

# Landscape forest cover and edge effects on songbird nest predation vary by nest predator

W. Andrew Cox · Frank R. Thompson III ·  
John Faaborg

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**Abstract** Rates of nest predation for birds vary between and within species across multiple spatial scales, but we have a poor understanding of which predators drive such patterns. We video-monitored nests and identified predators at 120 nests of the Acadian Flycatcher (*Empidonax vireescens*) and the Indigo Bunting (*Passerina cyanea*) at eight study sites in Missouri and Illinois, USA, during 2007–2010. We used an information-theoretic approach to evaluate hypotheses concerning factors affecting predator-specific and overall rates of predation at landscape, edge, and nest-site scales. We found support for effects of landscape forest cover and distance to habitat edge. Predation by Brown-headed Cowbirds (*Molothrus ater*) increased, and predation by rodents decreased as landscape forest cover decreased. Predation by raptors, rodents, and snakes increased as the distance to forest edges decreased, but the effect was modest and conditional upon the top-ranked model. Despite the

predator-specific patterns we detected, there was no support for these effects on overall rates of predation. The interactions between breeding birds, nest predators, and the landscapes in which they reside are scale-dependent and context-specific, and may be resistant to broad conceptual management recommendations.

**Keywords** Cause-specific mortality · Forest birds · Nest survival · Passerines

## Introduction

Anthropogenic habitat loss can have pervasive negative effects on wildlife that extend beyond the obvious reduction in habitat. The quality of remaining habitat may also be affected, resulting in reductions in species richness, abundance, and important demographic parameters (Lindenmayer and Fischer 2006). Reduction in the quality of remaining habitat is driven by biotic and abiotic factors that occur at multiple spatial scales. The landscape in which a habitat patch resides influences processes within it, can constrain effects at smaller spatial scales (Harper et al. 2005), and can be the dominant driver of species richness and abundance (e.g., Lindenmayer et al. 2009; Mohd-Azlan and Lawes 2011). Habitat characteristics at the patch scale such as the presence or density of edges can also have a profound influence on biotic processes (Murcia 1995). Further, habitat characteristics at the

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W. A. Cox (✉)  
Department of Fisheries and Wildlife Sciences, University  
of Missouri, 302 ABNR, Columbia, MO 65211, USA  
e-mail: wac253@mail.missouri.edu

F. R. Thompson III  
U.S.D.A. Forest Service Northern Research Station,  
University of Missouri, 202 ABNR, Columbia,  
MO 65211, USA

J. Faaborg  
Division of Biological Sciences, University of Missouri,  
105 Tucker Hall, Columbia, MO 65211, USA

scale of individual territories for animals can influence key demographic parameters such as population densities (e.g., Cornell and Donovan 2010), and rates of reproductive success (e.g., Martin 1992).

The literature on the relative importance of landscape, habitat and local (i.e., nest-site) effects on birds is well developed, as many species have demonstrated sensitivity to factors related to habitat fragmentation and loss at multiple spatial scales (Faaborg et al. 1995). Effects on rates of nest predation for breeding songbirds has been particularly well studied because nest survival is an important component of songbird demography (Donovan and Thompson 2001) and many species have experienced long-term population declines on the breeding (Robbins et al. 1989) and wintering grounds (Faaborg et al. 2010). For example, rates of nest predation may increase for forest songbirds as landscapes become less forested (Robinson et al. 1995), which in combination with a concomitant increase in rates of brood parasitism contributes to reduced population growth rates for songbirds across the United States (Lloyd et al. 2005). Further, proximity to forest edges can further exacerbate this problem by increasing the risk of nest predation for many species even when controlling for other landscape effects (Lloyd et al. 2005).

In many cases, however, habitat fragmentation and edge effects have not had demonstrable effects on nest predation. Edge effects may only be pronounced in moderately fragmented landscapes (Donovan et al. 1997) and more generally may be context dependent, influenced by biogeographic region, habitat type, and nest guild (Batáry and Báldi 2004). Further, in biogeographic regions with historically fragmented forests, nest predation rates may actually decline as fragmentation increases (Tewksbury et al. 1998). Thompson et al. (2002) proposed a hierarchical model to explain these discrepancies, in which factors that affect the risk of nest predation for songbirds operate at multiple spatial scales, with those operating at broad spatial scales providing constraints on local processes.

To explain variation of nest success across spatial scales, most researchers predictably invoke hypotheses about the identification, abundance, and/or activity of nest predators. The taxonomic focus of existing nest predator studies reveals the hypothesized mechanisms behind observed patterns of nest predation, as hypotheses typically focus on changes in abundance or activity of corvids, mesopredators (e.g., raccoons and

opossums), and rodents (e.g., mice and squirrels). Actual tests of such hypotheses are relatively rare and exhibit highly variable results, in part because of the taxon and context-dependent nature of the effects of forest fragmentation (Chalfoun et al. 2002). However, most studies of fragmentation effects on nest predators also suffer from a fundamental problem: the predators being investigated are only putatively important. Identifying species that are dominant nest predators in any habitat has proven difficult because nest predation events are infrequently observed and because artificial nest experiments designed to identify predators are biased (Faaborg 2004). In one study, for example, a predator group (snakes) that commonly depredated real nests was never recorded depredating an artificial nest, and video recordings showed that predators could not be reliably identified from marks made in plasticine eggs (Thompson and Burhans 2004).

Knowledge of important nest predators is imperative if land managers interested in optimizing breeding habitat for songbirds are to better understand why predation rates vary at different spatial scales (Stephens et al. 2003; Lahti 2009). We used video cameras to identify predators at the nests of forest songbirds at eight sites in the midwestern United States that spanned a gradient of landscape forest cover. We evaluated hypotheses regarding the relative importance of landscape, edge, and nest-site factors on predator-specific rates of nest predation. Specifically, we assessed previously invoked hypotheses about the mechanisms that drive increased rates of nest predation as landscape forest cover declines (Robinson et al. 1995) and as the distance to forest edges increases (Hoover et al. 2006). At a local scale we assessed whether nest-site foliage density, a habitat feature known to influence the risk of nest predation (Martin 1992) and one that can be controlled by land managers, influenced predator-specific predation rates. We predicted that landscape forest cover would be the primary determinant of predator-specific rates of predation because it strongly influences overall predation rates (Robinson et al. 1995) whereas edge and nest-site effects are often weak or absent (Burhans and Thompson 1998; Lahti 2001). Based on a review by Chalfoun et al. (2002) of landscape and edge effects on nest predators as well as literature on habitat selection by snakes (Blouin-Demers and Weatherhead 2001; Sperry et al. 2009), we predicted that landscape forest cover would most influence predation by

corvids, rodents, and mesopredators, and edge effects would most influence predation by corvids and snakes. The well established pattern of increased Brown-headed Cowbird (*Molothrus ater*) abundance and brood parasitism with increasing fragmentation (Thompson et al. 2000; Chace et al. 2005) coupled with strong evidence that cowbirds depredate nests (Arcese et al. 1996; Hoover and Robinson 2007) led us to predict that cowbirds would depredate nests more frequently in fragmented landscapes. Finally, we predicted that visually-oriented, diurnal predators such as raptors, corvids and cowbirds would exhibit reduced rates of predation on nests as stem density increased because of decreased nest visibility.

## Methods

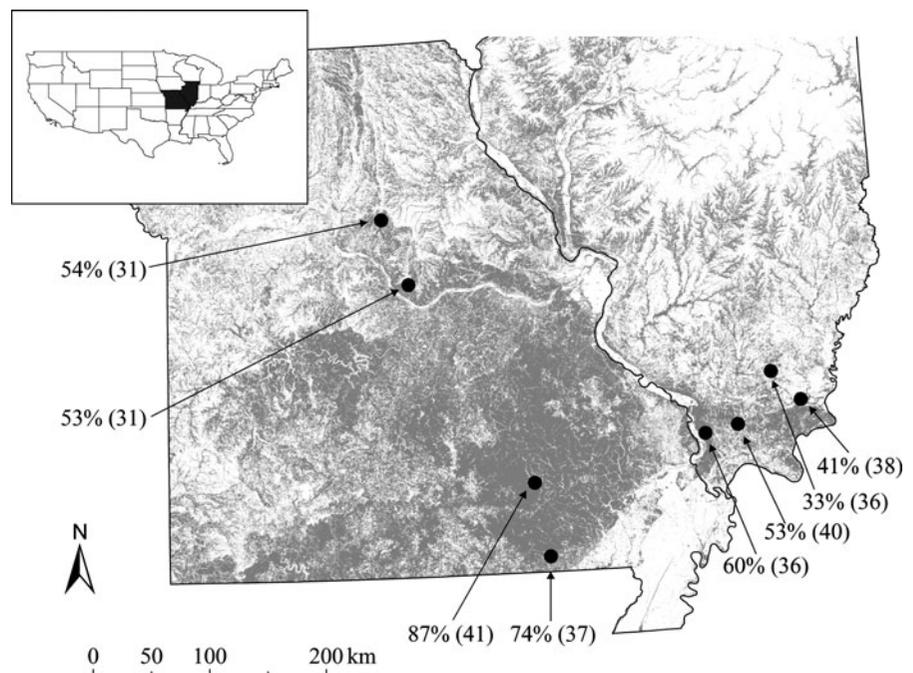
### Data collection

We selected eight study sites in Missouri and Illinois based on the presence of our focal species and a representative range of landscape forest cover in the midwestern United States (Fig. 1). We studied four sites in Missouri in 2007 and 2009 and four sites in Illinois in 2008 and 2010. All sites were >20 km from one another to ensure independence at the landscape

scale. Our focal species were the Acadian Flycatcher (*Empidonax vireescens*) and the Indigo Bunting (*Passerina cyanea*), which have shown differing responses to habitat fragmentation (Robinson et al. 1995). The Acadian Flycatcher typically nests in the sub-canopy of the forest interior, whereas the Indigo Bunting nests in shrubs and saplings near habitat edges and in forest openings with dense understory vegetation. We located nests using systematic search and behavioral cues. We filmed nests using eight vendor-built (Fuhrman Diversified, Inc.) and 16 user-built video systems (Cox et al. 2012a). We placed cameras 0.5–4.5 m from nests and camouflaged all components with small branches, leaves, and other vegetation to reduce the likelihood of the equipment influencing predator behavior (Herranz et al. 2002; Richardson et al. 2009). We did not set up cameras until after all eggs were laid in order to reduce the risk of nest abandonment. We tended to our cameras every 44–52 h to replace the battery and the SD memory card.

We used ArcMap 9.3 (ESRI 2008) to calculate forest and edge metrics for each nest. We merged land cover data for Regions 9, 11, and 12 from the 2001 National Land Cover Database (<http://www.mrlc.gov>) and reclassified land cover as forest (composed of deciduous, evergreen and mixed forests, shrub/scrub, and woody wetlands) or non-forest (all other land

**Fig. 1** Location of eight sites in a study of songbird nest predation in Missouri and Illinois, United States, 2007–2010. Forested habitat is gray and percentages indicate amount of forest cover in a 10 km radius extending from the center of each study site. The sample size of video-monitored nests at each site is in parentheses



types). We calculated percent forest cover in a 10-km radius around each nest using the Zonal Statistics tool in Hawth's Tools (Beyer 2004). We chose a 10-km buffer because it best explains variation in nest predation for forest songbirds in the United States (Lloyd et al. 2005). We digitized edges at our field sites using orthophotos from the 2009 National Agriculture Imagery Program (available at <http://www.apfo.usda.gov/FSA>). We considered all anthropogenic openings (e.g., large agricultural fields, open canopy roads, power lines, and wildlife food plots) as edges because the variation in predator-specific nest predation rates between birds that typically nest in these locations versus the forest interior suggest that the openings are preferentially used by nest predators (Cox et al. 2012b). We did not consider water/forest interfaces as edges. We then used the Nearest Feature tool to calculate the distance between each nest and the nearest edge. Thirteen shrub nests were located just outside the forest canopy in winged sumac (*Rhus copallinum*), blackberry (*Rubus* sp.) or other shrubby patches that composed a soft edge; these were assigned a distance of zero. We calculated stem density at each nest by counting all woody stems and trees greater than 1.3 m in height within a 5.64-m radius (i.e., 100 m<sup>2</sup>).

## Analysis

We used a multinomial logistic regression model programmed in the GLIMMIX procedure (SAS Institute 2008) to estimate rates of nest predation, which allowed us to have more response levels than typical binomial (0 = active, 1 = failed) nest fate approaches. The data consisted of each 24-h interval a nest was filmed and the status or response of each nest at the end of the interval. This approach allows for time-dependent or time-independent covariates and is essentially an extension of nest survival models (Dinsmore et al. 2002; Shaffer 2004) and traditional survival models (Allison 2010) to allow for multiple sources of mortality (Reidy and Thompson 2012). When modeling mortality using logistic regression, precision of parameter estimates depends on the number of mortality events, not the number of intervals an individual survives, so repeated observations of individuals do not represent pseudo replication (Allison 2010). Our response levels were: depredated by corvid, rodent, mesopredator, cowbird, snake, or raptor. Because we were interested in rates

of predation from these predator groups rather than nest survival per se, our final category grouped intervals in which nests were active with failures from predators that did not fall into the first five categories (e.g., other birds, humans), environmental factors, nest abandonment, nestling mortality not caused by predation, and nests with unknown fates (e.g., because of camera failure or technician error). We defined a predation event as the removal of  $\geq 1$  egg or nestling by a predator, but we only counted the initial predation event for nests that lost contents to a predator of the same species across multiple days.

We evaluated eight models representing predator-specific hypotheses of nest predation within an information-theoretic framework (Burnham and Anderson 2002). We ranked models by calculating Akaike's Information Criteria (AIC) and the difference between the top model and other candidate models ( $\Delta$ AIC). We used the  $\Delta$ AIC values to calculate weights ( $w_i$ ) to evaluate the relative support of each model in the candidate set. We considered models within four AIC units of the top-ranked model to be competitive and model-averaged parameter estimates across them.

We limited the complexity of our a priori candidate models because we knew that sample sizes for some predator groups would be small. We did not include a term for study site or year in any of our candidate models. We did not include a term for year because site level measurements were confounded with year effects since sites were visited in alternating years. However, we did evaluate the presence of year effects between Illinois sites in 2008 and 2010 and between Missouri sites in 2007 and 2009 by considering evidence ratios (i.e., ratio of Akaike weights between two models) for our null model versus a model with a term for year. Study site is sometimes included as a random effect in observational studies to account for potential correlated fates of observations from the same site. We could not consider site as a random effect because each site represented only a portion of the range of variation that was encompassed by all sites in one of the main effects of interest, percent forest cover, and therefore was confounded with it. However, in a separate analysis we compared support for a null model, site model, and percent forest cover model and found overwhelming support for the forest cover model. All candidate models included a term for nest stage and nesting species, as each is an important

predictor of predator-specific rates of nest predation (Cox et al. 2012b). A preliminary tolerance analysis of all covariates indicated no multicollinearity (Allison 1999; all tolerance values  $\geq 0.95$ ), so we were able to include any combination of our three covariates (forest cover, distance to edge, stem density) in our models. Our global model included all three covariates. We evaluated a model with only forest cover, but we did not evaluate a model with only edge or stem density as we hypothesized that local effects would be constrained by processes at broader spatial scales (Thompson et al. 2002). We evaluated two models with additive effects of distance to edge or stem density to the anticipated primary effect of forest cover, and we also included a model with a forest cover and edge interaction to represent the hypothesis that magnitude and slope of edge effects could vary across landscapes. In addition, we included models with species interaction terms, as flycatchers and buntings have previously demonstrated differing responses to landscape forest cover (Robinson et al. 1995) and because responses to increased proximity to forest edges can be highly variable (Batáry and Báldi 2004). Given that no more than four nests at any site within a year were depredated by the same predator group and that predator groups at each site almost assuredly consisted of multiple species and multiple individuals within each species, we did not attempt to account for spatial autocorrelation in our models.

We generated predicted probabilities of daily predator-specific rates of predation using unconditional (i.e., weighted model-averaged) parameter estimates across a range of covariate values that was representative of our sample. We generated predicted probabilities of overall predation by collapsing all predator response levels into one category, which also included predators that fell outside of the groups we tested [e.g., Yellow-billed Cuckoos (*Coccyzus*

*americana*), Wild Turkey (*Meleagris gallopavo*)]. We present unconditional parameter estimates with 95% confidence intervals; in some cases we also reference 85% confidence intervals for parameters in the top model to explain model selection results because model selection based on AIC supports parameters informative at this level (Arnold 2010).

## Results

We video-monitored 175 Acadian Flycatcher nests and 115 Indigo Bunting nests for a total of 3592 observation days during 2007–2010. We recorded 120 predation events from species that fell into the six predator groups. Predators included 44 raptors, 26 snakes, 21 corvids [18 were Blue Jays (*Cyanocitta cristata*)], 16 rodents, nine cowbirds, and four mesopredators. All nest contents were consumed at 113 of the 120 (94%) nests; at least one nestling successfully fledged concomitant with or after the predation event at the remaining seven nests. The mean distance between video-monitored nests at each site within a year was  $1211.7 \pm 14.4$  m ( $n = 2529$ ; 5%: 203.9 m, 95%: 2520.3 m), and we did not record multiple predator species at any nest. Study sites ranged from approximately 33–87% forest cover in a 10-km radius surrounding their center (Fig. 1). Nests for both species had similar levels of forest cover and similar stem densities, but bunting nests were typically much closer to forest edges (Table 1).

In our evaluation of year effects, evidence ratios suggest that the null model was supported 80.6 and 2.5 times more than the model with year for Missouri and Illinois, respectfully, so we concluded year effects were not important and did not confound interpretation of the fixed effects of interest in our study. The top ranked model from our set of eight candidate models

**Table 1** Mean, median, minimum, and maximum values of covariates used in analysis of predator-specific predation on songbird nests in Missouri and Illinois, 2006–2010

Variable	Acadian Flycatcher ( <i>N</i> = 175 nests)				Indigo Bunting ( <i>N</i> = 115 nests)			
	Mean	Median	Min	Max	Mean	Median	Min	Max
Forest cover (%/10 km <sup>2</sup> )	58.2	53.0	32.2	88.4	56.8	53.4	32.3	88.3
Distance to edge (m)	208.4	132.5	9.3	1164.2	52.3	14.7	0.0	850.6
Stems per 100 m <sup>2</sup>	25.8	24.0	2.0	126.0	25.0	22.0	0.0	93.0

included terms for landscape forest cover and distance to edge, whereas the second ranked model only included a term for landscape forest cover (Table 2). The top two models comprised 85% of the total weight of evidence and no other model was within four AIC units, so we calculated unconditional parameter estimates based on these two models. We concluded the effects of forest cover and edge on predator-specific rates of predation were similar for Acadian Flycatchers and Indigo Buntings and calculated predicted probabilities of predation for both species combined since there was no support for an interaction term for species (Table 2). The probability of predation by Brown-headed Cowbirds decreased with increasing landscape forest cover, whereas predation by rodents increased with increasing forest cover (Fig. 2a). Increased forest cover modestly increased the probability of predation by raptors and decreased the probability of predation by snakes, but model-averaged confidence intervals for these groups included zero (Fig. 2a). The magnitude of the effects of forest cover on predation rates by corvids and for overall predation was smaller yet (Fig. 2a).

We found support for the effect of distance to edge on nest predation. Based on model weights, the top model with edge effects was supported 1.75 times more than the next best model without edge effects (Table 2), but due to model selection uncertainty, unconditional parameter estimates for edge effects had 95% confidence intervals that included zero (Fig. 2b). Parameter estimates conditional on the top-ranked

model, however, suggested that overall rates of predation increased near forest edges ( $\beta = -0.0015$ ; 95% CI:  $-0.0029, -0.0001$ ), which may have been a consequence of the cumulative effect of edges on several predator groups; the probability of predation by raptors ( $\beta = -0.0020$ ; 85% CI:  $-0.0038, -0.0002$ ), snakes ( $\beta = -0.0054$ ; 85% CI:  $-0.0097, -0.0011$ ), and rodents ( $\beta = -0.0032$ ; 85% CI:  $-0.0061, -0.0003$ ) all tended to increase near forest edges.

## Discussion

We found support for our hypothesis that landscape forest cover influenced the probability of predation by cowbirds and rodents, but the most frequent predators (snakes, raptors, corvids) exhibited no response and overall rates of predation were invariant across the gradient of forest cover. Our top-ranked model indicated the presence of edge effects on overall predation rates and, to a lesser extent, on predation by rodents, raptors, and snakes. But these effects were modest and were not strongly supported in our unconditional model that averaged effects across the top models. Our results reinforce the importance of scale considerations and the strong influence of landscape scale factors on processes within habitat patches, but some of the predators influenced by forest composition and edge effects differed from our a priori predictions.

**Table 2** Model selection results for a priori candidate models describing predator-specific patterns of nest predation for Acadian Flycatchers and Indigo Buntings in the midwestern United States, 2007–2010

Model	$-2\text{Log}(L)$	$K^a$	AIC <sup>b</sup>	$\Delta\text{AIC}^c$	$w_i^d$
Forest cover + edge	1319.20	30	1379.20	0.00	0.54
Forest cover	1332.29	24	1380.29	1.09	0.31
Null	1347.51	18	1383.51	4.31	0.06
Forest cover + edge + stem	1312.37	36	1384.37	5.17	0.04
Forest cover + stem	1325.72	30	1385.72	6.52	0.02
Forest cover $\times$ edge	1337.80	24	1385.80	6.60	0.02
Edge $\times$ species	1339.42	24	1387.42	8.22	0.01
Forest cover $\times$ species	1342.81	24	1390.81	11.61	0.00

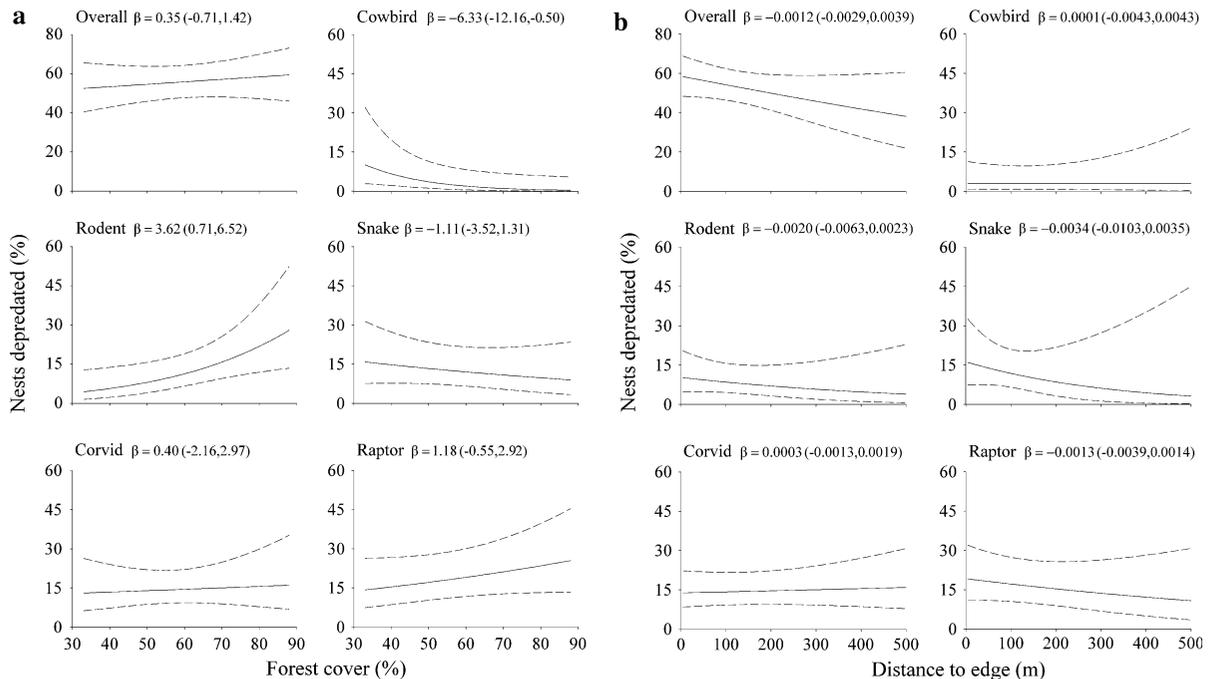
All models include terms for bird species and nest stage

<sup>a</sup> Number of parameters in the model

<sup>b</sup> Akaike's Information Criteria

<sup>c</sup> The difference between the current and top-ranked model's AIC<sub>c</sub> score

<sup>d</sup> Weight of evidence supporting the model



**Fig. 2** Modeled percentage of nests that lost  $\geq 1$  egg or nestling to a predator across the incubation and nestling periods as a function of **a** landscape forest cover and **b** proximity to a forest edge for two species of songbirds in the Midwestern United States, 2007–2010. The range of forest cover depicted in **a** represents the entire gradient sampled. Ninety percent of Acadian Flycatcher nests and  $>95\%$  of Indigo Bunting nests were within the range of edge distances in **b**. Inadequate sample size ( $N = 4$ ) precluded us from modeling rates for

mesopredators. Rates were estimated from parameters averaged across the two top-ranked models, with species and nest stage held constant. Rates are derived from daily probabilities of predation raised to the 24th power, which is the number of days of the post-lay nesting cycle averaged across both species. Dashed lines indicate 95% confidence intervals. Unconditional parameter estimates ( $\beta$ ) are presented with 95% confidence intervals in parentheses

### Effect of forest cover on nest predators

Some predator groups that have long been hypothesized to drive increased nest predation associated with reduced landscape forest cover either did not contribute meaningfully to overall rates of predation or were not influenced by landscape forest cover. Nearly half of the tests of landscape effects on nest predators reviewed by Chalfoun et al. (2002) focused on corvids and mesopredators, but neither group contributed to spatial variation in predation rates in this study. Predation by corvids was invariant across the gradient of forest cover, and mesopredators contributed so little to overall predation rates that we could not generate model-based estimates of predation for them. Rodents have also been hypothesized to drive landscape scale variation in nest survival (Chalfoun et al. 2002) and there is evidence that mouse densities are lower in continuous landscapes in the midwestern United States (Nupp and Swihart

2000). We detected a relationship between forest cover and predation by rodents (primarily *Peromyscus* sp.; Cox et al. 2012b), but its direction was opposite of what we predicted; rodents were essentially absent as nest predators in the least forested landscapes but were among the most important contributors to overall predation rates in highly forested landscapes. The unexpected response of rodents may in part reflect the problematic nature of grouping species. For example, two of 16 rodent predation events were by Southern Flying Squirrels (*Glaucomys volans*), densities of which increase as forests become more continuous (Nupp and Swihart 2000).

Cowbirds were the only predator that responded as predicted; they were absent as nest predators where forest cover was high and became increasingly important as forest cover decreased. Factors that influence the abundance and distribution of cowbirds are well studied (reviewed in Chace et al. 2005), as are

their impacts as brood parasites on the demography of host species (Trine et al. 1998). Recent video evidence (e.g., Benson et al. 2010) and strong indirect experimental evidence (Arcese et al. 1996; Smith et al. 2003; Hoover and Robinson 2007) confirm the importance of cowbirds as nest predators, but this component of their ecology has rarely been integrated into spatially explicit research on nest predation (zero tests for landscape or edge effects in Chalfoun et al. 2002). Given that they are nest predators and that their abundance increases with decreasing landscape forest cover (Thompson et al. 2000; Chace et al. 2005), it is not surprising that the risk of predation from cowbirds increases as well. Nevertheless, it remains unclear whether they are an important driver of overall increased rates of nest predation in less forested landscapes as seen in Robinson et al. (1995). Increased predation rates by cowbirds appeared to be compensated for by decreased predation from rodents, with overall predation rates remaining constant across the forest cover gradient. Further, even at the low end of the gradient where their impact was greatest, cowbirds accounted for a small fraction ( $\sim 13\%$ ) of the overall predation rate. Given that the brood parasitism rates we observed (maximum rate for a field site was 33% for buntings and 29% for flycatchers; W.A. Cox unpublished data) are substantially lower than what was been found elsewhere (e.g., Thompson et al. 2000; Tewksbury et al. 2006), greater insights into whether cowbirds drive increased rates of predation in landscape with little forest cover may require sampling in areas that are less forested (i.e.,  $<30\%$ ) and have higher parasitism rates than those we studied.

#### Effect of edges on nest predators

Edge effects on nest predation occur infrequently (Lahti 2001) and studies investigating predator-specific responses to edges usually fail to detect effects on predator abundance or activity (Chalfoun et al. 2002). Our evidence for edge effects on predator-specific rates of predation was conditional upon the top-ranked model and only had modest statistical support; it should therefore be considered exploratory. We may have lacked the temporal replication required to detect strong edge effects (Stephens et al. 2003) or may have benefitted by incorporating edge type into our analysis (Murcia 1995; but see Chapa-Vargas and Robinson 2006). In addition, edge effects are not always linear

with respect to landscape forest cover (Donovan et al. 1997), but concerns about model complexity precluded us from including additional terms in our models.

Nevertheless, several patterns emerged that are worth noting. First, all three predator groups (raptors, snakes, rodents) that demonstrated edge effects were influenced by edge in the predicted direction (i.e., increased predation rates near edges), which resulted in a cumulative effect of substantial support for edge effects conditional upon the top-ranked model. Second, raptors are frequent nest predators at our study sites and others (Benson et al. 2010; Conner et al. 2010) but we are not aware of any studies that have attempted to link them to spatial patterns of songbird nest predation. Studies on habitat use and resource selection by raptors in relation to landscape characteristics are needed if we are to better understand whether they positively respond to edges. Third, snakes had the largest parameter estimate of all predator groups for the edge term in the top-ranked model. The majority of depredation events by snakes were attributed to Black Rat Snakes (*Elaphe obsoleta*; Cox et al. 2012b), which have demonstrated preferences for edge habitat in past studies (Blouin-Demers and Weatherhead 2001; Sperry et al. 2009). Estimating snake densities is notoriously difficult (Weatherhead et al. 2010), but given their response to edge habitat and their importance as nest predators in different habitat types (Weatherhead and Blouin-Demers 2004; Thompson 2007), more work on how snake abundance and activity changes in response to landscape forest cover and habitat characteristics is needed. Finally, rodents were the only predator group to respond to both forest cover and edge effects, but they did so in a rather unintuitive way; rodent predation was highest in continuous landscapes where edge densities are lowest (Faaborg et al. 1995) and where edge effects are often absent in the Midwest (Donovan et al. 1997). Further, mouse densities in the Midwest may actually be lower near forest edges (Wolf and Batzli 2002) because of increased rates of predation near edges (Morris and Davidson 2000; Wolf and Batzli 2004). Clearly, estimation of predator abundance in conjunction with the use of cameras at nests would further strengthen our understanding of the mechanisms behind spatial variation in nest predation and may clarify such seemingly contradictory patterns.

## Conclusion and management implications

Many landscape metrics often fail to explain variation in songbird nest survival (Cottam et al. 2009; Falk et al. 2011). We detected substantial forest cover effects and modest edge effects on multiple nest predator groups, but none of our metrics were correlated with model-averaged overall rates of nest predation. These results exemplify the complex nature of nest predation and point to the difficulty in generalizing patterns of predation. The suite of predator groups we documented depredating flycatcher and bunting nests responded differently to factors at local and landscape scales, a scenario that may be the rule rather than the exception (Tewksbury et al. 2006; Klug et al. 2009; Benson et al. 2010). Potential interactions among predators probably further complicate our ability to predict forest cover and habitat effects on nest survival; many of the predator species we documented depredating nests also prey upon one another.

The complexity of the nest predator community highlights several challenges facing managers attempting to optimize habitat for breeding songbirds. First, landscape forest cover exerted the strongest influence on predator-specific rates of predation, with only modest edge effects and no nest-site effects apparent. These results are concordant with other studies that suggest landscape scale factors are often the dominant driver of biological processes (Lindenmayer et al. 2009; Mohd-Azlan and Lawes 2011) and can constrain processes at more local scales (Donovan et al. 1997; Thompson et al. 2002). Managers often have little control over landscape characteristics, however, making it difficult to implement effective management plans. Further, a local factor that managers do have control over (stem density) did not influence the risk of predation from any predator group. Second, interactions among predators and their varying responses to features at multiple spatial scales suggest that managing habitat to reduce the impact of one predator group may result in compensatory predation by another guild. Third, we have long recognized that spatial patterns of nest predation can differ across biogeographic regions because predator communities and ecology are often markedly different (Thompson 2007). For example, we recorded just two predation events by sciurids, but Red squirrels (*Tamiasciurus hudsonicus*) are thought to drive

landscape-scale patterns of nest predation in the Western United States (Tewksbury et al. 1998). But our study demonstrates that managers cannot assume that the suite of predators primarily responsible for nest failure at one site is the same at another even when the same predator species exist at both sites. Finally, even though the lack of an interaction term in the top-ranked model suggested that flycatchers and buntings responded similarly to landscape forest cover, this may not be true for ground or canopy nesting species. Habitat effects across spatial scales are often species-specific for birds (Robinson et al. 1995) and other taxa (Cushman 2006); larger or smaller species or those with different breeding phenologies or nest site locations may exhibit substantially different responses to the metrics we measured. Ultimately, the interactions between breeding birds, nest predators, and the landscapes in which they reside are scale-dependent and context-specific and may be resistant to broad conceptual management recommendations.

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