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Research Article

Cropland Edge, Forest Succession, and Landscape Affect Shrubland Bird Nest Predation

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ABSTRACT The effects of habitat edges on nest survival of shrubland birds, many of which have experienced significant declines in the eastern United States, have not been thoroughly studied. In 2007 and 2008, we collected data on nests of 5 shrubland passerine species in 12 early successional forest patches in North Carolina, USA. We used model selection methods to assess the effect of distance to cropland and mature forest edge on nest predation rates and additionally accounted for temporal trends, nest stage, vegetation structure, and landscape context. For nests of all species combined, nest predation decreased with increasing distance to cropland edge, by nearly 50% at 250 m from the cropland edge. Nest predation of all species combined also was higher in patches with taller saplings and less understory vegetation, especially in the second year of our study when trees were 4–6 m tall. Predation of field sparrow (*Spizella pusilla*) nests was lower in landscapes with higher agricultural landcover. Nest predation risk for shrubland birds appears to be greater near agricultural edges than mature forest edges, and natural forest succession may drive patterns of local extirpation of shrubland birds in early successional forest patches. Thus, we suggest that habitat patches managed for shrubland bird populations should be considerably large or wide (>250 m) when adjacent to crop fields and maintained in structurally diverse early seral stages. © 2011 The Wildlife Society.

KEY WORDS agricultural landscapes, early successional, habitat edge, nest predation, shrubland birds.

Predation is often the primary source of songbird nest failure and can have a significant influence on bird population dynamics (Martin 1992*a*, Donovan et al. 1995, Donovan and Thompson 2001). Populations of forest- and grassland-interior songbirds often experience higher rates of nest predation near habitat edges (e.g., Gates and Gysel 1978, Andrén and Angelstam 1988, Johnson and Temple 1990, Paton 1994, Winter et al. 2000). However, meta-analyses of edge effects on nest predation have not revealed a consistent pattern, and researchers have discovered that edge effects vary depending on surrounding landscape context and regional predator communities (Andrén 1995, Donovan et al. 1997, Heske et al. 2001, Lahti 2001, Chalfoun et al. 2002*a*).

Studies of avian nest predation in early successional forest and shrubland habitats (collectively, shrubland habitats) reflect the same inconsistency. Some studies failed to document negative edge effects on shrubland bird nest survival, whereas other studies showed that edge effects varied by edge type, bird species, and year (Chasko and Gates 1982, Suarez et al. 1997, King et al. 2001, Woodward et al. 2001, King and Byers 2002). Clarification of edge effects on nest predation is especially critical for shrubland bird populations, which have experienced more drastic declines than mature forest-breeding birds in the eastern United States (Askins 1993). Also, because edge effects vary by region and across landscape types, a more geographically complete picture of edge effects is needed (Paton 1994). Most studies of edge effects on shrubland bird nests are from forest-dominated landscapes in the northeastern and midwestern United States; agricultural landscapes and the southeastern United States remain under-represented (but see Riddle and Moorman 2010). Furthermore, higher predation risk at habitat edges has been hypothesized as a possible mechanism for edge avoidance and area-sensitivity behavior exhibited by several shrubland passerines (Schlossberg and King 2008, Ribic et al. 2009). Before this hypothesis is advanced, patterns of high predation risk near habitat edges in shrubland birds must be more clearly documented.

Edge effects may be difficult to detect because they can be obscured by other factors not accounted for in simplified study designs using traditional nest survival estimation techniques (i.e., the Mayfield estimator 1961). Recent developments in nest survival modeling represent an improvement over the commonly used Mayfield estimator because they go beyond comparisons of grouped nests and can assess the importance of multiple factors on nest survival, including variables specific to individual nests (reviewed in Jones and

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Guepel 2007). Using these methods, edge effects can be examined more directly by including a nest-specific distance-to-edge covariate in regression models rather than testing for differences among groups of nests placed in arbitrary distance-to-edge categories. These methods also can account for variation in nest-specific variables that can lead to biased estimates of nest survival, such as seasonal variation and differential survival among nest stages (Grant et al. 2005). Other site- or nest-specific variables that may influence predator abundance or a predator's ability to find nests, such as landscape composition and vegetation characteristics, can be modeled as well.

We examined the effects of habitat edges on nest predation of shrubland birds in agricultural landscapes. We modeled daily nest predation (DNP) relative to distance to mature forest and cropland edges and improved our ability to detect effects by incorporating additional variables that may influence nest predation, such as temporal variation, nest stage, vegetation structure, and landscape context. We sought to identify how these factors influenced nest predation through predictive modeling of DNP rates.

STUDY AREA

We studied shrubland bird nest predation in 12 early successional forest habitat patches located in northeastern North Carolina during the 2007 and 2008 breeding seasons. The patches were planted 3–7 yr prior to our study as forested riparian buffers in the North Carolina Conservation Reserve Enhancement Program (CREP). This state and federal cooperative program provides monetary incentives to private landowners to restore agricultural land near streams and other waterways to natural vegetation. The landscape surrounding our patches was a mosaic of forested and cultivated land, though there was noticeable local variation in percentages of these 2 landcover types. Dominant forest types were second-growth and mature pine (*Pinus* spp.)–oak (*Quercus* spp.) woodlands in the uplands and gum (*Nyssa* spp.)–cypress (*Taxodium* spp.) swamps in low-lying areas. The most common crops grown in the region were corn, soybeans, cotton, and tobacco.

METHODS

Site Selection

We selected patches of various sizes and shapes to acquire a sample of nests with a wide range and distribution of distance-to-habitat-edge values. Patches ranged in size from 2.2 ha to 24.9 ha, with a mean and median area of 7.4 ha and 4.0 ha, respectively. Patches varied in shape from nearly linear patches 40 m wide to nearly square or triangular-shaped patches. Each patch had roughly equal proportions of adjacent habitat edge types—approximately half mature forest, half cropland. All patches were established by planting loblolly pine (*Pinus taeda*) in rows, generally in a 3-m by 3-m grid. Various species of hardwood trees (most commonly, *Quercus* spp.) also were planted in some of the patches but never constituted more than 20% of the total patch area. Natural regeneration of grass, forbs, shrubs, and trees occurred on all sites, but structure and composition of naturally regenerated vegetation varied within and among sites because of differences in soil characteristics, seed sources, and landowners' mowing and herbicide treatments. All patches were separated by at least 2 km.

Nest Monitoring

We searched the 12 habitat patches for nests of blue grosbeak (*Passerina caerulea*), field sparrow (*Spizella pusilla*), indigo bunting (*P. cyanea*), prairie warbler (*Dendroica discolor*), and yellow-breasted chat (*Icteria virens*). All 5 focal species are open cup nesters that generally nest in shrubs or young trees, most often within 4 m of the ground. We conducted ≥ 2 complete searches of each patch during the 2007 and 2008 breeding seasons by systematically walking rows of planted trees and searching available shrub and tree nest substrates. We searched during the period 8 May to 30 July and randomized the order in which we searched patches the first time. We conducted the second search approximately 1 month after the first. We found additional nests opportunistically or with partial searches focused on bird behavior. We monitored all nests every 3–4 days to record nest stage, number of eggs or nestlings, parental activity, brown-headed cowbird (*Molothrus ater*) nest parasitism, and nest fate. We determined the transition between the incubation and nestling stage based on presence of both eggs and nestlings in the nest or by aging nestlings based on development patterns. For nests found in the nest building stage, we recorded the date when the first egg was laid, or we estimated that date based on the assumption that birds laid one egg per day. We considered a nest from which ≥ 1 nestling fledged as a successful nest. When we could not locate fledglings near a nest, we determined success or failure based on nest evidence (e.g., droppings in the nest, nest condition) and parental behavior (e.g., carrying food, frantic calling). We determined cause of nest failure as depredation (eggs or nestlings were removed from the nest or destroyed), desertion (we observed no adult activity at or around the nest for >2 weeks), parasitism (parasitized by brown-headed cowbirds and no nestlings of the host species survived to fledging), or weather (nests knocked down or eggs or nestlings ejected due to extreme weather events). We determined the Universal Tranverse Mercator coordinates of each nest with a Global Positioning System (GPS) unit, and used this location to measure the straight-line distance to the nearest cropland and mature forest edge in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA).

Patch Characteristics

We measured vegetation within each patch between 15 June and 1 August of both years using a reduced version of the BBIRD protocol (Martin et al. 1997). We randomly sampled 5 pairs of concentric 5-m- and 11.3-m-radius circular plots. We took vegetation measurements in both years at the same 5 points in each patch and included vegetation height, woody stem density, and ground cover estimates. We measured vegetation height by selecting one shrub or sapling within each 11.3-m-radius plot that visually appeared to represent the average height of the dominant shrubs or saplings in the plot, and then we averaged this value over all 5 plots. We counted the number of small woody plant stems (0.5–3 m tall) with their base inside the 5-m-radius plot. We added counts from all 5 sample plots and calculated small woody stem density as stems/m^2. Woody plants <0.5 m tall were accounted for in visual estimates of ground cover, which we separated into 4 types: bare ground–litter, graminoid, forb, and woody. We estimated percent of each cover type within the 5-m plots and averaged these estimates across all 5 plots in a habitat patch.

We delineated the cropland and mature forest edges of individual patches using spatially referenced aerial photo data and on-screen digitizing in ArcGIS 9.2. We did not consider narrow strips of early-successional habitat <10 m wide that were connected to a patch as part of that patch. We measured landscape context by quantifying the proportion of agricultural cover within 2.5 km of the edge of each habitat patch. We based habitat type designations on the 2001 National Landcover Dataset (NLCD), which was created from 2001 Landsat satellite imagery (Homer et al. 2004). Agricultural cover combined the total percentage of 2 NLCD cover types: cultivated crops and pasture/hay. We chose to measure habitat at this landscape scale (approximately 20 km^2) for 2 reasons: 1) to make comparisons with another study in the region that used the same scale and observed greater shrubland bird nest success in agricultural-dominated landscapes than forest-dominated landscapes (Riddle and Moorman 2010) and 2) because it is sufficiently large to influence the abundance of common nest predators in our study area, even those with larger home ranges, such as raccoons (*Procyon lotor*; Gehring and Swihart 2003). Five of our 2.5-km landscapes partially overlapped with landscapes of a neighboring patch. Although this overlap among landscapes may constitute a degree of pseudoreplication, we believe that inclusion of this covariate into our modeling can still lead to useful explanations of how landscapes might affect nest survival (Hargrove and Pickering 1992).

Data Analysis

We evaluated the evidence for an effect of distance-to-edge on DNP using an information-theoretic model selection approach (Burnham and Anderson 2002). We created a set of generalized linear models of daily nest survival relative to distance-to-edge and other nest- and patch-specific covariates in Program MARK, which compares competing models using Akaike's Information Criterion (AIC; Akaike 1973, Dinsmore et al. 2002). We included only successful and depredated nests in our analysis, which allowed us to later convert daily nest survival estimates computed in MARK into DNP rates (1—daily nest survival). Although we acknowledge that other sources of nest failure such as nest abandonment and parasitism may be natural processes and an important component of nest survival, we wanted to focus specifically on identifying only nest predation risk relative to nest and patch characteristics. We considered the effects of a common set of covariates on DNP of all 5 species combined and for field sparrow and indigo bunting separately, 2 species for which we had adequate sample sizes. We believe that pooling of nest data across all 5 species was justified because all of these species build open-cup nests at similar heights from the ground and the duration of their nesting cycle and nesting seasons correspond. We modeled the following 5 covariates and developed a priori hypotheses about how each might influence nest predation:

1. Between- and within-year temporal patterns: Differences in nest predation between years may be caused by factors such as yearly increases in regional or local nest predator abundance (e.g., Rotenberry and Wiens 1989). Nest predation rates also may vary within a breeding season because of seasonal changes in nest-concealing vegetation or seasonal variability in predator abundance and movement (Burhans et al. 2002, Grant et al. 2005). We did not hypothesize any particular pattern relative to temporal effects. However, because within-season temporal variation has been observed to be nonlinear for some shrubland breeding passerines, we considered both linear and quadratic within-season trends in our modeling (Grant et al. 2005, Burhans et al. 2010).
2. Nest stage: Predation rates of passerine nests can differ among and within the egg-laying, incubation, and nestling stages (Burhans et al. 2002, Grant et al. 2005). Because we did not determine exact nest age, we grouped nests in the laying and incubation stages together into an egg stage. We hypothesized that DNP would be higher in the nestling stage than the egg stage because of increased activity at the nest associated with feeding nestlings, but we did not hypothesize any specific trends within nest stages.
3. Distance to mature forest and cropland edge: We hypothesized nests closer to habitat edges would have higher DNP rates because nest predators may use edges more readily than other habitats (e.g., Durner and Gates 1993, Dijak and Thompson 2000, Chalfoun et al. 2002*b*). However, because nest predation rates may differ at different types of edges, we expected that the distance-to-edge effect might differ between our 2 edge types (Suarez et al. 1997). Thus, we included 2 separate covariates: nest distance from a mature forest edge and nest distance from a cropland edge.
4. Within-patch shrub–sapling height: Nest predation often is lower in more heterogeneous habitats with dense foliage because these habitats provide better concealment for nests and make searching more difficult for nest predators (Martin 1993, Moorman et al. 2002). Our most direct estimates of nest concealing vegetation, ground cover and small woody stem density, had high variances (e.g., mean proportional standard error (PSE) = 0.54 for % bare ground cover and PSE = 0.88 for small woody stem density), so we used mean shrub–sapling height as a surrogate because we could more precisely estimate it (PSE = 0.16) and because we expected nest-concealing

understory vegetation to decrease as it was shaded out by increasingly taller trees. Because of the loss of nest-concealing understory cover as trees get taller, we hypothesized that nest predation would be higher in patches with high mean shrub–sapling height.

5. Percent agriculture within 2.5 km of patch: Preliminary evidence suggests that nest survival may be higher in agriculture-dominated landscapes for some shrubland bird species in this region (Riddle and Moorman 2010). Thus, we hypothesized that patches in landscapes with higher percent agriculture within 2.5 km would have lower nest predation. Though we make this specific hypothesis, we consider our assessment of this covariate's effect as exploratory, especially given the overlap in some of the 2.5-km landscapes in our study, which limits us to more inductive inferences (Hargrove and Pickering 1992).

We modeled the 2 categorical covariates, nest year and stage, as group covariates in Program MARK, resulting in a total of 4 groups. To model within-year and within-stage variation in nest predation, we allowed nest predation to vary over time (day of season) within year and within nest stage groups and fit the data to either a linear or quadratic trend (denoted as T or TT, respectively). The remaining covariates—distance to mature forest edge, distance to cropland edge, mean shrub–sapling height, and percent agriculture within 2.5 km—were continuous covariates. The latter 2 covariates were patch-specific and we assigned all nests found in a patch the shrub–sapling height and percent agriculture value of that patch.

We used a hierarchical modeling approach where we modeled temporal and nest stage effects as nuisance parameters first and then added the additional habitat and distance-to-edge covariates to the best of these models (Dinsmore and Dinsmore 2007; see Table 1 for models described below). This approach reduced the total number of models fit while still accounting for the most important nuisance parameters in our habitat models. We first fit an intercept-only model where we estimated DNP across all groups (hereafter the constant predation model; model 1). Next, we modeled differences in DNP between years and stages (models 2 and 3). Then we modeled linear (T) and quadratic (TT) trends in DNP within each year and each stage (models 4–7). To the single best model from these first 7 models (ΔAIC = 0) we added our remaining covariates. First, we modeled the effects of distance to forest edge and distance to cropland edge singly and then combined (models 8–10). We then modeled the effects of shrub–sapling height and percent agriculture within 2.5 km singly and combined (models 11–13). Because of considerable tree growth between 2007 and 2008 (mean increase in shrub–sapling height across all 12 patches = 1.6 m, SE = 0.6), we expected the effect of shrub–sapling height to differ each year. For this reason, we modeled an interaction term between temporal effects (e.g., year) and shrub–sapling height in models where the 2 effects were combined. Finally, we added the shrub–sapling height and percent agriculture covariates to each of the 3 distance-to-edge covariate models singly and combined (models 14–22). Each continuous covariate appeared in 8 models. We fit all models using a logit link function and thus we reported estimates of covariate effects (hereafter, betas or estimates) on the logit scale.

Table 1. Model set and number of model parameters (*K*) for modeling daily nest predation of shrubland birds in North Carolina, USA, 2007 and 2008 relative to nest- and patch-specific covariates using Akaike's Information Criterion model selection. "T" and "TT" denote linear and quadratic trends in daily nest predation, respectively. Continuous covariates included are: distance to mature forest edge (DE For), distance to cropland edge (DE Crop), mean shrub–sapling height (SSHgt), year and mean shrub–sapling height interaction (Year × SSHgt), and percent agriculture cover within 2.5 km (PctAg).

Model	*K*
1) Constant predation	1
2) Year	2
3) Stage	2
4) T within years	3
5) TT within years	5
6) T within stages	3
7) TT within stages	5
8) (Best 1–7) + DE For	(Best 1–7) + 1
9) (Best 1–7) + DE Crop	(Best 1–7) + 1
10) (Best 1–7) + DE For + DE Crop	(Best 1–7) + 2
11) (Best 1–7) + SSHgt + (Year × SSHgt)	Variable
12) (Best 1–7) + PctAg	(Best 1–7) + 1
13) (Best 1–7) + SSHgt + (Year × SSHgt) + PctAg	Variable
14–16) (Model 8) + (Models 11–13)	Variable
17–19) (Model 9) + (Models 11–13)	Variable
20–21) (Model 10) + (Models 11–13)	Variable

To identify which covariates in our models were good predictors of nest predation, we assessed the strength of evidence from our model selection results first by identifying covariates that appeared consistently in the best models in the set and then examined the beta estimates of covariate effects. Instead of making inferences based on beta estimates from a single best model, we calculated model averaged beta estimates and their 95% confidence intervals for each of the continuous covariates—distance to forest edge, distance to cropland edge, shrub–sapling height, interactions between shrub–sapling height and temporal effects, and percent agriculture. Model averaged estimates are an average of all the estimates of a particular covariate across models containing that covariate, weighted by each model's Akaike weight (Burnham and Anderson 2002). Model averaged estimates are an improvement over single-model estimates because the former account for uncertainty in the model selection process. Program MARK calculates beta estimates and 95% confidence intervals relative to nest survival, so we changed the sign of our model averaged betas and adjusted the confidence interval to reflect the covariates' effect relative to nest predation. Because model selection methods consider weight of evidence rather than results of statistical hypothesis tests, we do not indicate whether beta estimates were significant. Instead, we considered model averaged beta estimates with 95% confidence intervals that did not overlap zero to be strong evidence of a covariate effect. If an estimate's confidence interval increasingly overlapped zero, the certainty with which we could say a covariate effect was in fact positive or negative was weakened and the evidence for a biological effect weakened accordingly.

Once we identified covariate effects with strong support in each analysis, we used the model that contained all of these covariates and their beta estimates to predict changes in DNP across a range of covariate values. To examine covariate effects individually, we fixed values for all but one covariate in the model and calculated an estimate of DNP back-transformed from the logit scale for a range of values and then graphed the results. We predicted changes in DNP only within the range of covariate values in our study.

A key assumption of Program MARK nest survival models is that the fates of all nests in a sample are independent (Dinsmore et al. 2002). Although nests in each of our study patches were distributed in close proximity, we suggest that statistical dependence among nest fates within the same patch was negligible. Approximate nest densities in our patches ranged from 0.5 active nests/ha to 1.5 active nests/ha at any given time. At these densities, it is unlikely that a predator would easily detect a nest neighboring the one that it just depredated, especially in densely vegetated early successional habitats. If predators were consequentially discovering neighboring nests, we likely would have observed cases where neighboring nests within a patch were depredated during the same nest check interval. In fact, this occurred only 4 times during our entire study. To provide more information regarding the degree of variability in nest predation that was related to the patch in which a nest was located, we ran an all-species-combined model that included a random effect of patch and no other covariates. We ran the model in Program MARK using the Markov-Chain Monte Carlo estimation function. We used one hyperdistribution parameter and the default priors provided by Program MARK. The model estimated $\mu = -0.81$ (SE $= 0.48$) with 2.5- and 97.5-percentile credible intervals of -1.70 and 0.13, respectively, and $\sigma = 0.28$ (SE 0.15) with a 2.5- and 97.5-percentile credible interval of 0.04 and 0.61, respectively.

RESULTS

We monitored 320 nests during the 2 seasons. Predation accounted for most of the 173 nest failures (88.4%); desertion (9.2%), parasitism (1.2%), and weather (1.2%) accounted for the remainder. After removing nests that failed due to these latter 3 factors, we analyzed data from 300 nests of all species combined (effective sample size [n] = 2,827 exposure days), which included 131 field sparrow, 71 indigo bunting, 44 blue grosbeak, 28 yellow-breasted chat, and 26 prairie warbler nests. We had reasonable effective sample sizes to analyze field sparrow and indigo bunting nest data separately ($n = 1{,}188$ and 722, respectively). Frequency of nest parasitism by brown-headed cowbirds was low; only 19 of 320 nests we located were parasitized (6.3%) and only 2 of these failed as a result of being parasitized.

Distance to mature forest edge ranged from 2 m to 276 m (median = 38 m, $\bar{x} \pm$ SE $= 54 \pm 46$ m) and distance to cropland edge ranged from 1 m to 362 m (median = 44 m, $\bar{x} \pm$ SE $= 81 \pm 82$ m) among all species' nests. Distance to forest edge and distance to cropland edge were not correlated ($R^2 = 0.01$). Nests of all species combined and nests of field sparrows were distributed proportional to the habitat available in relation to distance to nearest edge (cropland or forest), whereas indigo buntings placed nests nearer to patch edges (Fig. 1).

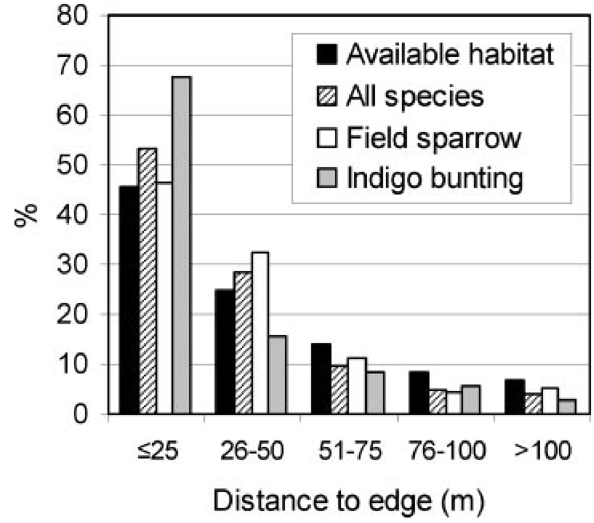

Figure 1. Percent of habitat available compared to percent of shrubland bird nests located within 5 distance-to-edge categories in early successional forested riparian buffers in North Carolina, USA, 2007 and 2008.

Estimates of mean shrub–sapling height of each patch in 2007 ranged from 2.1 m to 4.7 m ($\bar{x} \pm$ SE $= 3.2 \pm 0.8$ m); 2008 estimates ranged from 3.6 m to 5.9 m ($\bar{x} \pm$ SE $= 4.8 \pm 0.7$ m). Mean shrub–sapling height estimates were positively correlated with percent bare ground cover estimates ($R^2 = 0.54$ across both years of data). The strength of this correlation differed between 2007 ($R^2 = 0.01$) and 2008 ($R^2 = 0.42$), indicating that substantial shading out of understory vegetation did not occur until 2008 (Fig. 2). Percent agriculture cover within 2.5 km ranged from 18.2% to 46.3% ($\bar{x} \pm$ SE $= 33.9 \pm 8.4$%).

All Species Combined

In the analysis of all species combined, the between-year effects model (Table 1, model 2) was the best of the temporal

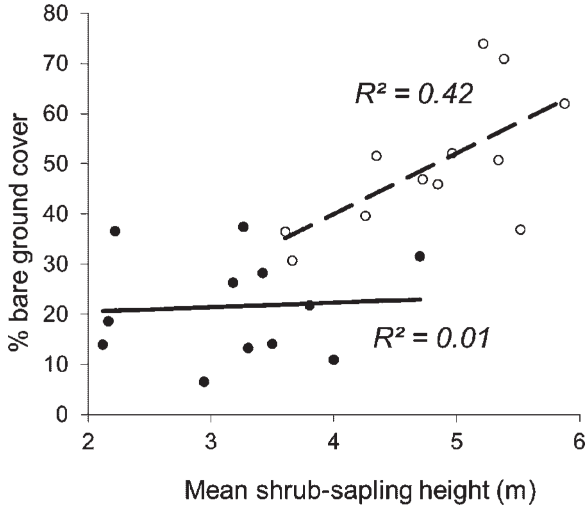

Figure 2. Linear relationship and correlation coefficient between within-patch estimates of mean shrub–sapling height and percent bare ground cover in 2007 (filled dots and solid line) and 2008 (open dots and dashed line) for 12 early successional forested riparian buffers in North Carolina, USA.

Table 2. Effective sample size (n) and estimates of daily nest predation (DNP) and standard error (SE) for shrubland birds in early successional forested riparian buffers in North Carolina, USA, 2007 and 2008. We calculated yearly estimates from the between-year effects model (daily nest predation = Year) and the overall estimate from the constant predation model.

		2007		2008		Overall	
Species	n	**DNP**	**SE**	**DNP**	**SE**	**DNP**	**SE**
All species	2,827	0.041	0.005	0.058	0.006	0.049	0.004
Field sparrow	1,188	0.033	0.007	0.074	0.010	0.053	0.006
Indigo bunting	722	0.045	0.008	0.078	0.023	0.051	0.008
Blue grosbeak	476	0.033	0.011	0.047	0.014	0.040	0.009
Yellow-breasted chat	227	0.062	0.023	0.061	0.021	0.061	0.015
Prairie warbler	222	0.038	0.017	0.021	0.014	0.030	0.011

and nest stage effect models (Akaike weight [w_i] = 0.42) and this model indicated that DNP was higher in 2008 than in 2007 (Table 2). Thus, we included a year effect in all remaining models with continuous covariates.

We documented strong evidence that distance to cropland edge, shrub–sapling height, and the interactive effect of year and shrub–sapling height had an effect on nest predation rates of all species' nests combined, because these covariates appeared consistently in the best models (Table 3) and the confidence intervals of their beta estimates did not overlap zero (Table 4). The beta estimate of distance to cropland edge was negative, which indicated that nest predation was higher for nests that were nearer the cropland edge (Table 4). A predictive graph of DNP based on the best model in the set, which contained distance to cropland edge (DE Crop), shrub–sapling height (SSHgt), and the interactive effect of year and shrub–sapling height (DNP = Year + DE Crop + SSHgt + Year × SSHgt), shows how nest predation decreased farther away from the cropland edge. The model predicted that nest predation in 2008 was reduced from its highest level at the cropland edge (where DNP = 0.056) by 25% and 50% at approximately 110 m and 265 m from the cropland edge, respectively (Fig. 3).

The interactive nature of the year and shrub–sapling height effects indicates that the effect of shrub–sapling height differed between 2007 and 2008. Indeed, a predictive graph of DNP based on the best model in the set illustrates this difference. Predicted DNP did not differ greatly across the range of mean shrub–sapling heights in 2007, but in 2008, it more than doubled from 0.05 to 0.11 in patches with mean shrub–sapling heights ranging from 3.6 m to 6.0 m, respectively (Fig. 4). These predicted trends in DNP relative to mean shrub–sapling height correspond very closely with the relationship between mean shrub–sapling height and percent bare ground cover; there appears to be a concurrent increase in nest predation as percent bare ground cover increases (Fig. 2). Confidence intervals for estimates of distance to forest edge and percent agriculture in the landscape overlapped zero considerably (Table 4), which provided little evidence that these covariates influenced nest survival of all species combined.

Table 3. Delta Akaike's Information Criterion (ΔAIC, difference in AIC from minimum in each model set), model weight (w_i), and −2 log likelihood (−2 log) for the best models (ΔAIC ≤ 2) and the constant predation model of shrubland bird daily nest predation relative to nest- and patch-specific covariates in North Carolina, USA, 2007 and 2008. Continuous covariates included are: distance to mature forest edge (DE For), distance to cropland edge (DE Crop), mean shrub–sapling height (SSHgt), year and mean shrub–sapling height interaction (Year × SSHgt), and percent agriculture cover within 2.5 km (PctAg). The all species combined data set includes nests of field sparrow, indigo bunting, blue grosbeak, yellow-breasted chat, and prairie warbler.

	Analysis		
Model description	**ΔAIC**[a]	w_i	**−2 Log**
All species combined			
Year + DE Crop + SSHgt + Year × SSHgt	0.00	0.25	794.87
Year + DE Crop + SSHgt + Year × SSHgt + PctAg	0.86	0.16	793.71
Year + DE For + DE Crop + SSHgt + Year × SSHgt	1.48	0.12	794.34
Year + DE Crop	1.66	0.11	800.53
Constant predation	8.34	0.00	811.23
Field sparrow			
Year + PctAg	0.00	0.27	342.95
Year + DE For + PctAg	0.99	0.17	341.93
Year + DE Crop + PctAg	1.87	0.11	342.81
Constant predation	12.23	0.00	359.20
Indigo bunting			
Year	0.00	0.18	208.48
Constant predation	0.38	0.14	210.87
Linear trend within years	1.64	0.08	208.10
Year + PctAg	1.65	0.08	208.11
Year + DE Crop	1.73	0.07	208.19
Stage	1.79	0.07	210.27
Year + DE For	1.99	0.06	208.45

[a] Minimum AIC: 804.89 for all species combined, 348.97 for field sparrow, and 212.50 for indigo bunting.

Table 4. Model-averaged beta estimates (β) with standard error (SE) and 95% confidence intervals for continuous covariate effects on daily nest predation of shrubland birds in North Carolina, USA, 2007 and 2008. Covariates include: distance to mature forest edge (DE For), distance to cropland edge (DE Crop), mean shrub–sapling height (SSHgt), year and mean shrub–sapling height interaction (Year × SSHgt), and percent agriculture cover within 2.5 km (PctAg). All species combined includes nests of field sparrow, indigo bunting, blue grosbeak, yellow-breasted chat, and prairie warbler.

Covariate	β	SE	95% CI
All species combined			
DE For	0.0014	0.0018	−0.0021 to 0.0048
DE Crop[a]	−0.0027	0.0012	−0.0051 to −0.0004
SSHgt[a]	0.41	0.18	0.06 to 0.75
Year × SSHgt[a]	−0.51	0.25	−0.99 to −0.03
PctAg	−0.016	0.014	−0.043 to 0.012
Field sparrow			
DE For	0.0025	0.0024	−0.0022 to 0.0072
DE Crop	−0.0011	0.0018	−0.0046 to 0.0024
SSHgt	0.27	0.23	−0.18 to 0.72
Year × SSHgt	−0.39	0.37	−1.11 to 0.32
PctAg[a]	−0.053	0.023	−0.098 to −0.008
Indigo bunting			
DE For	−0.0006	0.0040	−0.0084 to 0.0072
DE Crop	−0.0012	0.0022	−0.0055 to 0.0032
SSHgt	0.67	0.54	−0.39 to 1.73
Year × SSHgt	−0.74	0.57	−1.87 to 0.38
PctAg	−0.016	0.025	−0.065 to 0.033

[a] Strong evidence of a covariate effect, where CI does not overlap zero.

Field Sparrow

Field sparrow nest predation also differed between the 2 yr of our study (Table 2), and again the model containing a between-year effect (Table 1, model 2) was the best of the temporal and nest stage models ($w_i = 0.69$). Percent agriculture within 2.5 km, which appeared consistently in best models (Table 3), was the only covariate for which we found strong evidence for an effect on field sparrow nest predation (Table 4). The effect was negative, indicating that DNP on field sparrow nests was lower in patches located in landscapes with higher percent agriculture. The effect was more pronounced in 2008, when predicted DNP in landscapes with 20% agricultural cover was >3 times higher than predicted nest predation in landscapes with 45% agricultural cover (DNP = 0.16 and 0.05, respectively).

In contrast to the pooled species analysis, there was no compelling evidence that distance to edge, mean shrub–sapling height, and the interaction of year and mean shrub–sapling height were good predictors of field sparrow nest predation; they appeared in best models infrequently (Table 3) and confidence intervals for the beta estimates all overlapped zero substantially (Table 4). However, the trends

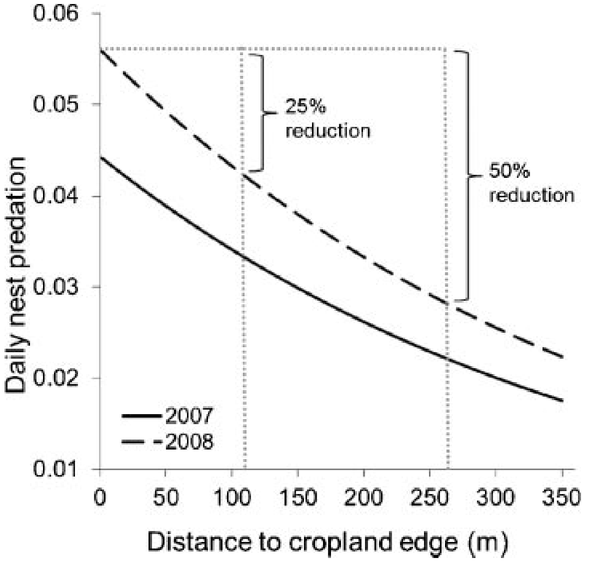

Figure 3. Predicted daily nest predation at varying distances from the cropland edge (DE Crop) for 5 shrubland bird species in early-successional forested riparian buffers in North Carolina, USA, 2007 and 2008. We based predictions on estimates from the model (daily nest predation = Year + DE Crop + SSHgt + Year × SSHgt), where shrub–sapling height (SSHgt) was held constant at its mean value of 3.82 m.

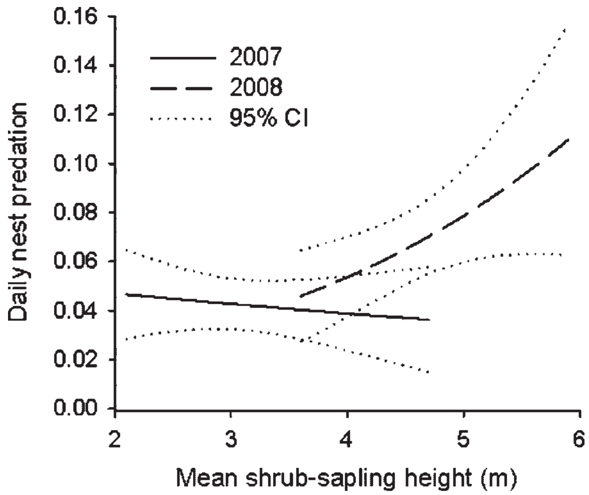

Figure 4. Predicted daily nest predation for 5 shrubland bird species in early-successional forested riparian buffer patches with varying mean shrub–sapling height (SSHgt) in North Carolina, USA, 2007 and 2008. We based predictions on the model (daily nest predation = Year + DE Crop + SSHgt + Year × SSHgt), where distance to cropland edge (DE Crop) was held constant at its median value, 44 m.

of the beta estimates of these covariates were the same as in the pooled species analysis.

Indigo Bunting

The between-year effect model was the best of the temporal and nest stage effects models in the indigo bunting analysis ($w_i = 0.33$), and nest predation was higher in 2008 than in 2007 (Table 2). There was no strong evidence that any of the covariates were good predictors of predation on indigo bunting nests; models containing these covariates received little support (Table 3) and confidence intervals of all covariate betas overlapped zero substantially (Table 4). Again, however, the direction of the beta estimates of distance to cropland edge, mean shrub–sapling height, year and mean shrub–sapling height interaction, and percent agriculture within 2.5 km were the same as in the pooled species and field sparrow analyses.

DISCUSSION

Our results indicate that the effect of edges on predation rates of shrubland bird nests varied by edge type. Predation risk was higher near cropland habitat edges for all species combined but was not higher near mature forest edges in any analysis. The magnitude and precision of the cropland edge effect we observed in the pooled data diminished when we analyzed nests of the 2 most abundant species separately, but the direction of the effect was consistent. Thus, we conclude that predation risk for shrubland bird nests in agricultural landscapes may be marginally higher near cropland edges, but not near mature forest edges.

Our findings are consistent with those of Suarez et al. (1997), who observed a similar pattern of higher predation risk for indigo buntings near abrupt, agricultural edges than near gradual, shrubland-forest edges in southern Illinois. Other studies also documented no clear patterns of increased nest predation near shrubland-forest edges for shrubland songbirds, including several of our focal species (field sparrow, indigo bunting, yellow-breasted chat, and prairie warbler; Woodward et al. 2001, Weatherhead et al. 2010). Moorman et al. (2002) also reported no increases in nest predation near early successional or mature forest edges for hooded warblers (*Wilsonia citrina*), which nest in forest understory shrubs. In contrast, some studies have shown increased predation of shrubland bird nests near forested edges in clearcuts and utility right-of-ways (Rudnicky and Hunter 1993, Vander Haegen and DeGraff 1996, King and Byers 2002). However, the heavily forested landscapes and primary predators (i.e., corvids and small mammals) of these studies conducted in the northeastern United States differed markedly from those in our study. We suspect that the primary nest predators in our study area were snakes, raccoons, opossums (*Didelphus virginiana*), American crows (*Corvus brachyrhynchos*), and blue jays (*Cyanocitta cristata*). This predator community was much more similar to those mentioned by Suarez et al. (1997), Woodward et al. (2001), Moorman et al. (2002), and Weatherhead et al. (2010), whose studies were all conducted in the midwestern or southeastern United States. Given that edge effects on nest predation vary depending on regional predator communities, the consistency of our results to those with similar predator communities is expected (Chalfoun et al. 2002*a*).

Patterns of habitat use by primary nest predators may help explain why we observed higher nest predation at cropland edges. Both American crows and raccoons may concentrate activity at cropland edges, where they occasionally exploit row crops as an additional food source (Best et al. 1990, Suarez et al. 1997, Dijak and Thompson 2000). The black rat snake (*Elaphe obsoleta*), a common species in the southeastern United States known to depredate songbird nests, preferentially selects field-forest edge habitats where thermoregulatory conditions are optimal (Weatherhead and Charland 1985, Durner and Gates 1993, Blouin-Demers and Weatherhead 2001). We suspect that the shrubland-cropland edges also would provide the thermoregulatory conditions that might attract snakes, which may have contributed to increased nest predation near cropland edges in our study. We make this suggestion with caution, because the link between high snake activity in a given habitat type and higher nest predation rates in that habitat type has not been well established, even though seasonal snake activity levels are sometimes correlated with seasonal patterns in songbird nest survival (Sperry et al. 2008, 2009; Weatherhead et al. 2010).

The less abrupt transition of vegetation conditions at shrubland-forest edges might explain the lack of negative edge effects observed for shrubland birds nesting near these edges, because vegetation structure may discourage predator movement, especially for raccoons and other meso-mammals, and provide better nest concealment (Suarez et al. 1997, Heske et al. 1999). Changes in vegetation structure within a patch along the distance-to-edge gradient also may result in edge effect patterns, including those we observed. However, vegetation structure in patches in our study appeared more related to soil moisture and topography than to proximity to edge (C. Shake, North Carolina State University, unpublished report).

Predation of shrubland bird nests also was higher in patches with taller vegetation. This effect was strong in 2008, when most patches exceeded 4 m in height. We believe that higher nest predation in patches with high mean shrub–sapling height may have been the result of reductions in understory vegetation associated with natural forest succession. As saplings became increasingly tall within our patches (i.e., >4 m), ground cover vegetation diminished as it was shaded out by overhead canopy. This pattern coincided with our predictions of increased nest predation in habitat patches. Although we cannot make a causal link between the 2 patterns, the importance of ground cover and understory vegetation for providing nest concealment and alternative nest sites to reduce the probability of predation is well-documented (Martin 1992*b*, 1993; Moorman et al., 2002; but see Peak, 2003). We suggest that the reduction in nest survival associated with natural forest succession we observed could be one mechanism for local extirpation of early successional birds in regenerating forest habitat patches (Keller et al. 2003, Schlossberg and King 2009). However, we acknowledge that the duration of our study was too short to definitively draw this conclusion and suggest that this possibility should be explored experimentally. Concurrent monitoring of changes in shrubland bird nest predation, shrubland bird abundance, and nest-site vegetation over several years would provide critical information about the mechanisms and timing of forest successional effects on local shrubland bird population dynamics.

Nest predation also appears to have been influenced by the landscape surrounding a habitat patch. Field sparrow nest predation was considerably lower in habitat patches with high percent agricultural cover within 2.5 km. Our results are similar to those of Riddle and Moorman (2010), who documented higher nest success of indigo buntings and blue grosbeaks in agriculture-dominated landscapes than in forest-dominated landscapes in eastern North Carolina. However, our observations are contrary to observations in the midwestern United States, where forest-breeding birds experience higher nest predation rates in areas with higher percent agricultural cover because mammalian and avian nest predators are often more abundant in these landscapes (Andrén 1995, Robinson et al. 1995, Dijak and Thompson 2000). Differences in these findings may be related to differences in the range of landscapes studied. Robinson et al. (1995) examined landscapes where percent agricultural composition was as high as 90%, whereas percent agriculture in landscapes in our study did not exceed 47%. Differences in nest predator communities and variation in predator response to landscape composition also might explain these differences. However, because we did not directly identify nest predators or estimate relative predator abundance, we refrain from speculating on these differences.

Our landscape-level findings build support for a hypothesis that deserves more rigorous evaluation, especially because it runs contrary to well-documented patterns observed in similar systems. Specifically, future research should explore why nest predation of some shrubland birds may be lower in more highly agricultural landscapes in the southeastern United States. Studies would be most useful if they also directly identified nest predator communities and quantitatively linked predator abundance to landscape composition (e.g., Thompson and Burhans 2003).

Many other components of breeding productivity that we did not measure (e.g., nest density, individual female fecundity, and fledgling survival) also influence shrubland bird population dynamics in habitat patches. Future assessment of how patch characteristics affect these components would provide a more complete picture of the contribution of a given habitat patch to population change. Breeding productivity is not the only relevant bird response variable when considering adequate patch width or size for shrubland birds. Abundance and patch occupancy of some shrubland birds also are influenced by patch size; many species avoid mature forest edges and some are area-sensitive (Rodewald and Vitz 2005, Schlossberg and King 2008, Lehnen and Rodewald 2009, Shake 2009). Our findings provide no evidence for the hypotheses that shrubland birds avoid mature forest edges because they experience lower nest success there, suggesting that other mechanisms for edge avoidance behavior may be more important (Bollinger and Switzer 2002, Ribic et al. 2009). However, nest predation may still play a role in causing edge avoidance for other edge types, particularly when habitat patches are adjacent to cropland. Future research should compare edge avoidance behavior at different types of shrubland edges and, more importantly, attempt to identify how large or wide a patch should be to support diverse and abundant shrubland bird communities (e.g., Shake 2009).

MANAGEMENT IMPLICATIONS

When restoring early successional and shrubland habitat adjacent to row crop agriculture, we suggest that land managers consider patches wider than 250 m to provide nesting habitat away from cropland edges where nest predation risk may be as much as 2 times higher. Maintenance of early successional forest and shrubland habitats with structurally diverse grass, herbaceous, and low shrub vegetation also can be an important management tool to reduce nest predation on shrubland birds. Schlossberg and King (2009) showed that continual creation of early successional forest habitat at 10- to 15-yr intervals would help maximize shrubland bird density and diversity. Given that our oldest sites were established no more than 7 yr prior to our study, we suggest that shorter intervals may be more appropriate, especially in habitats or regions like ours where vegetation growth and succession occur more rapidly. We acknowledge that implementation of this recommendation is dependent on management objectives; clearing and reinitiating succession is not an option for managers trying to achieve a mature forest community (e.g., for permanent riparian buffers or timber production). However, in these instances we would encourage use of management practices such as precommercial thinning or more widely spaced planting arrangements to help maintain understory vegetation for longer periods. In some regions or vegetation types, prescribed fire may be the appropriate disturbance to maintain early successional conditions. With great regional variation in growing conditions and vegetation types, the disturbance interval and type will clearly need to be tailored to local situations. Finally, our results suggest that in regions where agriculture does not compose >50% of the land base habitat restoration projects in landscapes with more agricultural cover may provide greater benefits for some shrubland bird species than those in more heavily forested landscapes. However, we caution that the evidence for this effect was not consistently strong for all shrubland species and again suggest that more research of shrubland bird nest survival is needed in regions where landscape effects have not been well-studied and where nest predator communities have not been identified.

Habitat restoration aimed at increasing populations of shrubland birds in agricultural landscapes should consider the impact of cropland edges, forest succession, and landscape composition when creating early successional habitat patches. The effects of these factors are likely to be complex and dependent on local and regional nest predator communities. Until biologists learn more about the complex interactions between shrubland bird communities and their nest predators, we suggest that land managers maintain reasonably large or wide shrubland habitats in early stages of succession with structurally complex vegetation.

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