Linking snake behavior to nest predation in a Midwestern bird community

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Abstract. Nest predators can adversely affect the viability of songbird populations, and their impact is exacerbated in fragmented habitats. Despite substantial research on this predator–prey interaction, however, almost all of the focus has been on the birds rather than their nest predators, thereby limiting our understanding of the factors that bring predators and nests into contact. We used radiotelemetry to document the activity of two snake species (rat snakes, *Elaphe obsoleta*; racers, *Coluber constrictor*) known to prey on nests in Midwestern bird communities and simultaneously monitored 300 songbird nests and tested the hypothesis that predation risk should increase for nests when snakes were more active and in edge habitat preferred by both snake species. Predation risk increased when rat snakes were more active, for all nests combined and for two of the six bird species for which we had sufficient nests to allow separate analyses. This result is consistent with rat snakes being more important nest predators than racers. We found no evidence, however, that nests closer to forest edges were at greater risk. These results are generally consistent with the one previous study that investigated rat snakes and nest predation simultaneously. The seemingly paradoxical failure to find higher predation risk in the snakes' preferred habitat (i.e., edge) might be explained by the snakes using edges at least in part for non-foraging activities. We propose that higher nest predation in fragmented habitats (at least that attributable to snakes) results indirectly from edges promoting larger snake populations, rather than from edges directly increasing the risk of nest predation by snakes. If so, the notion of edges per se functioning as ecological "traps" merits further study.

Key words: Coluber constrictor; edge; Elaphe obsoleta; field; forest; fragmentation; Midwest, USA; nest predation; racer; rat snake; snake behavior; songbirds.

INTRODUCTION

Nest failure due to predation is a potent force affecting populations and communities of nesting birds (Ricklefs 1969, Martin 1988). As many bird species decline (e.g., Askins 2000), the need to understand nest predation has moved from being an ecological to a conservation imperative. For most of its history, the investigation of the interaction between birds and their nest predators has focused almost exclusively on the consequences of nest predation for birds (Weatherhead and Blouin-Demers 2004), although not because the importance of studying the nest predators has gone unrecognized (e.g., Paton 1994, Marzluff and Restani 1999, Schmidt 1999, Chalfoun et al. 2002, Lima 2002, Larivière 2003, Stephens et al. 2003). An impediment to

studying nest predators was identifying them and quantifying their relative importance. Increasing use of video surveillance of nests is overcoming that problem (Thompson 2007), opening the way for studies that investigate both birds and their nest predators. Here we investigate whether spatial and temporal patterns of nest predation in a Midwestern bird community can be explained by habitat selection and activity of two snake species that prey on their nests.

Increased nest predation is widely associated with increased habitat fragmentation, where the fragments are characterized by greater ratios of edge to interior habitat (Faaborg et al. 1995). Although the ecological effects of fragmentation and edge are often confounded (Ries et al. 2004, Fletcher et al. 2007), nest predators apparently respond positively to both (Chalfoun et al. 2002). Recent evidence has implicated snakes as important nest predators that may respond to fragmentation and edge in ways that contribute to increased nest predation in fragmented habitats (Weatherhead and Blouin-Demers 2004). First, reviews of studies in North America that have monitored nests using video cameras indicate that snakes are major nest predators (Weatherhead and Blouin-Demers 2004, Thompson 2007).

Second, telemetry studies of snakes known to be nest predators have found that these snakes preferentially use forest edges (Weatherhead and Charland 1985, Blouin-Demers and Weatherhead 2001a, Carfagno and Weatherhead 2006, Sperry et al. 2009). In the first study to investigate predatory snakes and nesting birds simultaneously, Sperry et al. (2008) found that seasonal variation in predation risk for two endangered bird species in Texas was associated with temporal variation in snake activity. In that study there was no clear association between predation risk and snake habitat use (including edge), despite the snakes in that study preferring edges (Sperry et al. 2009). Our central goal here was to follow that same approach of studying birds and snakes simultaneously to determine if spatiotemporal variation in the risk of nest predation was associated with either snake activity or snake habitat preferences.

Previous studies of Midwestern bird communities have documented edge and fragmentation effects on nest predation (Robinson et al. 1995, Brawn and Robinson 1996, Suarez et al. 1997, Heske et al. 1999, Morse and Robinson 1999). Snakes accounted for 87% of 30 documented cases (observations and video recording) of nest predation made over the course of those studies (S. K. Robinson and A. Suarez, unpublished data). Those observations are consistent with data from other studies in the same region, where snakes accounted for 63% of 86 instances of nest predation (Thompson et al. 1999, Thompson and Burhans 2003). In those studies rat snakes (Elaphe obsoleta) were the single most important predator, accounting for 36% of all documented predation events (see Plate 1). Racers (Coluber constrictor) accounted for only 8% of all nest predation in those studies, but we included them here because they were abundant at our study site. At our site in southern Illinois both snake species preferentially use edge habitat between forest and old fields during the bird-nesting season, with rat snakes otherwise being forest specialists and racers being field specialists (Carfagno et al. 2006). The general prediction we test is that predation risk for nests should be highest in forest–field edges and should increase over the avian nesting season as snakes become more active. Because rat snakes appear to be more important nest predators than racers, relative to racers, rat snake habitat use and activity should be better predictors of predation risk.

METHODS

We conducted the study in 2003 at the Cache River State Natural Area in southern Illinois. Habitat in the 3 × 4 km study area was a mosaic of mature upland and bottomland forest and old fields in various stages of succession. As indicated previously, the two snake species we studied were chosen because of their documented role as avian nest predators and because they co-occur in areas characterized by the interface of forest and old fields (Keller and Heske 2000, Carfagno and Weatherhead 2006). Rat snakes and racers are

similar in size and although both species climb trees, rat snakes are much more arboreal than racers (Carfagno and Weatherhead 2006). Both species exploit a diverse suite of avian and mammalian prey (Klimstra 1959, Fitch 1963a, b, Weatherhead et al. 2003), although birds are a more important component of rat snake diets (Carfagno et al. 2006), probably reflecting their more arboreal nature.

The snake data we use were part of a four-year telemetry study of habitat use and movements of rat snakes and racers, the general methods for which are provided by Carfagno and Weatherhead (2006). In 2003 we tracked 12 rat snakes and 12 racers throughout the bird-nesting season. Snakes were usually located every other day. Each time a snake was located we mapped its position using GPS. We used Hawth's Analysis Tools (Beyer 2004) in ESRI ArcGIS version 9 to calculate the straight-line distance between successive locations. That distance was divided by the number of days elapsed between locations to estimate daily distance moved. Individual values were then averaged across snakes within species to obtain mean daily activity values for each species for a given time period.

Bird methods

We searched for bird nests from 15 April through 15 August 2003 in the same areas where snakes were being monitored, which included successional fields and forests in the uplands and the floodplain of the Cache River. We balanced our nest-searching effort so that all habitats and parts of the study area were searched with roughly equal effort. Once a nest was located, its contents were checked, GPS coordinates were taken, and nest height was recorded. Nests were flagged to facilitate relocating them, with flags placed at least 3 m from the nest to minimize cues that could be used by predators. Nests were monitored every three days and their contents recorded. Nest monitoring ceased when nests were empty or had no signs of activity for at least three consecutive visits. When nests had survived long enough to fledge, a concerted effort was made to search for fledglings in the vicinity of the nest to confirm fledging. Nests located in dense foliage of old fields were checked at the greatest distance possible to minimize disturbing vegetation around the nest in ways that might provide a clue for predators. High nests were checked with poles with mirrors attached. GPS locations were used to map all nests and determine their distance from the nearest edge.

Statistical methods

We used an information-theoretic approach (Burnham and Anderson 2002), following the logistic exposure methods described by Shaffer (2004), to evaluate support for 23 candidate models that could potentially influence nest survival and to calculate daily nest survival rates. Models were developed using habitat, temporal, and snake activity variables, all two-way

Table 1. Number of nests monitored, average nest height, observation days, daily survival rate (DSR), and 95% confidence intervals of DSR for the six most common bird species studied in southern Illinois in 2003.

Species	N	Nest height (m)	Obs. days	DSR	95% CI
Acadian Flycatcher	31	5.44 ± 0.50	479	0.956	0.934–0.971
Blue-gray Gnatcatcher	19	2.55 ± 0.29	278	0.950	0.918–0.969
Field Sparrow	49	0.52 ± 0.05	519	0.944	0.920–0.960
Indigo Bunting	81	1.07 ± 0.10	964	0.948	0.932–0.960
Northern Cardinal	35	1.79 ± 0.16	378	0.912	0.878–0.937
Yellow-breasted Chat	29	0.87 ± 0.09	369	0.956	0.929–0.973

combinations of these variables, a global model (all variables combined), and a null model (intercept only). Habitat models included macro-habitat type (upland forest, bottomland forest, old field or successional field), distance to habitat edge (meters), and nest height (meters). Temporal models included seasonal effects (day of year). Snake activity models included average daily rat snake distance traveled and average daily racer distance traveled. We ran one analysis with all bird species combined (excluding those with <2 nests) and separate analyses for each of the six most common species. We included models incorporating effects of species in the overall analysis, resulting in a total of 26 candidate models. All analyses were conducted in SAS (SAS Institute 2004) using PROC GLM (Shaffer 2004).

We tested for multicollinearity using the tolerance values from PROC REG (SAS Institute, Cary, North Carolina, USA) and the global model (all variables included) was tested for overdispersion using Pearson χ^2 test statistic (Burnham and Anderson 2002). In the overall and individual species analyses we found little evidence of model problems with multicollinearity (all $\hat{c}$'s = 0.95–1.24) or overdispersion (all tolerance values $\geq$ 0.48). We evaluated relative support for models using Akaike's Information Criteria with small sample bias adjustment (AIC_c). Models were considered important if ΔAIC_c (difference between the AIC_c of each model and the lowest AIC_c value) was $\leq$2.0 AIC units (Burnham and Anderson 2002). We also derived parameter importance weights to estimate the plausibility of habitat and snake factors as determinants of predation risk.

We determined if nests were located closer to edges than expected using a chi-square analysis. For this analysis we defined edge as habitat within 15 m of the interface between open habitat (e.g., field, river) and forest (Blouin-Demers and Weatherhead 2001a, Carfagno and Weatherhead 2006). Expected edge proportions were determined by choosing locations a random distance and direction from snake locations (Carfagno and Weatherhead 2006).

All means are presented $\pm$ standard error.

RESULTS

We monitored a total of 300 nests of 19 species, resulting in 3820 observation days (range of species observation days = 7–964; mean = 212.06 $\pm$ 57.71). Among the six most common bird species sampled, Acadian Flycatcher nests had the highest survival rates and Northern Cardinals the lowest (Table 1). Most nests were found in successional field habitats, although habitat use and distance-to-habitat edges varied among species (Table 2). The number of nests of all species found in edges was proportional to the availability of edges ($\chi^2 = 0.28$, $P = 0.60$). The same was true for five of the six most common species ($\chi^2 = 0.27$–3.09, $P = 0.08$– 0.60), but field sparrows did nest in edges less often than expected by chance ($\chi^2 = 8.64$, $P < 0.01$).

Radiotelemetry produced a total of 280 rat snake locations (23.33 $\pm$ 3.55 locations per snake, mean $\pm$ SE) and 452 racer locations (37.67 $\pm$ 4.12 locations per snake) during the time that birds were nesting. Racers moved further per day on average than rat snakes (70.87 $\pm$ 2.76 m and 49.23 $\pm$ 2.07 m, respectively; see Carfagno and Weatherhead 2008). We observed no seasonal variation in activity for either snake species, but daily variation in movement was substantial for both species (Fig. 1). Daily movement by rat snakes was not correlated with movement by racers ($R^2 = 0.01$). A reason for the lack of correlation was that racer activity

Table 2. Number of nests in each habitat type and distance to habitat edge (mean $\pm$ SE) for all bird species combined and for the six most common species sampled in southern Illinois in 2003.

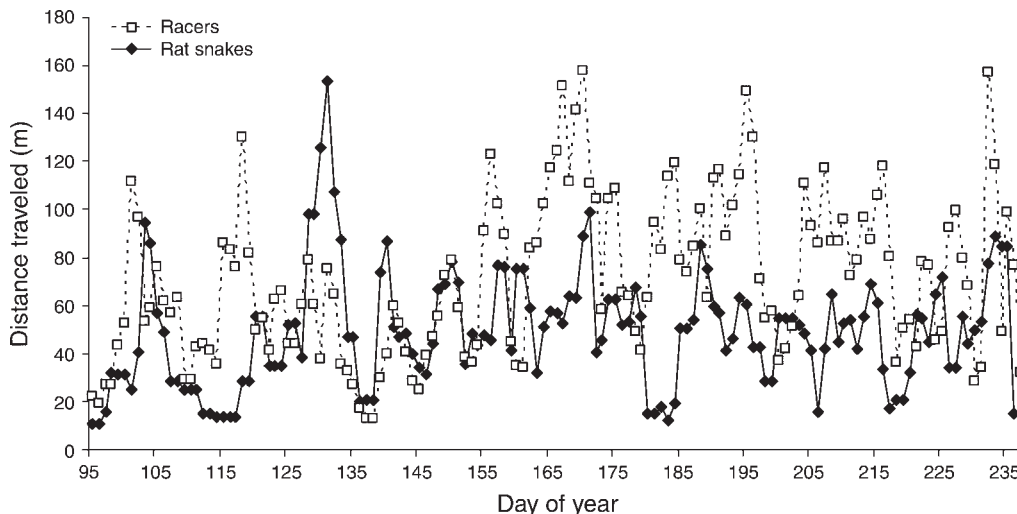| Species	Bottomland forest	Upland forest	Old field	Successional field	Distance to edge (m)
All species	34	43	34	189	84.3 ± 4.9
Acadian Flycatcher	14	17	0	0	56.6 ± 11.5
Blue-gray Gnatcatcher	0	0	5	14	134.2 ± 24.0
Field Sparrow	0	0	13	36	119.4 ± 13.2
Indigo Bunting	5	5	7	64	73.5 ± 9.2
Northern Cardinal	5	7	3	20	55.6 ± 11.3
Yellow-breasted Chat	0	0	3	26	89.9 ± 13.7

Fig. 1. Daily mean distance traveled per snake for rat snakes *Elaphe obsoleta* (solid line, solid triangles) and racers *Coluber constrictor* (dashed line, open squares) in southern Illinois, 2003. Day 1 is 1 January.

was much more closely tied to temperature than was rat snake activity ($R^2 = 0.42$, $P < 0.01$ vs. $R^2 = 0.14$, $P = 0.09$; Fig. 2). ANCOVA confirmed that the slopes of the relationships between activity and temperature differed between the two snake species ($F_{1,39} = 15.31$, $P < 0.01$).

For the analysis including nests of all species, the model including rat snake activity and nest height was the highest ranked (Table 3). Nest survival was negatively associated with rat snake activity (model averaged estimate = -0.004, CL: -0.014, 0.007, all values are mean and 95% CL) and positively associated with nest height (0.025, CL: $= -0.228$, 0.279), although the 95% CI for both model-averaged estimates included zero. Effects of bird species, habitat, distance to edge, and racer activity were not strong and none of these variables was included in any of the highest ranked models. Importance weights indicated that rat snake activity was over twice as plausible as any other variable

in explaining overall variation in the probability of nest predation (Table 4).

In the analyses of individual bird species, rat snake activity was the highest ranked model for both Blue-gray Gnatcatchers and Field Sparrows (Table 3). For both species, rat snake activity was also present in most of the competing models, which resulted in rat snake activity having high importance weights for both species (Table 4). Nest survival was negatively associated with rat snake activity for both species. Although the 95% confidence intervals for the model-averaged estimates encompassed zero, the proportion of nests that failed was highest when rat snakes were most active (Fig. 3). For Acadian Flycatchers, racer activity was the highest ranked model, although contrary to expectation, the direction of the effect was positive (model averaged estimate = 0.007, CL: -0.009, 0.023). However, the confidence intervals again indicated uncertainty. Preda-
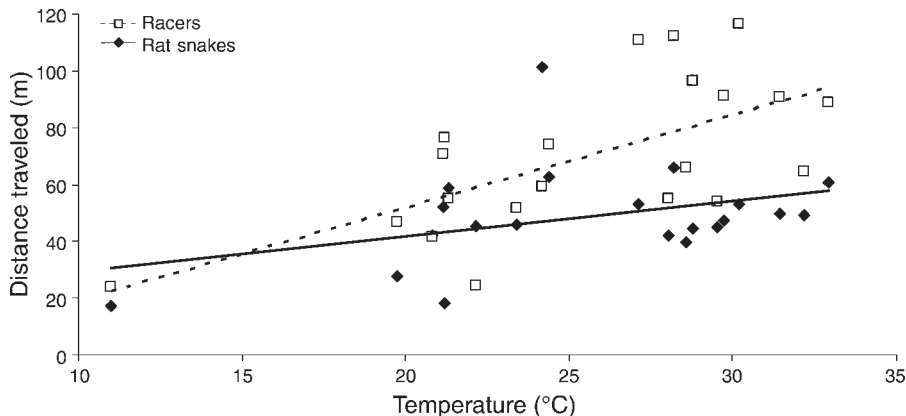

Fig. 2. Distance traveled per week for rat snakes and racers relative to daily maximum temperature each week in southern Illinois in 2003.

TABLE 3. Model selection results from logistic exposure analyses examining habitat, temporal, and snake activity (indicated by rat snake and racer, respectively) effects on daily nest survival of the six most common bird species in southern Illinois in 2003.

Species, competing models	K	ΔAIC_c	w_i
Combined species			
Rat snake and nest height	3	0.00	0.27
Rat snake and season	3	1.12	0.16
Rat snake	2	1.29	0.14
Acadian Flycatcher			
Racer and habitat	3	0.00	0.21
Racer and season	3	1.12	0.12
Global model	7	1.21	0.12
Habitat	2	1.30	0.11
Blue-gray Gnatcatcher			
Rat snake	2	0.00	0.16
Rat snake and habitat	3	0.60	0.12
Rat snake and season	3	0.52	0.08
Rat snake and nest height	3	0.58	0.07
Rat snake and edge distance	3	0.73	0.07
Rat snake and racer	3	0.84	0.06
Null model	1	0.91	0.06
Field Sparrow			
Rat snake	2	0.00	0.12
Null model	1	0.15	0.11
Rat snake and racer	3	0.85	0.08
Racer	2	1.37	0.06
Season	2	1.53	0.06
Rat snake and season	3	1.78	0.05
Rat snake and edge distance	3	1.83	0.05
Rat snake and habitat	3	1.93	0.05
Habitat	2	1.96	0.05
Rat snake and nest height	3	1.96	0.05
Indigo Bunting			
Nest height	2	0.00	0.15
Nest height and season	3	0.22	0.13
Season	2	0.23	0.09
Nest height and rat snake	3	1.08	0.06
Rat snake and season	3	1.79	0.06
Null model	1	1.83	0.06
Nest height and edge distance	3	1.93	0.06
Nest height and racer	3	1.96	0.05
Northern Cardinal			
Null model	1	0.00	0.17
Rat snake	2	0.65	0.12
Season	2	1.36	0.09
Nest height	2	1.90	0.07
Edge distance	2	1.91	0.07
Racer	2	1.98	0.06
Yellow-breasted Chat			
Null model	1	0.00	0.14
Nest height	2	1.06	0.08
Habitat	2	1.42	0.07
Edge distance	2	1.52	0.06
Racer	2	1.62	0.06
Season	2	1.73	0.05

Notes: Only the highest ranked models ($\leq 2\ \Delta AIC_c$) are presented. K is the number of parameters in each model including the intercept, ΔAIC_c is the difference between each model and the model with the lowest ΔAIC_c score, and w_i describes the relative support for each model.

tion risk for cardinals and chats appeared unrelated to snake activity.

The model-averaged estimates suggested that nest survival was positively associated with nest height for four species (Field Sparrow, Indigo Bunting, Northern Cardinal, and Yellow-breasted Chat), but negative for Acadian Flycatchers and Blue-gray Gnatcatchers. The two species with negative relationships were also the species with the highest nests (Table 1).

Habitat type was included in the highest ranked models only for Acadian Flycatchers. Flycatcher daily nest survival was lower in bottomland forests (0.92, CL: 0.87, 0.96) compared to upland forest (0.97, CL: 0.94, 0.98). We did not find evidence supporting an effect of distance to edge or seasonal effects on daily nest survival for any species (Table 3). Although these variables were present in a few of the competing models, they were only present in combination with more supported variables. For cardinals and chats, interpretation of our model selection is difficult because the null model was the highest ranked model (Table 3), indicating that the explanatory variables used in the analyses did not have a strong effect on daily nest survival.

DISCUSSION

Three general patterns emerged from our results. First, nest predation risk increased when snakes were active, and although racers are more active than rat snakes, it was rat snake activity that emerged as the better predictor of predation risk. This was consistent with our prediction that rat snakes should be more important because they account for more nest predation than racers. Even for Field Sparrows, which nest in habitat used more by racers than rat snakes, it was still rat snake activity that predicted predation. This is consistent with Thompson et al.'s (1999) observations that rat snakes are more important nest predators than racers in old fields. Second, contrary to our prediction, nests closer to edges were not at greater risk of predation. The only habitat feature that was associated with predation risk was nest height, and the nature of that association differed among bird species. Third, none of the patterns we found was strong, suggesting either that we did not record important variables that do predict predation risk, or that predation is highly stochastic. Some unexplained variation is likely to be a consequence of us focusing only on snakes, given that other predators almost certainly accounted for some predation.

The lack of strong edge effects on nest predation is generally consistent with results from other studies in the nearby Shawnee National Forest of southern Illinois (Robinson and Wilcove 1994, Marini et al. 1995). For example, in a study of Kentucky Warblers (*Oporornis formosus*), Morse and Robinson (1999) found strong edge effects on brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) but no edge effects on nest predation. Hoover et al. (2006) found some effect of edge on nest predation rates on Acadian Flycatchers but the decline was gradual over a 1.5-km distance from edges and thus might not have been detectable on the scale of this study. More generally, results of studies on

TABLE 4. Importance weights for individual parameters as determined by summing AIC weights from all models in which the parameter appeared for all bird species combined and for the six most common species sampled in southern Illinois in 2003.

Parameter	Species						
	All	ACFL	BGGN	FISP	INBU	NOCA	YBCH
Rat snake	0.78	0.21	0.57	0.40	0.21	0.32	0.18
Racer	0.04	0.53	0.15	0.24	0.16	0.21	0.21
Nest height	0.36	0.21	0.20	0.17	0.50	0.20	0.28
Habitat	0.09	0.67	0.27	0.19	0.05	0.06	0.23
Season	0.27	0.35	0.20	0.20	0.44	0.25	0.21
Edge distance	0.13	0.22	0.17	0.20	0.16	0.20	0.23
Species	0.16						

Notes: AIC weights were calculated from logistic exposure nest survival analyses. Snake activity is indicated by rat snake and racer, respectively. ACFL is Acadian Flycatcher, BGGN is Blue-gray Gnatcatcher, FISP is Field Sparrow, INBU is Indigo Bunting, NOCA is Northern Cardinal, YBCH is Yellow-breasted Chat.

edge effects in North America have also been inconsistent in finding an association between proximity to edge and probability of nest predation (Fletcher et al. 2007).

The association we found between snake behavior and nest predation is similar to results from a study of rat snakes and two endangered songbirds in Texas. Risk of predation increased as rat snakes became more active (Sperry et al. 2008), but nests in habitat preferred by the snakes were not more likely to be preyed on (Sperry et al. 2009). Similar outcomes are needed from more than two studies before we can be confident that there is a general pattern, but the current evidence does invite speculation. The fact that nests are at greater risk when their most important predator is more active is consistent with expectations and raises no obvious questions, whereas the failure to find that nests in habitats preferred by those predators are not at greater risk is puzzling. However, Blouin-Demers and Weatherhead (2001*a*) demonstrated that rat snakes prefer edges for thermoregulation and thus often spend time in edges for reasons unrelated to foraging. Specifically, females use edges more when eggs are developing and both sexes use edges more when shedding and when digesting a meal (Blouin-Demers and Weatherhead 2001*a, b*). Failure to find higher nest predation in edges ceases to be problematic if we assume that when snakes are engaged in these other activities they are not simultaneously foraging.

Even though edges did not increase nest predation directly, they probably had indirect effects. When Weatherhead and Charland (1985) initially documented a preference for edges by rat snakes, they speculated that rat snake populations would benefit from a small-scale mosaic of forest and field, i.e., fragmented forest habitat. Because edges provide ecological services for the snakes, habitats with abundant edges should support larger snake populations. Testing the hypothesis that rat snake density is higher in fragmented than unfragmented forest will be challenging for two reasons. First, the test requires finding relatively large areas of unfragmented forest that is otherwise similar to fragmented forest. Second, there are no simple survey methods for

estimating rat snake density, so relatively intensive studies of the snakes will be necessary (e.g., Blouin-Demers and Weatherhead 2002). If we are correct that higher predation in fragmented habitat results indirectly from the effect of edge on predator populations, the hypothesis that edges function as ecological "traps" for birds (e.g., Gates and Gysel 1978, Schlaepfer et al. 2002) would be challenged.

Linking snake behavior to nest predation as we have done here is a step forward in understanding the relationship between birds and their nest predators. However, more refined approaches to addressing this problem should soon be possible. Ideally one would like
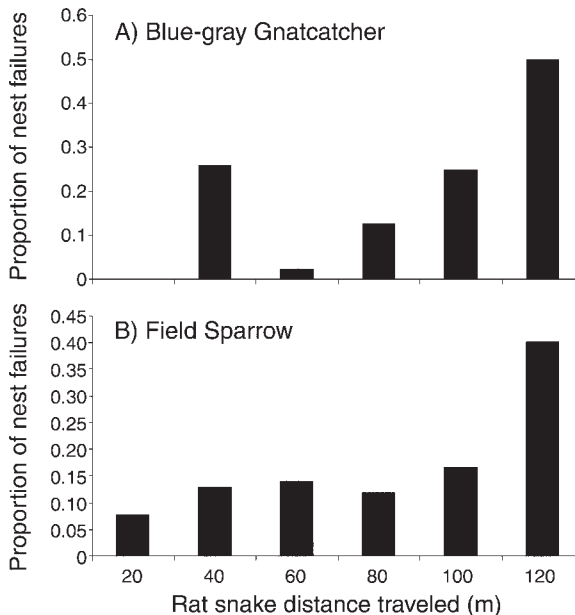

FIG. 3. The number of nests that failed as a proportion of the total nests checked at increasing increments of mean daily rat snake distance traveled (m) for (A) Blue-gray Gnatcatchers and (B) Field Sparrows in southern Illinois in 2003. Only species for which rat snake activity was included as a competing model in logistic exposure nest survival analyses are presented.

PLATE 1. A black rat snake climbing a tree in the Cache River State Natural Area in southern Illinois, USA. Photo credit: G. L. F. Carfagno.

to document all movements by individual snakes rather than estimating snake activity from changes in locations determined every other day. Automated telemetry will make that a realistic possibility (e.g., Crofoot et al. 2008). If this technology is coupled with video monitoring of nests, it will be possible to link the behavior of individual snakes to the attributes of the nests they prey on. For example, it should be possible to identify the features of nests or of parental behavior that apparently made nests of some species more vulnerable to rat snake predation in this study. In a recent study using video cameras, Benson et al. (*in press*) demonstrated that predation patterns associated with specific predators are apparent only when nests preyed on by other predators are excluded from analyses. Data generated by combining telemetry and camera technologies will help us determine both the scope for selection to modify avian nesting behavior to reduce the risk of snake predation and the potential for managers to intervene in this predator–prey relationship to protect nests of birds of conservation concern.

LITERATURE CITED

Askins, R. A. 2000. Restoring North America's birds: lessons from landscape ecology. Yale University Press, London, UK.

Benson, T. J., J. D. Brown, and J. C. Bednarz. *In press*. Indentifying predators clarifies predictors of nest success in a temperate passerine. Journal of Animal Ecology.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. ⟨http://www.spatialecology.com/htools⟩

Blouin-Demers, G., and P. J. Weatherhead. 2001a. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forest. Ecology 82:2882–2896.

Blouin-Demers, G., and P. J. Weatherhead. 2001b. An experimental test of the link between foraging, habitat selection and thermoregulation in black rat snakes (*Elaphe obsoleta obsoleta*). Journal of Animal Ecology 70:1006–1013.

Blouin-Demers, G., and P. J. Weatherhead. 2002. Implications of movement patterns for gene flow in black rat snakes (*Elaphe obsoleta*). Canadian Journal of Zoology 80:1162–1172.

Brawn, J. D., and S. K. Robinson. 1996. Source–sink population dynamics may complicate the interpretation of long-term census data. Ecology 77:3–12.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and mulitmodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Carfagno, G. L. F., E. J. Heske, and P. J. Weatherhead. 2006. Does mammalian prey abundance explain forest-edge use by snakes? Ecoscience 13:293–297.

Carfagno, G. L. F., and P. J. Weatherhead. 2006. Intraspecific and interspecific variation in use of forest-edge habitat by snakes. Canadian Journal of Zoology 84:1440–1452.

Carfagno, G. L. F., and P. J. Weatherhead. 2008. Energetics and space use: intraspecific and interspecific comparisons of movements and home ranges of two Colubrid snakes. Journal of Animal Ecology 77:416–424.

Chalfoun, A. D., M. J. Ratnaswany, and F. R. Thompson III. 2002. Songbird nest predators in forest–pasture edge and forest interior in a fragmented landscape. Ecological Applications 12:858–867.

Crofoot, M. C., I. C. Gilbya, M. Wikelski, and R. W. Kays. 2008. Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. Proceedings of the National Academy of Sciences 105:577–581.

Faaborg, J., M. C. Brittingham, T. M. Donovan, and J. Blake. 1995. Habitat fragmentation in the temperate zone. Pages 357–380 *in* T. M. Martin and D. M. Finch, editors. Ecology and management of neotropical migratory birds. Oxford University Press, New York, New York, USA.

Fitch, H. S. 1963a. Natural history of the black rat snake (*Elaphe o. obsoleta*) in Kansas. Copeia 1963:649–658.

Fitch, H. S. 1963b. Natural history of the racer, *Coluber constrictor*. University of Kansas Publications of the Museum of Natural History 15:351–488.

Fletcher, R. J., Jr., L. Reis, J. Battin, and A. D. Chalfoun. 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? Canadian Journal of Zoology 85:1017–1030.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field–forest ecotones. Ecology 59:871–883.

Heske, E. J., S. K. Robinson, and J. D. Brawn. 1999. Predator activity and predation on songbird nests on forest–field edges in east-central Illinois. Landscape Ecology 14:345–354.

Hoover, J. P., T. H. Tear, and M. E. Baltz. 2006. Edge effects reduce the nesting success of Acadian Flycatchers in a

moderately fragmented forest. Journal of Field Ornithology 77:435–436.

Keller, W. L., and E. J. Heske. 2000. Habitat use by three species of snakes at the Middle Fork Fish and Wildlife Area, Illinois. Journal of Herpetology 34:558–564.

Klimstra, W. D. 1959. Foods of the racer, *Coluber constrictor*, in southern Illinois. Copeia 1959:210–214.

Larivière, S. 2003. Edge effects, predator movements, and the travel-lane paradox. Wildlife Society Bulletin 21:315–320.

Lima, S. L. 2002. Putting predators back into behavioral predator–prey interactions. Trends in Ecology and Evolution 17:70–75.

Marini, M., S. K. Robinson, and E. J. Heske. 1995. Effects of edges on nest predation and nest predators. Biological Conservation 74:203–213.

Martin, T. E. 1988. Processes organizing open-nesting bird assemblages: competition or nest predation? Evolutionary Ecology 2:37–50.

Marzluff, J. M., and M. Restani. 1999. The effects of forest fragmentation on avian nest predation. Pages 5–23 *in* J. A. Rochelle, L. A. Lehmann, and J. Wisniewski, editors. Forest fragmentation: wildlife and management implications. Brill Academic Publishing, Leiden, The Netherlands.

Morse, S. A., and S. K. Robinson. 1999. Nesting success of a migratory songbird in a multiple-use forest landscape. Conservation Biology 13:327–337.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17–26.

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

Ries, L., R. J. Fletcher, Jr., J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. Annual Review of Ecology, Evolution and Systematics 35:491–522.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional effects of forest fragmentation on the nesting success of migratory birds. Science 267:1987–1990.

Robinson, S. K., and D. S. Wilcove. 1994. Impacts of forest fragmentation on breeding populations of neotropical migrants. Bird Conservation International 4:233–249.

SAS Institute. 2004. The SAS system for windows, version 9.1. SAS Institute, Cary, North Carolina, USA.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 128:474–480.

Schmidt, K. A. 1999. Foraging theory as a conceptual framework for studying nest predation. Oikos 85:151–160.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.

Sperry, J. H., D. A. Cimprich, R. G. Peak, and P. J. Weatherhead. 2009. Is nest predation on two endangered bird species higher in habitats preferred by snakes? Ecoscience 16:111–118.

Sperry, J. H., R. G. Peak, D. A. Cimprich, and P. J. Weatherhead. 2008. Snake activity affects seasonal variation in nest predation risk for birds. Journal of Avian Biology 39:379–383.

Stephens, S. E., D. N. Koons, J. J. Rotella, and D. W. Wiley. 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation 115:101–110.

Suarez, A. V., K. S. Pfennig, and S. K. Robinson. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. Conservation Biology 11:928–935.

Thompson, F. R., III. 2007. Factors affecting nest predation on forest songbirds in North America. Ibis 149:98–109.

Thompson, F. R., III, and D. E. Burhans. 2003. Predation of songbird nests differs by predator and between field and forest habitats. Journal of Wildlife Management 67:408–416.

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.

Weatherhead, P. J., G. Blouin-Demers, and K. M. Cavey. 2003. Seasonal and prey-size dietary patterns of black rat snakes (*Elaphe obsoleta obsoleta*). American Midland Naturalist 150:275–281.

Weatherhead, P. J., and M. B. Charland. 1985. Habitat selection in an Ontario population of the snake, *Elaphe obsoleta*. Journal of Herpetology 19:12–19.