benefits may even be possible if, for example, defensive scolding leads to mobbing and/or attracts larger predators to prey on the offending snake (see Withgott 1996). Also, where the risk to the defender appears small, the potential for future reproductive success is not likely to be diminished.

Our results differed from those in comparable studies in Missouri and Texas, where snakes (primarily *Scotophis* and *Lampropeltis* spp.) were common nest predators (Stake et al. 2005, Reidy et al. 2009). The frequency of partial predation in Wisconsin was much higher than that found in Missouri and Texas. Also, no incubating or brooding adults were killed by snakes in our study, whereas Reidy et al. (2009) recorded six mortality events at 133 video-recorded nests. Furthermore, Reidy et al. (2009) did not report any nest defense. A possible explanation for all these differences is that the snake species encountered on their study areas were generally larger than those on ours. The small size of snakes (relative to the birds) in our study may explain the high frequency of defense, the higher proportion of partial predation, and the lower risk to adult birds compared to the studies farther south.

Our observations of multiple snake visits to individual nests, as well as the short intervals between some visits to the same nest by different snakes, suggest that snakes might use chemical cues left by their own and other species. Ford (1982) demonstrated species specificity of sex pheromone trails among sympatric and allopatric species of gartersnakes (*Thamnophis* spp.). Such mechanisms could be used by foraging snakes, particularly among those in the subfamily *Colubrinae*, like the milksnake, that commonly prey upon other snakes. Further evidence that snakes use chemical cues left by other snakes includes a study by Clark (2007), which demonstrated that timber rattlesnakes (*Crotalus horridus*) use conspecific chemical cues to select ambush sites.

Future Directions

While we did not design our studies explicitly to study nest defense, using video cameras at nests has allowed us to document behaviors of nest predators as well as those expressed by defending birds. As digital technologies progress, fewer logistical constraints associated with video recording at nests will exist (Cox et al., chapter 15, this volume). This will allow increased use of video camera systems explicitly for studying nest defense. For instance, a camera with a wider field of view aimed at the general nest area, in addition to a camera close to the nest, would likely improve the chance of recording additional events and behaviors associated with nest defense. Ideally, wireless cameras would be aimed at different angles and distances from the nest. Adding an audio component to the video recording would permit detection of vocal behaviors, such as chipping and scolding to alert a mate or harass a potential predator.

There should also be considerable potential to study defensive behaviors with experimental manipulations, using video recording of both real and simulated encounters. For instance, parental response relative to snake size could be tested with model snakes (preferably with some sort of mechanical animation to increase realism). Simulated encounters would be particularly useful when the behaviors elicited can be compared with those of real encounters, such as those described in our study.

Future studies could use video of bird responses to real and simulated predators to help identify general versus specialized defensive behaviors, and the degree to which learning plays a role in whether and how the nest is defended. General responses are those that entail the same postures and behavior regardless of type of predator.

Specialized responses are those that are unique to a type of predator. For instance, some passerines exhibit aggression toward cowbirds (*Molothrus* spp.) (Tewksbury et al. 2002, Ellison and Sealy 2007) but respond to most other predators only with alarm calls (Gill and Sealy 2004).

We focused on snakes in this paper, but there are many other predators of grassland bird nests (Pietz et al., chapter 1, this volume). In fact, Pietz and Granfors (2005) recorded more defense directed at mammals (16 accounts, from mice to raccoons, *Procyon lotor*) than at snakes (two plains gartersnakes, *Thamnophis radix*) in Minnesota and North Dakota. In all our studies from which the data for this paper were taken, nest defense of any type against mammalian predators was rare (i.e., two cases, both involving thirteen-lined ground squirrels, *Ictidomys tridicemlineatus*; unpubl. data). Comparative studies of nest defense behaviors among different bird species and taxa of predators would be particularly interesting.

Although we acknowledge the biases associated with our camera systems for detecting nest defense, these systems have already provided much unprecedented information. With continued application and improved technology, we hope further research will address some of the questions raised by our findings. For example, future researchers may be able to determine whether the behavioral variation we observed in nest defense reflects species differences, anatomic or phylogenetic constraints, or individual differences related to a bird's prior experience with a type of predator. The exploration of nest defense using video cameras is just beginning.

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LITERATURE CITED

Arcese, P., M. K. Sogge, A. B. Marr, and M. A. Patten. 2002. Song Sparrow (*Melospiza melodia*). Birds of North America No. 704, Academy of Natural Sciences, Philadelphia, PA.

Breitwisch, R. 1988. Sex differences in defence of eggs and nestlings by Northern Mockingbirds, *Mimus polyglottos*. Animal Behavior 36:62–72.

Brunton, D. H. 1986. Fatal antipredator behavior of a Killdeer. Wilson Bulletin 98:605–607.

Caro, T. M. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, IL.

Clark, R. W. 2007. Public information for solitary foragers: timber rattlesnakes use conspecific cues to select ambush sites. Behavioral Ecology 18:487–490.

Cochrane, T. S., and H. H. Iltis. 2000. Atlas of Wisconsin prairie and savanna flora. Technical Bulletin 191. Wisconsin Department of Natural Resources, Madison, WI.

Crother, B. I. (editor). 2008. Scientific and standard English names of amphibians and reptiles of North American north of Mexico. Herpetological Circular No. 37. Society for the Study of Amphibians and Reptiles, Salt Lake City, UT. <http://www.ssarherps.org/pdf/HC_37_6thEd.pdf> (22 September 2010).

Curtis, J. T. 1959. The vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press, Madison, WI.

Edmunds, M. 1974. Defense in animals. Longman Group Limited, Essex, UK.

Ellison, K., and S. G. Sealy. 2007. Small hosts infrequently disrupt laying by Brown-headed Cowbirds and Bronzed Cowbirds. Journal of Field Ornithology 78:379–389.

Ford, N. B. 1982. Species specificity of sex pheromone trails of sympatric and allopatric garter snakes (*Thamnophis*). Copeia 1:10–13.

Gill, S. A., and S. G. Sealy. 2004. Functional reference in an alarm signal given during nest defence: seet calls of Yellow Warblers denote brood-parasitic Brown-headed Cowbirds. Behavioral Ecology and Sociobiology 56:71–80.

Grubb, T. C., Jr. 1998. Tufted Titmouse. Stackpole Books, Mechanicsburg, PA.

Guzy, M. J., C. A. Ribic, and D. W. Sample. 2002. Helping at a Henslow's Sparrow nest in Wisconsin. Wilson Bulletin 114:407–409.

Hakkarainen, H., P. Ilmonen, V. Koivunen, and E. Korpimäki. 1998. Blood parasites and nest defense behaviour of Tengmalm's Owls. Oecologia 114:574–577.

Hansell, M. 2000. Bird nests and construction behavior. Cambridge University Press, Cambridge, UK.

Knight, R. L., and S. A. Temple. 1986. Methodological problems in studies of avian nest defense. Animal Behavior 34:561–566.

Knight, R. L., and S. A. Temple. 1988. Nest-defense behavior in the Red-winged Blackbird. Condor 90:193–200.

Lanyon, W. E. 1995. Eastern Meadowlark (*Sturnella magna*). Birds of North America No. 160, Academy of Natural Sciences, Philadelphia, PA.

Larsen, T., T. A. Sordahl, and I. Byrkjedal. 1996. Factors related to aggressive nest protection behavior: a comparative study of holarctic waders. Biological Journal of the Linnean Society 58:409–439.

Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485–513.

Martin, S. G., and T. A. Gavin. 1995. Bobolink (*Dolichonyx oryzivorus*). Birds of North America No. 176, Academy of Natural Sciences, Philadelphia, PA.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101–127.

Pietz, P. J., and D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. Journal of Wildlife Management 64:71–87.

Pietz, P. J., and D. A. Granfors. 2005. Parental nest defense on videotape: more reality than "myth." Auk 122:701–705.

Reidy, J. L., M. M. Stake, and F. R. Thompson III. 2009. Nocturnal predation of females on nests: an important source of mortality for Golden-cheeked Warblers? Wilson Journal of Ornithology 121:416–421.

Renfrew, R. B., and C. A. Ribic. 2003. Grassland passerine nest predators near pasture edges identified on videotape. Auk 120:371–383.

Richardson, T. W., T. Gardali, and S. H. Jenkins. 2009. Review and meta-analysis of camera effects on avian nest success. Journal of Wildlife Management 73:287–293.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1–48.

Rugg, D. J. 2003. TableSim: a program for analysis of small-sample categorical data. USDA Forest Service General Technical Report NC-232. USDA Forest Service, North Central Research Station, St. Paul, MN.

Stake, M. M., F. R. Thompson III J. Faaborg, and D. E. Burhans. 2005. Patterns of snake predation at songbird nests in Missouri and Texas. Journal of Herpetology 39:215–222.

Tewksbury, J. J., T. E. Martin, S. J. Hejl, M. J. Kuehn, and J. W. Jenkins. 2002. Parental care of a cowbird host: caught between the costs of egg-removal and nest predation. Proceedings of the Royal Society of London, Series B 269:423–429.

Thompson, F. R., III, W. Dijak, and D. E. Burhans. 1999. Video identification of predators at songbird nests in old fields. Auk 116:259–264.

Weatherhead, P. J., and G. Blouin-Demers. 2004. Understanding avian nest predation: why ornithologists should study snakes. Journal of Avian Biology 35:185–190.

Wheelwright, N. T., and J. D. Rising. 1993. Savannah Sparrow (*Passerculus sandwichensis*). Birds of North America No. 45, Academy of Natural Sciences, Philadelphia, PA.

Withgott, J. H. 1996. Natural history notes: *Elaphe obsoleta obsoleta* (foraging). Herpetological Review 27:81–82.