ABSTRACT

SHAKE, COREY SCOTT. Considerations for Conservation of Shrubland Birds in Early Successional Forest Habitat. (Under the direction of Dr. Christopher E. Moorman).

Populations of many bird species associated with shrubland habitats are declining in the eastern United States, but incentive programs that restore shrubland or early-successional forest habitat on privately-owned land may help to ameliorate these declines. The habitat patches created by these programs are highly variable in size, shape, and surrounding habitat matrix, and it is unclear how these characteristics affect patch occupancy and nest survival of shrubland passerines. Our first objective was to determine how patch area, patch shape, and extent of forest cover in the surrounding landscape affect shrubland bird species' occupancy of early-successional forest habitat patches and, for species that were area-sensitive, we sought to identify minimum area requirements. Our second objective was to determine if nest predation was higher at habitat edges, and whether patch vegetation structure or the landscape surrounding a patch influenced nest predation rates.

To study patch occupancy, we surveyed 35 individual habitat patches in 2007 and 43 in 2008 for the presence of nine shrubland birds in North Carolina, USA. We then modeled individual patch occupancy probability of five of these species relative to patch area, patch shape, and % forest cover within 1 km of the patch. We documented evidence of area-sensitivity for yellow-breasted chat (*Icteria virens*) and prairie warbler (*Dendroica discolor*), and estimated minimum area requirements of 2.3 and 1.1 ha, respectively. Blue grosbeaks (*Passerina caerulea*) also were area-sensitive in irregularly-shaped patches. Predicted individual patch occupancy probability was >0.9 in patches ≥5.5 ha for all area-sensitive species. Shape index alone and proportion of forest cover were not important predictors of occupancy for shrubland birds. Restored shrubland and early-successional forest in agricultural landscapes can provide habitat for many shrubland birds, but patches should be >5 ha to maximize shrubland bird diversity.

To study nest predation, we collected data on nests of five shrubland passerine species during the 2007 and 2008 breeding seasons 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 accounted for other sources of variation, including 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 extinction of shrubland birds in regenerating 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.

Considerations for Conservation of Shrubland Birds in Early Successional Forest Habitat

by
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A thesis submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Master of Science

Fisheries and Wildlife Sciences

Raleigh, North Carolina

2009

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BIOGRAPHY

Corey Shake grew up in the town of Fruitland, Idaho, surrounded by farms in the foreground and mountains in the distance. His parents were both school teachers, and his father couldn't help himself from going fishing and bringing along his boys. As such, for the rest of his life, Corey couldn't help himself from enjoying two things: the act of learning and enjoying wild creatures and places. After high school, he couldn't think of what else to do other than study animals and keep learning, so he attended the University of Idaho to study wildlife biology, and graduated with a bachelor's degree in 2005. Now he's continued this trend by coming to North Carolina State University to study wildlife science. His coming to Raleigh, North Carolina has, however, expanded his interests to include the enjoyment of porch sitting, eating raw peanuts, cane pole fishing, and riding city buses. These new stimuli, along with meeting extraordinary people, a trip to the Alaskan wilderness, and reading some influential books, have prompted uncertainty in his mind about his future aspirations. However, it’s likely that he’ll go on being a wildlife biologist because he won't be able to escape his adoration of all things wild and scenic. He also expects that he will someday settle into living amongst farm fields within sight of at least a single mountain range.

ACKNOWLEDGMENTS

First I must thank those who, without their participation, all of this research would not have happened. The landowners of northeastern North Carolina were more than obliging when asked if I could conduct research on their properties; a few even drove me around their property or let me use their golf cart to tour the property myself and one gave my old work truck a jump when I needed it.

My parents, Ann and Terry Shake, were also undeniably critical to this thesis in countless ways. Their support of me throughout my post-high education has been generous and they have always given me great freedom to pursue what fascinates me. Their efforts before I left home may have been most important to sustain me through my academic career; they taught me to desire and enjoy learning. The rest of my family, especially those that I am closest to, my brother and grandparents, have been equally supportive and perhaps, more importantly, an inspiration for me to live life more fully and compassionately. I can’t mention my family without mentioning my closest friends who, like family, have provided me with immeasurable inspiration and happiness.

My graduate advisor, Dr. Chris Moorman, has been essential to my academic and professional development in many ways, but I believe his greatest contribution to my growth has come from the great example he set as a devoted wildlife conservationist. His enthusiasm for natural history and bird watching has helped me recall my own strong interest in these things when I’ve been overwhelmed by statistical methods and data analysis. My graduate committee has been invaluable for their diverse perspectives, varied expertise, insightful criticism, and insistence that I think critically and broadly about my work. From my committee, I'd like to thank Dr. Mike Burchell of the Department of Biological and Agricultural Engineering for acquiring funding for this project and for providing a field vehicle. Dr. Jason Riddle (University of Wisconson- Stevens Point), Dr. Ken Pollock (North Carolina State University) and Dr. Steve Dinsmore (Iowa State University) have been extremely helpful in developing my study design, learning how to use data analysis programs, and interpreting my results.

Many professionals outside the academic community have been helpful to my research, especially those associated with the Conservation Reserve Enhancement Program (CREP) in North Carolina. In particular, I'd like to thank Natalie Woolard, the CREP manager, and Charles Bowden for their help in giving me useful background on the program, taking me on site visits, and facilitating communication with county extension agents, NRCS staff, and landowners.

Lastly, I'd like to thank those agencies who provided financial or in-kind support for my research. The North Carolina Department of Environment and Natural Resources Division of Soil and Water Conservation provided generous funding for my assistantship and field supplies. The North Carolina Wildlife Resources Commission (WRC) provided housing for both field seasons at the Tillery Game Lands Wildlife Depot. The WRC's Gold House, with its screened-in back porch and pond full of turtles, frogs, and skinny bass was my finest housing in North Carolina and extremely important for the maintenance of my well-being after spending too much time in the city.

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CHAPTER 1

Patch Area Affects Shrubland Bird Occupancy

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Abstract

Populations of many shrubland bird species are declining in the eastern United States. Incentive programs that restore shrubland or early-successional forest habitat on privately-owned land may help to ameliorate these declines. However, the habitat patches created by these programs are highly variable in size, shape, and surrounding habitat matrix and it is unclear how these characteristics affect patch occupancy by shrubland passerines. Our objective was to determine if shrubland birds avoided small or irregularly-shaped habitat patches and for area-sensitive species, to identify their minimum area requirements. Additionally, we sought to determine if the proportion of mature forest cover in the landscape influenced patch occupancy. We surveyed 35 individual habitat patches in 2007 and 43 in 2008 for the presence of nine shrubland birds. We then modeled individual patch occupancy probability of five of these species relative to patch area, patch shape, and % forest cover within 1 km of the patch. We documented evidence of area-sensitivity for yellow-breasted chat (*Icteria virens*) and prairie warbler (*Dendroica discolor*), and estimated minimum area requirements of 2.3 and 1.1 ha, respectively. Blue grosbeaks (*Passerina caerulea*) also were area-sensitive in irregularly-shaped patches. Predicted individual patch occupancy probability was >0.9 in patches ≥5.5 ha for all area-sensitive species. Shape index alone and proportion of forest cover were not important predictors of occupancy for shrubland birds. Restored shrubland and early-successional forest in agricultural landscapes can provide habitat for many shrubland birds, but patches should be >5 ha to maximize shrubland bird diversity.

Key Words: area-sensitive, landscape, minimum area requirement, occupancy modeling, shrubland birds

1. Introduction

Many wildlife species associated with disturbance-dependent habitats have declined as a consequence of habitat loss in the eastern United States (Askins 1993, Dessecker and McAuley 2001, Hunter et al. 2001, Litvaitus 2001). Most of these habitat losses have resulted from changes in spatial and temporal patterns of disturbance types such as fire, timber harvest, land clearing, and agricultural practices (Warner 1994, Lorimer 2001, Brawn et al. 2001). Some of the most substantial declines are evident in populations of bird species that breed in early-successional forest and shrubland habitats (hereafter referred to as shrubland birds; Brawn et al. 2001, Hunter et al. 2001). Some shrubland birds, such as the prairie warbler (*Dendroica discolor*), are now considered high conservation priority species in North America (Partners in Flight Watch List Species, Rich et al. 2004).

Silviculture and prescribed fire are common conservation practices used to create or maintain early-successional habitat (Thompson and DeGraaf 2001), but other habitat restoration options are available. In the eastern and midwestern U. S., where a large percentage of land is privately owned, there are a number of federal and state conservation programs and initiatives that focus on habitat restoration on private land. Many of these programs are associated with federal legislation known as the Farm Bill (i.e., the 2008 Food, Conservation, and Energy Act), which already has resulted in the restoration of millions of hectares of agricultural land to wildlife habitat (Natural Resources Conservation Service 2000, Gray and Teels 2006). The Conservation Reserve Enhancement Program (CREP) is a state and federal cooperative Farm Bill program that aims to reduce erosion, improve water quality, and restore wildlife habitat in environmentally sensitive areas (Farm Service Agency

2009). Forested riparian buffers, tree plantings established adjacent to water courses (e.g., ditches, streams, swamps), are a common conservation practice used to achieve CREP goals. Over 300 000 ha of riparian buffers currently are enrolled in CREP or other Farm Bill programs in the eastern U.S. (Farm Service Agency 2008). In their early seral stages, these forested riparian buffers have potential to provide habitat for shrubland bird species. However, the design requirements for forested riparian buffers vary from program-to-program and state-to-state, and individual buffer design is further influenced by individual landowner objectives. Consequently, the size and shape of buffers can vary considerably.

Habitat patch area influences whether some bird species will occupy a patch (e.g., Robbins et al. 1989, Vickery et al. 1994, Helzer and Jelsinki 1999). Those species whose occurrence or abundance increases with increasing patch area are considered to be area-sensitive (Freemark and Collins 1992). Patterns of species' occurrence within a patch, or occupancy, relative to patch area have not been thoroughly studied for shrubland birds, and minimum patch area requirements for shrubland bird species have not been estimated. However, many studies of shrubland bird abundance in regenerating group-selection timber harvests showed that some shrubland species were absent from habitat patches <1 ha (Annand and Thompson 1997, Robinson and Robinson 1999, Costello et al. 2000, Moorman and Guynn 2001). Studies in larger patches have provided mixed results; some found weak evidence of area-sensitivity for a few species (Rudnicky and Hunter 1993, Rodewald and Vitz 2005, Askins et al. 2007, Chandler et al. 2009, Lehnen and Rodewald 2009) while others found no evidence of area-sensitivity (Krementz and Christie 2000). Patch shape may also influence patch occupancy for some grassland bird species (Helzer and Jelskinki 1999), but no studies have directly addressed the effect of patch shape on shrubland bird occurence. However, there is considerable evidence that suggests many shrubland birds avoid habitat edges and may avoid irregularly-shaped patches (Schlossberg and King 2008).

Although riparian buffers typically are implemented in predominately agricultural landscapes, considerable regional and local differences in landscape composition surrounding riparian buffers are likely. Variation in the landscape surrounding a habitat patch can explain a large proportion of the variation in grassland and forest bird communities (e.g., Bakker et al. 2002, Rodewald and Bakermans 2005), but studies of landscape effects on shrubland birds are few and the results are mixed. The occurrence of some shrubland birds in managed forest landscapes in the southeastern U.S. was related to landscape-scale habitat features (Mitchell et al. 2001), but abundance of shrubland birds in clearcuts and beaver meadows in the northeastern U.S. was not related to landscape variables measured at the 1-km scale (Askins et al. 2007, Chandler et al. 2009). Overall, much remains to be clarified regarding the effects of landscape composition on shrubland bird habitat habitat use.

Most studies of shrubland bird occupancy and abundance have not accounted for the detectability of species, an important source of bias in estimates based on bird count data (Nichols et al. 2000, MacKenzie et al. 2002). New methods of estimating occupancy that account for the probability of detecting a species are now available. These methods allow researchers to assess the influence of patch variables on individual species' patch occupancy and whether a particular variable influences the probability of detection (MacKenzie et al. 2006). Using these new methods, we conducted an observational study to determine if and how patch size and shape and landscape context influence shrubland bird occupancy of

CREP early-successional forested riparian buffer habitat patches. Our overall objectives were: (1) to detect patterns of area-sensitivity and edge avoidance in shrubland bird species; (2) to determine minimum area requirements for species that exhibit area-sensitivity; and (3) to determine if landscape composition influences shrubland bird occupancy.

2. Methods

2.1 Study Area and Habitat Patch Selection

We studied CREP early-successional forested riparian buffers located in six counties in northeastern North Carolina, all within Partners in Flight's South Atlantic Coastal Plain Bird Conservation Region (Rich et al. 2004). Landscapes in this region were a mosaic of forest and cultivated land, though there was noticeable local variation in percentages of these two landcover types. Landscapes within 1 km of our study patches averaged 50% (SE = 14) forest, 38% (SE = 10) agricultural land, 11% (SE = 8) other (includes grassland, shrubland, early-successional, barren, open water, and developed cover types). The dominate forest types were second-growth and mature pine-oak (*Pinus* spp.-*Quercus* spp.) woodlands in the uplands and gum-cypress (*Nyssa sylvatica-Taxodium* spp.) swamps in low-lying areas. The most common crops grown in the region were corn, soybeans, cotton, and tobacco.

In 2007, we surveyed 35 early successional forested riparian buffer habitat patches for the occurrence of nine focal shrubland bird species (Table 1). In 2008, we surveyed eight additional habitat patches to increase our sample size, expand the range and distribution of patch sizes and shapes, and broaden the geographic scope of our study (Fig. 1). The 43 study habitat patches ranged in size from 0.3 to 24.9 ha (mean = 6.1, SE = 5.7). A comparison of these 43 habitat patches to 100 randomly-selected CREP riparian buffer patches drawn from a Geographic Information System (GIS) database showed the distributions of patch area in both samples were similar, though there were more patches <1 ha in the random sample (Fig. 2, median = 3.8 ha for study patches; mean = 6.1 and median = 2.7 ha for randomly-selected patches). We selected patches that were close in age (4 to 7 years since planting) with relatively similar hardwood and pine planting arrangements. 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. Additionally, we selected patches with roughly equal proportions of adjacent habitat types—approximately half woodland and half cropland, a common configuration of CREP riparian buffers in North Carolina. All patches were spaced at least 1 km apart.

2.2 Bird Occupancy Sampling

We sampled each habitat patch along a single 150-m-long straight-line transect to determine presence-absence for all nine focal species. The start point and direction of the transect were randomly determined for each patch, with the constraint that the transect line was completely within the patch. Two independent observers walked the transect at the same pace and recorded birds as present or absent at unlimited distances from the transect anywhere within the habitat patch boundaries. We considered observations in the first 10 m of adjacent habitat types as within the habitat patch, because many of our focal species that maintained a territory inside the patch characteristically perched on tall trees at the edge of patches to sing or forage at the edge of cultivated fields. We sampled from transects of the same length and for the same duration (mean ± SE = 20 ± 1 minutes) for all habitat patches because occurrence data sampled proportional to patch area can falsely indicate area-sensitivity (Halia 1986, Horn et al. 2000). Our 150-m-long transect was sized as such to fit within our smallest and most linear patches. To ensure that observations were made independently, the observers were staggered 10 m apart along the transect line and instructed to avoid looking at the other observer for cues. Each patch was surveyed once per breeding season between 15 May and 15 June, and the same two observers sampled all patches during each year. All surveys were conducted from sunrise until 0900 EST and only in the absence of high winds and rain.

2.3 Patch Characteristics

To measure size and shape of our habitat patches, we delineated the perimeters of individual patches using spatially-referenced aerial photo data in a GIS. Patch size and perimeter were calculated with ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA). We calculated each patch's shape index, which is a measure of the deviation in perimeter of a given patch from the perimeter of a circular patch of the same area (Eqn. 1). Our use of this metric avoids the high correlation between a standard perimeter-area ratio metric and area, which is useful to differentiate area and shape effects on a given response variable. A perfectly circular patch has a shape index of 1, and the index value increases as a patch becomes more irregularly-shaped (Fig. 3).

Equation 1. $$\text{Shape index} = \text{perimeter} / [2\sqrt{(\pi * \text{area})}]$$

We measured the proportion of mature forest habitat within 1 km of each habitat patch in ArcGIS 9.2 using the most recent National Landcover Dataset cover type data, which was created from 2001 Landsat satellite imagery (Homer et al. 2004). The 1-km scale has been used widely and shown to influence bird communities (e.g., Saab 1999, Rodewald and Bakermans 2006). We reclassified four vegetation cover types into one mature forest classification: evergreen forest, deciduous forest, mixed forest, and woody wetlands (see Homer et al. 2004 for all cover types). We used percent mature forest habitat as our landscape variable in occupancy modeling for two reasons: (1) most of our focal bird species do not breed in mature forest habitat and thus may not readily colonize shrubland habitat patches isolated in landscapes with high levels of inhospitable mature forest habitat (Dunning et al. 1995) and (2) mature forest habitat is classified from Landsat imagery with much higher accuracy than early-seral forest habitat (Sader et al. 1991).

2.4 Data Analysis

We used an independent double-observer bird sampling approach because it allowed for estimation of each observer's probability of detection for each species, which can be used to adjust a naïve estimate of occupancy when detection probability is <1 (MacKenzie et al. 2006). Occupancy (ψ) is defined as the proportion of sites occupied, and detection probability (p) as the probability that a species will be detected within a sample area, given that it is present within that sample area. In our sampling design, each independent observer's survey was treated as a simultaneous, but separate visit to each patch. Therefore, our estimates of detection probability are conditional on both the presence of a species and the availability of that species during the 20-minute count period (Nichols et al. 2009). We used Program PRESENCE 2.0 (Hines 2006) to analyze our occupancy data, which allowed us to compare models using Akaike Information Criterion (AIC) model selection (Burnham and Anderson 2002). This information-theoretic approach allowed us to assess the influence of covariates on species occupancy and detection probability by examining the evidence from a set of competing models (Burnham and Anderson 2002). Because our data were collected over two seasons, we used multi-season models in Program PRESENCE, which estimate colonization (γ) and local extinction (ε) rates between the two seasons. For models that include covariates, Program PRESENCE also estimates individual patch occupancy, which is defined as the probability that a species will occupy a given patch. Individual patch occupancy estimates from single-covariate models can be used to create a predictive graph that illustrates the magnitude of the effect of a given covariate. We used the original parameterization of Mackenzie et al.'s (2006) multi-season models, where occupancy in the first season, seasonal colonization, and local extinction are estimated and occupancy in the second season is a derived parameter. Multi-season models, which estimate covariate effects over all years of data, allowed us to determine if the patterns observed were consistent across years. Although we did not survey eight of the 43 patches in 2007, missing observations are acceptable and accommodated for in multi-season models (MacKenzie et al. 2006: 195).

We developed a model set based on *a priori* hypotheses that patch occupancy of nine scrub-successional birds may be affected by patch area, shape index, and/or landscape composition. We first fit the data to a baseline model where occupancy was constant across all patches and did not vary with any patch-specific covariates (denoted as $\psi(.)$, Table 2, Model 1). Next, we modeled occupancy relative to area and hypothesized that if a species is area-sensitive, it will have reduced individual patch occupancy in smaller patches (i.e., a positive effect of area; Table 2, Model 2). We then modeled occupancy relative to shape index and hypothesized that species which avoid edges will show reduced individual patch occupancy in irregularly-shaped patches (i.e., a negative relationship with shape index; Table 2, Model 3). Next, we modeled the effect of percent forest cover within 1 km, and hypothesized that occupancy would be lower in patches surrounded by high percent forest cover (i.e, a negative relationship; Table 2, Model 4). We also hypothesized that area-sensitivity may be more pronounced in patches with high shape index and thus, we modeled an interaction between area and shape index (Table 2, Model 5). Finally, we modeled our three covariates in all possible combinations (Table 2, Models 6-10).

We also hypothesized that detection probability (*p*) may differ among each observer for some species, due to variation in observers' level of experience, hearing ability, or judgment of distance to observed birds. To examine this effect, we ran the same ten models described above, but allowed *p* to vary among each of four observers (denoted *p*(obs); Table 2, models 11-20). We left colonization (γ) and local extinction (ε) parameters constant in all models because we did not expect them to vary for any species relative to any of the measured covariates which were static between the two years, but rather, to respond more substantially to regional abundance patterns and population dynamics (Haila 1986, Boulinier et al. 2001).

To identify which covariates in our models were good predictors of patch occupancy, we assessed the strength of evidence from our model selection results and from model estimates of covariate effects. First, we examined whether the best models in the set explained the data better than constant occupancy models (i.e., $\psi(.)\ldots$). Next, we identified which covariates consistently were included in the best models in the set. The final and most critical evidence, however, was the estimates of covariate effects and their standard errors (hereafter, “beta estimates” or “betas”). Instead of reporting beta estimates from a single best model, we reported model averaged betas and their standard errors to account for uncertainty in the model selection process. Model averaged estimates are a weighted average of all the estimates of particular covariate across models containing that covariate, weighted by each model’s Akaike weight (Burnham and Anderson 2002: 150-167). Because the inclusion of interaction effects in a model alters the estimates of the individual effect of covariates involved in the interaction, we excluded area and shape estimates in the four interaction models from the model-averaging. We calculated 95% confidence intervals for each model-averaged estimate (95% CI = estimate ± 1.96*standard error; Donovan and Hines 2007). Estimates whose confidence interval did not overlap zero were considered to provide strong evidence of a covariate effect while those whose confidence intervals were nearly centered on zero were considered to provide little to no evidence of a covariate effect.

For species that showed strong evidence of a covariate effect, we graphed individual patch occupancy estimates and their 95% confidence intervals relative to the covariate of interest. These graphs were created using the individual patch occupancy estimates from the lowest AIC value, single-covariate model that contained the covariate of interest. These graphs allowed us to display the magnitude of the covariate’s effect and, in cases where area was the covariate of interest, we used the model predictions to identify the area value at which we would expect the individual patch occupancy point estimate to be equal to 0.5. We suggested this value as a minimum-area requirement, because we would expect the probability that a species will occupy a patch smaller than this to be less than completely random (after Robbins et al. 1989, Vickery et al. 1994). We also identified what we termed the "optimal area value", which was the area value at which the model predicted the individual patch occupancy point estimate to be equal to 0.9. This optimal area value provided a minimum area that would ensure with greater certainty that a species would occupy a given habitat patch.

3. Results

The 43 study habitat patches ranged in shape index and forest cover from 1.12 to 3.32 (mean = 1.76, SE = 0.52) and 24 to 81% (mean = 50%, SE = 14)., respectively.

Occupancy was high for indigo buntings, field sparrows, and common yellowthroats and low for brown thrasher (Table 3). Because these four species occupied nearly all or none of the patches, we excluded them from the model selection analysis. Detection probability for all species was relatively high (Table 3), but model selection analysis for the remaining five species indicated that the best models were those that accounted for differences in detection probability among the four observers (…*p*[obs]; Table 4).

Patch area was a good predictor of patch occupancy for two species: yellow-breasted chat and prairie warbler. Area was consistently in the best of the yellow-breasted chat occupancy models, and these models received considerably more support than constant occupancy models (Table 4). The model-averaged beta estimate for patch area did not overlap zero, providing strong evidence for a positive effect of patch area on yellow-breasted chat occupancy (Table 5, Fig. 4). Patch area was consistently in the best models in the prairie warbler results as well (Table 4), and the confidence interval of the model-averaged beta estimate for patch area only slightly overlapped zero, indicating moderately strong evidence of a patch area effect (Table 5, Fig. 4). We estimated a minimum area requirement (where individual patch occupancy probability = 0.5) and an optimal area value (where individual patch occupancy probability = 0.9) of 2.3 ha and 4.4 ha, respectively, for yellow-breasted chat and 1.1 and 5.5 ha, respectively, for prairie warbler (Fig. 4). Although area appeared consistently in the best models in the eastern towhee and white-eyed vireo analyses, models containing area were only a slight improvement over the constant occupancy models and the confidence intervals of the beta estimates overlapped zero substantially, providing no compelling evidence of area-sensitivity for these species (Tables 4 and 5).

Blue grosbeak patch occupancy also appeared unrelated to patch area when the covariate was considered alone, but the area-shape index interaction model received nearly equal support to the best model in the set (Table 4). The model-averaged beta estimate of the area-shape index interaction effect on blue grosbeak occupancy was strongly positive (Table 5). The positive effect of area on individual patch occupancy was more pronounced in patches with high shape index (3.3) than in those with the mean shape index of 1.8, and in patches where shape index = 3.3, blue grosbeak's minimum area requirement and optimal area value were 2.8 and 4.1 ha, respectively (Fig. 5).

We documented no compelling evidence for an effect of shape index alone or percent forest cover within 1 km on occupancy of our focal species. Both covariates did not appear consistently in the best models and confidence intervals of their model-averaged beta estimates overlapped zero substantially for all five species (Tables 4 and 5).

4. Discussion

Among the factors we considered, patch area had the most significant influence on patch occupancy of shrubland birds. Two of our nine focal species, yellow-breasted chat and prairie warbler, were area-sensitive, exhibiting low patch occupancy in our smallest patches. Also, blue grosbeak was area-sensitive in very linear, irregularly-shaped patches. Similar patterns of absence from small habitat patches <1 ha have been observed for yellow-breasted chat, prairie warbler, field sparrow, and eastern towhee (Annand and Thompson 1997, Robinson and Robinson 1999, Moorman and Guynn 2001, Alterman et al. 2005). Other studies have shown that although the abundance of some of shrubland bird species may increase with increasing patch area, particularly yellow-breasted chat and eastern towhee, individuals will occupy patches as small as 3 ha (Krementz and Christie 2000, Rodewald and Vitz 2005, Askins et al. 2007, Lehnen and Rodewald 2009). DeGraaf and Yamasaki (2003) suggested that shrubland birds require patches at least 0.8 ha in size. Our analysis to identify minimum area requirements, the first of its kind for shrubland birds, indicates that yellow-breasted chats and prairie warblers require patches of at least 2.3 and 1.1 ha, respectively. If patches are very linear or irregularly-shaped, area requirements may be as much as 3 ha for blue grosbeak. However, patches ≥5.5 ha may be most ideal when creating habitat for shrubland birds, because we would expect a high probability that all three area-sensitive species would occupy patches of this size.

The proximate cause of area-sensitivity for some shrubland birds may be edge avoidance in small or very linear patches that are almost entirely edge habitat (Schlossberg and King 2008). Ultimate causes of edge avoidance by shrubland birds remain uncertain, though some potential mechanisms have been investigated. Edge avoidance behavior and bird use of small early-successional habitat patches does not seem to be related to variation in food abundance and vegetation structure (Rodewald and Vitz 2005, Champlin et al. 2009). Increased nest predation near edges may explain shrubland bird aversion to edges. In fact, negative edge effects on nest success of shrubland birds have been documented (Suarez et al. 1997, King and Byers 2002), including at cropland edges in our study area (Shake 2009). However, nest success did not decline at mature forest-shrubland edges elsewhere (Woodward et al. 2001, Moorman et al. 2002) and breeding productivity also was not lower in smaller patches (Lehnen and Rodewald 2009, Krementz and Christie 2000). Detailed studies of population demographics (e.g., breeding productivity, adult survival) of the most area-sensitive shrubland birds (e.g., yellow-breasted chat) in relation to edges of different types would be useful to clarify the mechanisms influencing edge-avoidance behavior.

Although we predicted that occupancy of edge-avoiding species such as field sparrow, indigo bunting, prairie warbler, and yellow-breasted chat would decrease in irregularly-shaped patches with high shape index, we discovered no strong evidence that shape index alone influenced patch occupancy of these species. Although shrubland birds may have lower abundance in irregularly-shaped patches (Schlossberg and King 2008), edge effects may not preclude occupancy of patches, given that patches meet minimum area requirements. Also, our habitat patches may not have been sufficiently narrow or irregularly-shaped to preclude occupancy. Our most linear habitat patch was, on average, approximately 30 m wide and occupied by all of our focal species. In contrast, field sparrows and prairie warblers were absent from early-successional field borders <3 m wide in this region (J. Riddle, personal communication).

Percent forest cover in landscapes surrounding habitat patches did not appear to influence patch occupancy for shrubland birds. Askins et al (2007) also documented no response to landscape composition within 1 km of clearcut patches in Connecticut for shrubland specialist birds. Shrubland birds may occupy patches regardless of the extent of forest cover in the surrounding landscape, because they are adapted to colonize ephemeral habitat patches isolated in forested landscapes (Askins et al. 2007). Disturbances that historically maintained shrubland habitats in the eastern United States, such as beavers, wind, and fires, generally were small and isolated in a heavily-forested matrix (Askins 2001, Askins et al. 2007).

Shrubland-breeding passerines require relatively small habitat patches and occupy landscapes with varying amounts of forest and agricultural cover compared to area-sensitive forest- and grassland-breeding passerines that may require habitat patches greater than 50 ha (Robbins et al. 1989, Herkert 1994, Vickery et al. 1994) and landscapes with extensive contiguous habitat (Ambuel and Temple 1983, Askins et al. 1987),. However, because of evidence of area-sensitivity, edge avoidance, and decreased nest survival near agricultural edges, we suggest that patch size should be an important consideration when shrubland habitats are created or managed for shrubland birds (Degraaf and Yamasaki 2003, Schlossberg and King 2008, Lehnen and Rodewald 2009, Shake 2009). We recommend that shrubland patches should be >5 ha in size to ensure habitat use by the entire community of shrubland birds that we considered. Furthermore, the evidence that most shrubland birds occupy patches regardless of landscape composition is encouraging for habitat restoration programs in highly agricultural landscapes that are targeted at conservation of shrubland birds. The overall high occupancy rates in our study indicate that restored early-successional forest in agricultural landscapes can provide habitat for many declining shrubland birds, but patches must be of adequate size to maximize shrubland bird diversity.

Acknowledgments

We thank W. Ricks and J. Trutwin for field assistance and G. Hess and T. Simons for their very helpful reviews of this manuscript. This study was funded by a grant from the North Carolina Department of Environment and Natural Resources, Division of Soil and Water Conservation.

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Tables and Figures

Table 1. Nine shrubland bird focal species surveyed for in early-successional forested riparian buffer habitat patches in North Carolina, USA, 2007-2008.

Common name (Species Code)	**Scientific Name**
Blue grosbeak (BLGR)	*Passerina caerulea*
Brown thrasher (BRTH)	*Toxostoma rufum*
Common yellowthroat (COYE)	*Geothlypis trichas*
Eastern towhee (EATO)	*Pipilo erythrophthalmus*
Field sparrow (FISP)	*Spizella pusilla*
Indigo bunting (INBU)	*Passerina cyanea*
Prairie warbler (PRAW)	*Dendroica discolor*
White-eyed vireo (WEVI)	*Vireo griseus*
Yellow-breasted chat (YBCH)	*Icteria virens*

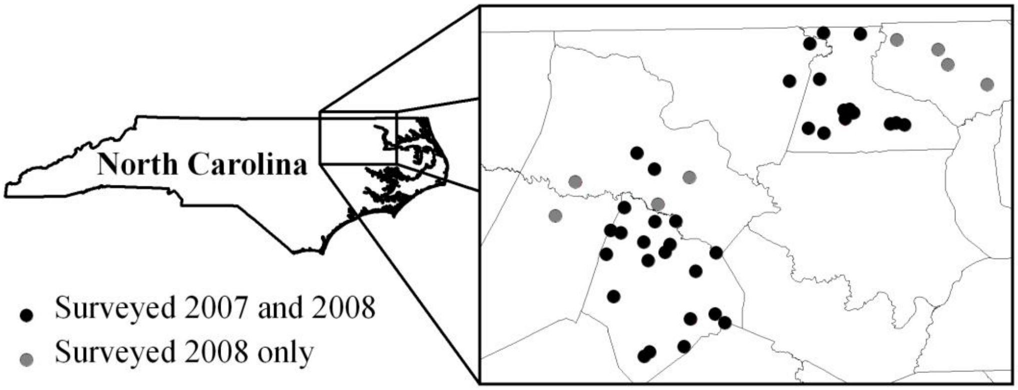


Figure 1. Location of 43 early successional forested riparian buffer habitat patches surveyed for shrubland bird occurrence in North Carolina, USA, 2007-2008.

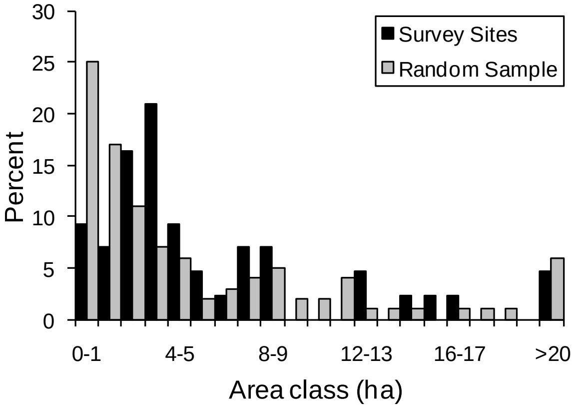
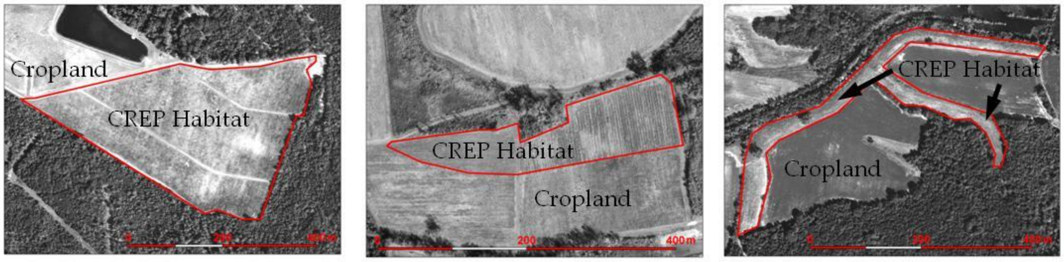


Figure 2. Histogram showing % of total habitat patches in 1 ha area classes for survey sites (*n* = 43) and randomly-selected habitat patches (*n* = 100) in North Carolina, USA, 2007-2008.



Area = 3.4 ha SI = 3.32 Area = 2.6 ha SI = 1.70 Area = 12.6 ha SI = 1.29

Figure 3. Examples of area and shape index (SI) of three early-successional forested riparian buffer habitat patches surveyed for bird occurrence in North Carolina, USA, 2007-2008. Base maps are 2003 orthophoto images and red lines indicate habitat patch edges.

Table 2. Model set and number of model parameters (K) for multi-season occupancy modeling of shrubland birds in North Carolina, U.S.A, 2007-2008. Occupancy (ψ) for each species is modeled relative to three patch-specific covariates: area, shape index (SI), and percent forest cover within 1 km of each patch (%Forest). Detection probability (p) was held constant (p(.) in models 1-10) or allowed to vary by observer (p(obs) in models 11-20). Colonization (γ) and local extinction (ε) parameters were left constant in all models.

Model	**K**
(1) ψ(.) γ(.) ε(.) p(.)	4
(2) ψ(area) γ(.) ε(.) p(.)	5
(3) ψ(SI) γ(.) ε(.) p(.)	5
(4) ψ(%Forest) γ(.) ε(.) p(.)	5
(5) ψ(area + SI + area*SI) γ(.) ε(.) p(.)	7
(6) ψ(area + SI) γ(.) ε(.) p(.)	6
(7) ψ(area + %Forest) γ(.) ε(.) p(.)	6
(8) ψ(SI + %Forest) γ(.) ε(.) p(.)	6
(9) ψ(area + SI + %Forest) γ(.) ε(.) p(.)	7
(10) ψ(area + SI + area*SI + %Forest) γ(.) ε(.) p(.)	8
(11-20) Models 1-10, but with p(obs)	Original + 3

Table 3. Patch occupancy (ψ) and detection probability (p) during the breeding season for nine shrubland bird species in early-successional forested riparian buffer habitat patches (n = 35 in 2007 and n = 43 in 2008) in North Carolina, U.S.A. (in order of highest occupancy to lowest). Estimates are from the constant occupancy and detection probability model, $\psi(.)\ \gamma(.)\ \varepsilon(.)\ p(.)$.

Species	ψ (SE)		p (SE)
	2007	2008	
Indigo bunting	0.97 (0.03)	0.95 (0.06)	1.00 (0.00)
Field sparrow	0.97 (0.03)	0.86 (0.18)	0.96 (0.10)
Common yellowthroat	0.97 (0.03)	0.88 (0.22)	1.00 (0.00)
Prairie warbler	0.82 (0.07)	0.74 (0.07)	0.98 (0.01)
Yellow-breasted chat	0.81 (0.07)	0.65 (0.07)	0.96 (0.02)
Eastern towhee	0.80 (0.07)	0.82 (0.06)	0.90 (0.03)
Blue grosbeak	0.79 (0.08)	0.69 (0.07)	0.83 (0.04)
White-eyed vireo	0.54 (0.09)	0.69 (0.08)	0.77 (0.05)
Brown thrasher	0.09 (0.05)	0.14 (0.05)	0.87 (0.09)

Table 4. Top models (ΔAIC < 2) and best constant occupancy model (ψ(.)…) for patch occupancy of seven scrub-successional bird species in early-successional forested riparian buffer habitat patches in North Carolina, USA, 2007-2008. Occupancy (ψ) for each species is modeled relative to three patch-specific covariates: area, shape index (SI), and percent forest cover within 1 km (%Forest). Detection probability was modeled as constant, *p*(.), or varied by observer, *p*(obs). Colonization (γ) and local extinction (ε) were constant in all models and omitted from model descriptions.

Species	Model	ΔAIC [a]	w_i	- 2*Log Likelihood
BLGR	ψ (.) *p*(obs)	0.00	0.24	158.74
	ψ (area + SI + area*SI) *p*(obs)	0.09	0.23	152.82
	ψ (%Forest) *p*(obs)	1.57	0.11	158.31
	ψ (SI) *p*(obs)	1.72	0.11	158.45
	ψ (area + SI + area*SI + %Forest) *p*(obs)	1.86	0.09	152.59
	ψ (area) *p*(obs)	2.00	0.09	158.74
EATO	ψ (area) *p*(obs)	0.00	0.33	132.07
	ψ (area + %Forest) *p*(obs)	1.80	0.13	131.87
	ψ (area + SI) *p*(obs)	1.99	0.12	132.06
	ψ (.) *p*(obs)	2.57	0.09	136.64
PRAW	ψ (area) *p*(obs)	0.00	0.24	85.02
	ψ (area + SI) *p*(obs)	0.66	0.17	83.68
	ψ (area + %Forest) *p*(obs)	1.60	0.11	84.63
	ψ (area + SI + %Forest) *p*(obs)	1.93	0.09	82.95
	ψ (.) *p*(obs)	4.26	0.03	91.28
WEVI	ψ (area) *p*(obs)	0.00	0.28	159.66
	ψ (area + SI) *p*(obs)	1.01	0.17	158.67
	ψ (.) *p*(obs)	1.95	0.11	163.61
	ψ (area + %Forest) *p*(obs)	2.00	0.10	159.66
	ψ (area + SI + %Forest) *p*(obs)	2.00	0.10	157.66

table continued next page…

YBCH	ψ (area + SI) *p*(obs)	0.00	0.20	94.06
	ψ (area + SI) *p*(.)	0.63	0.15	100.69
	ψ (area + SI + %Forest) *p*(obs)	1.19	0.11	93.25
	ψ (area) *p*(obs)	1.23	0.11	97.29
	ψ (area) *p*(.)	1.75	0.08	103.81
	ψ (area + SI + %Forest) *p*(.)	1.80	0.08	99.86
	ψ (area + %Forest) *p*(obs)	1.86	0.08	95.92
	ψ (.) *p*(obs)	12.88	0.00	110.94

[a] Minimum AIC = 172.74 for BLGR; 148.07 for EATO; 101.02 for PRAW; 159.66 for WEVI; 112.06 for YBCH.

Table 5. Model-averaged beta estimates, standard error, and 95% confidence intervals of covariate effects on occupancy of early-successional forested riparian buffer habitat patches by seven shrubland bird species in North Carolina, USA, 2007-2008. Estimates and confidence intervals are on the logit scale.

Species	β (SE)	95% C.I.
Area		
BLGR	-0.06 (2.14)	-4.25, 4.13
EATO	2.01 (1.59)	-1.10, 5.12
PRAW	2.68 (1.44)	-0.13, 5.49
WEVI	0.96 (1.80)	-2.57, 4.50
YBCH	6.00 (1.94)	2.20, 9.80 [a]
Shape index		
BLGR	0.29 (1.98)	-3.58, 4.16
EATO	0.05 (2.00)	-3.88, 3.97
PRAW	-0.54 (1.94)	-4.35, 3.26
WEVI	-0.41 (2.38)	-5.08, 4.26
YBCH	-0.80 (1.32)	-3.38, 1.79
Area-shape index interaction		
BLGR	12.10 (1.36)	9.43, 14.77 [a]
EATO	1.14 (2.88)	-4.50, 6.79
PRAW	-0.81 (2.00)	-4.72, 3.11
WEVI	-2.96 (1.85)	-6.59, 0.67
YBCH	-0.02 (6.08)	-11.95, 11.90
% forest within 1 km		
BLGR	-0.25 (2.88)	-5.88, 5.39
EATO	-0.28 (2.18)	-4.55, 3.99
PRAW	0.32 (1.93)	-3.46, 4.10
WEVI	-0.05 (3.00)	-5.93, 5.83
YBCH	-0.49 (1.46)	-3.36, 2.37

[a] 95% confidence interval does not include zero; indicates strong evidence for covariate effect.

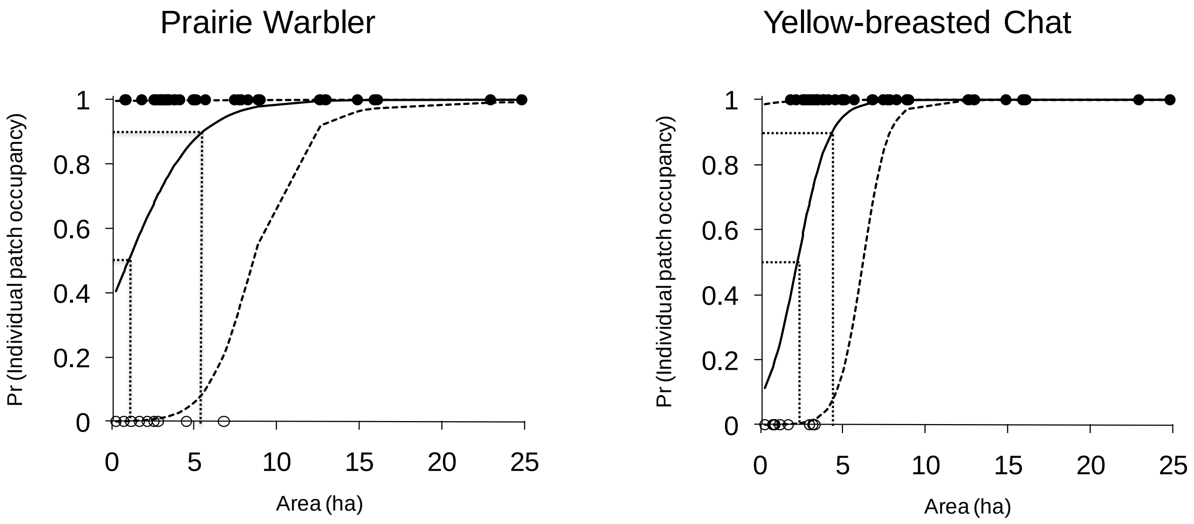


Figure 4. Individual patch occupancy estimates (solid lines) and 95% confidence intervals (dotted lines) relative to patch area, and occurrence data (closed dots = present, open dots = absent) for prairie warbler (*Dendroica discolor*) and yellow-breasted chat (*Icteria virens*) in early-successional forested riparian buffer habitat patches in North Carolina, USA, 2007-2008. Also shown are minimum area requirement (Pr[individual patch occupancy] = 0.5) and optimal area (Pr[individual patch occupancy] = 0.9) estimates. All estimates were calculated in Program PRESENCE using the multi-season model ψ(area) γ(.) ε(.) *p*(obs).

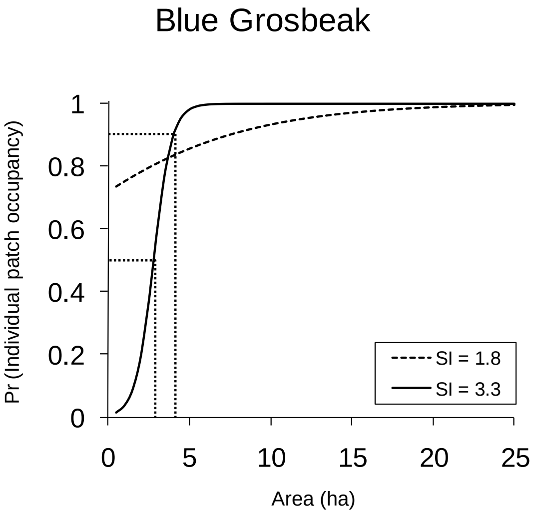


Figure 5. Predicted individual patch occupancy estimates relative to patch area at two shape index values for blue grosbeak in early-successional forested riparian buffer habitat patches in North Carolina, USA, 2007-2008. Shape index values represent the mean (1.8) and an extreme high (3.3) from our sample of patches. Occupancy estimates were calculated using beta estimates from the area-shape index interaction occupancy model, ψ(area + SI + area*SI) γ(.) ε(.) p(.).

CHAPTER 2

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 U.S., have not been thoroughly studied. In 2007 and 2008, we collected data on nests of five shrubland passerine species in 12 early successional forest patches in North Carolina, U.S.A. We used model selection methods to assess the effect of distance to cropland and mature forest edge on nest predation rates and accounted for other sources of variation, including 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 extinction of shrubland birds in regenerating 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.

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

The Journal of Wildlife Management: 00(0): 000-000, 200X

Predation is often the primary source of songbird nest failure and can have a significant influence on bird population dynamics (Martin 1992a, 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 (Lahti 2001), 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, Chalfoun et al. 2002a).

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 (Chasko and Gates 1982, King et al. 2001), while others showed that edge effects varied by edge type, bird species, and year (Suarez et al. 1997, 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 U.S. (Askins 1993). 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 U.S.; agricultural landscapes and the southeastern U.S. remain under-represented (but see Riddle 2007).

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, Mayfield 1961). Recent developments in nest survival modeling represent a significant 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 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 conducted a study to examine the effects of habitat edges on nest predation of shrubland birds in agricultural landscapes. We modeled daily nest predation 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 daily nest predation 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 to 7 years 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. We selected patches of varying size and shape 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 to 24.9 ha, with a mean and median area of 7.4 and 4.0 ha, respectively. Patches varied in shape from relatively 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. The landscape surrounding our patches was a mosaic of forested and cultivated land, though there was noticeable local variation in percentages of these two landcover types. The dominate forest types were second-growth and mature pine-oak woodlands (*Pinus* spp.-*Quercus* spp.)

in the uplands and gum-cypress swamps (*Nyssa sylvatica-Taxodium* spp.) in low-lying areas. The most common crops grown in the region were corn, soybeans, cotton, and tobacco.

METHODS

Nest monitoring.— We searched our 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 five focal species are open cup nesters that generally nest in shrubs or young trees, most often within 4 m of the ground. We conducted at least two 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 patches were searched the first time. We conducted the second search approximately one month after the first. We found additional nests opportunistically or with partial searches focused on bird behavior. We monitored all nests every three to four 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 estimated that date based on the assumption that the birds laid one egg per day. We considered a nest from which at least one 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 (no adult activity was observed 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/nestlings ejected due to extreme weather events). We determined the Universal Tranverse Mercator coordinates of each nest with a Garmin 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, California, USA).

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 five pairs of concentric 5-m and 11.3-m radius circular plots. Vegetation measurements were taken in both years at the same five points in each patch, and included vegetation height, woody stem density, and ground cover estimates. We measured vegetation height by selecting a single shrub or sapling within each 11.3-m radius plot that visually appeared to represent the average height of the dominant shrubs/saplings in the plot, and then averaged this value over all five plots. We counted the number of small woody plant stems (0.5-3 m tall) with their base inside the 5-m radius plot and the number of large woody stems (>3 m tall) within the 11.3-m radius plot. We added counts from all five sample plots and calculated small and large woody stem density as stems/m^2 and stems/ha, respectively. Woody plants <0.5 m tall were accounted for in visual estimates of ground cover, which was separated into four types: bareground/litter, graminoid, forb, and woody.

We estimated percent of each cover type within the 5-m plots and averaged these estimates across all five 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. Narrow strips of early-successional habitat <10 m wide that were connected to the patch were not considered part of the patch. We measured landscape context by quantifying the proportion of agricultural cover within 2.5 km of the edge of each habitat patch. Habitat type designations were based 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 two NLCD cover types: cultivated crops and pasture/hay. We chose to measure habitat at this landscape scale (approximately 20 km^2) for two reasons: (1) because shrubland bird nest success in the region was greater in agricultural-dominated landscapes than forest-dominated landscapes at this scale (Riddle 2007); 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).

Data Analysis

We evaluated the evidence for an effect of distance-to-edge on daily nest predation 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 daily nest predation 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 daily nest predation of all five species combined and for field sparrow and indigo bunting separately, two species for which we had adequate sample sizes (S. Dinsmore, personal communication). We believe that pooling of nest data across all five 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 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 single 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.
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 what we termed the “egg” stage. We hypothesized that daily nest predation 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 that nests closer to habitat edges would have higher daily nest predation rates because nest predators may use edges more readily than other habitats (e.g., Durner and Gates 1993, Dijak and Thompson 2000). However, because nest predation rates may differ at different types of edges (Suarez et al. 1997), we expected that the distance-to-edge effect might differ between our two edge types.

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 and foliage density, 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 it was more precisely estimated (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. Evidence suggests that nest survival may be higher in agriculture-dominated landscapes for some shrubland bird species in this region (Riddle 2007). Thus, we hypothesized that patches in landscapes with higher % agriculture within 2.5 km would have lower nest predation.

Our two categorical covariates, nest year and stage, were modeled as group covariates in Program MARK, resulting in a total of four 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 % agriculture within 2.5 km—were continuous covariates. The latter two covariates were patch-specific and all nests found in a patch were assigned the shrub/sapling height and % agriculture value of that patch.

To reduce the total number of models in our set, we used a hierarchical modeling approach, where we modeled temporal and nest stage effects first and then added additional covariates to the best of these models (Dinsmore and Dinsmore 2007; see Table 1 for models described below). We first fit an intercept-only model where daily nest predation was estimated across all groups (hereafter referred to as “constant predation” model; model 1). Next, we modeled differences in daily nest predation between years and stages (model 2 and

3). Then we modeled linear (T) and quadratic (TT) trends in daily nest predation within each year and each stage (models 4 – 7). To the single best model from these first seven 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 % 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 be different for each year. For this reason, we modeled an interaction term between temporal effects (e.g., year) and shrub/sapling height in models where the two effects were combined. Finally, we added the shrub/sapling height and % agriculture covariates to each of the three distance to edge covariate models singly and combined (models 14 – 22). Each continuous covariate appeared in eight models. All models were fit using a logit link function, and thus we reported estimates of covariate effects (hereafter, “betas” or “estimates”) on the logit scale.

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 our continuous covariates—distance to forest edge, distance to cropland edge, shrub/sapling height, interactions between shrub/sapling height and temporal effects, and % 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). They are an improvement over single-model estimates because they 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 daily nest predation 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 daily nest predation back-transformed from the logit scale for a range of values and then graphed the results. We predicted changes in daily nest predation only within the range of covariate values in our study.

RESULTS

We monitored 320 nests during the two seasons. Predation accounted for most of the 173 nest failures (88.4%), while desertion (9.2%), parasitism (1.2%), and weather (1.2%)

accounted for the remainder. After removing nests failed due to these latter three factors, we analyzed data from 300 nests of all species combined (effective sample size (*n*) = 2827 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* = 1188 and 722, respectively). The frequency of nest parasitism by brown-headed cowbirds was low in our study; only 19 of 300 nests analyzed were parasitized (6.3%) and only two of these failed as a result of being parasitized.

Distance to mature forest edge ranged from 2 to 276 m (median = 38 m, mean ± SE = 54 ± 46 m) and distance to cropland edge ranged from 1 to 362 m (median = 44 m, mean ± SE = 81 ± 82 m) among all species' nests. Distance to forest edge and distance to cropland edge were not correlated ($R^2 = 0.01$). Fifty-six to 61% of all nests were within 50 m of forest and cropland edges, and field sparrows nested less frequently and indigo bunting nested more frequently within 25 m of the forest edge (Fig. 1).

Estimates of mean shrub/sapling height of each patch in 2007 ranged from 2.1 to 4.7 m (mean ± SE = 3.2 ± 0.8), while 2008 estimates ranged from 3.6 to 5.9 m (mean ± SE = 4.8 ± 0.7). As we expected, mean shrub/sapling height estimates were positively correlated with % bare ground cover estimates ($R^2 = 0.54$ across both years of data). This strength of this correlation differed greatly 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% (mean ± SE = 33.9 ± 8.4).

In the analysis of all species combined, the between-year effects model (Table 1, model 2) was the best of the temporal and nest stage effect models (Akaike weight [w_i] = 0.42) and this model indicated that daily nest predation (DNP) was higher in 2008 than in 2007 (Table 2). Thus, a year effect was included 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 3). A predictive graph of daily nest predation based on the best model in the set, which contained distance to cropland edge, shrub/sapling height, 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 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 daily nest predation based on the best model in the set illustrates this difference. Predicted daily nest predation 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 to 6.0 m, respectively (Fig. 4). These predicted trends in daily nest predation relative to mean shrub/sapling height correspond very closely with the relationship of mean shrub/sapling height and % bare ground cover; there appears to be a concurrent increase in nest predation as % bare ground cover increases (Fig. 2). Confidence intervals for estimates of distance to forest edge and % agriculture in the landscape overlapped zero considerably (Table 4), which provided little evidence that these covariates influence nest survival of all species combined.

Field sparrow nest predation also differed between the two years 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 daily nest predation on field sparrow nests was lower in patches located in landscapes with higher % agriculture. The effect was more pronounced in 2008, where predicted daily nest predation in landscapes with 20% agricultural cover was over three times higher than predicted nest predation in landscapes with 45% agricultural cover (DNP = 0.16 and DNP = 0.05, respectively; Fig. 5). 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 of the beta estimates of these covariates were the same as in the pooled species analysis.

The between-year effect model was the best of the temporal and nest stage effects models in the indigo bunting analysis as well ($w_i = 0.33$), and nest predation was higher in 2008 than in 2007 (Table 2). There was no strong evidence that suggested that any of our 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 % 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 varies 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 observed in the pooled data diminished when we analyzed nests of the two most abundant species separately, but the direction of the effect was still positive. 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 edges in southern Illinois. In Missouri, Woodward et al. (2001) also observed no significant increase in nest predation near mature forest edges for field sparrows, indigo buntings, and for combined nests of five focal species nearly identical to ours (with northern cardinal [*Cardinalis cardinalis*] instead of blue grosbeak). Moorman et al. (2002) reported no increases in nest predation near early successional/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 U.S. 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 in Suarez et al. (1997), Woodward et al. (2001), and Moorman et al. (2002). Given that edge effects on nest predation vary depending on regional predator communities (Chalfoun et al. 2002a), the consistency of our results to those with similar predator communities is expected.

Habitat use and abundance patterns of primary nest predators may help explain why we observed higher nest predation at cropland edges but not at mature forest edges. Higher nest predation near cropland edges may have been the result of increased nest depredation by predators that frequently use habitat edges adjacent to crop fields. 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, Dijak and Thompson 2000, Suarez et al. 1997). To explain the lack of a mature forest edge effect, we argue that black rat snakes

(*Elaphe obsoleta obsoleta,* perhaps the most common snake in our study habitats) and raccoons may not concentrate activity at mature forest edges (as documented by Dijak and Thompson 2000, Blouin-Demers and Weatherhead 2001, Chalfoun et al 2002b) when early successional habitat is available nearby, because both species select shrubland or early successional forest habitats disproportionate to their availability (Weatherhead and Charland 1985, Durner and Gates 1993, Chamberlin et al. 2003).

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 our habitat patches. Although we cannot make a causal link between the two 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 1992b, 1993, Moorman et al. 2002). We suggest that the reduction in nest survival associated with natural forest succession we observed could be one mechanism for local extinction 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.

Nest predation also was influenced by the landscape surrounding a habitat patch. Field sparrow nest predation was considerably lower in habitat patches with high % agricultural cover within 2.5 km. Our results are similar to those of Riddle (2007), 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 U.S., where forest-breeding birds experience higher nest predation rates in areas with higher percent agricultural cover (Robinson et al. 1995) because mammalian and avian nest predators are often more abundant in these landscapes (Andrén 1995, Dijak and Thompson 2000). The 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 our landscapes was not above 47%. Differences in nest predator communities and variation in predator's response to landscape composition might also explain these differences. However, because we did not directly identify nest predators or estimate predators' relative abundance in our study area, we refrain from speculating on these differences. Future studies of shrubland bird nest survival would be most useful if they directly identified nest predator communities (e.g., Thompson and Burhans 2003) and quantitatively linked predator abundance to landscape composition.

Providing habitats that increase nest survival likely will contribute to stabilizing shrubland bird populations. However, 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. Furthermore, breeding productivity is not the only relevant bird response variable when considering adequate patch width or size. Patch occupancy and abundance of shrubland birds also are influenced by patch size; many species avoid edges and some are area-sensitive (Rodewald and Vitz 2005, Schlossberg and King 2008, Shake 2009).

MANAGEMENT IMPLICATIONS

When restoring early successional and shrubland habitat adjacent to rowcrop agriculture, we suggest that land managers should 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 – 15 year intervals would help maximize shrubland bird density and diversity. Given that our oldest sites were established no more than 7 years 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 pre-commercial thinning or more widely-spaced planting arrangements to help maintain understory vegetation for longer periods. Finally, our results also suggest that habitat restoration projects in landscapes with higher 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 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.

ACKNOWLEDGMENTS

We appreciate the hard work of field technicians W. Ricks and J. Trutwin and the input on study design and analysis from J. Riddle. We thank S. Dinsmore, G. Hess, and T. Simons for their helpful reviews of this manuscript. This study was funded by a grant from the North Carolina Department of Environment and Natural Resources, Division of Soil and Water Conservation.

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Associate Editor:

TABLES AND FIGURES

Table 1. Model set and number of model parameters (K) for modeling daily nest predation of shrubland birds relative to nest- and patch-specific covariates using AIC 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 % 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

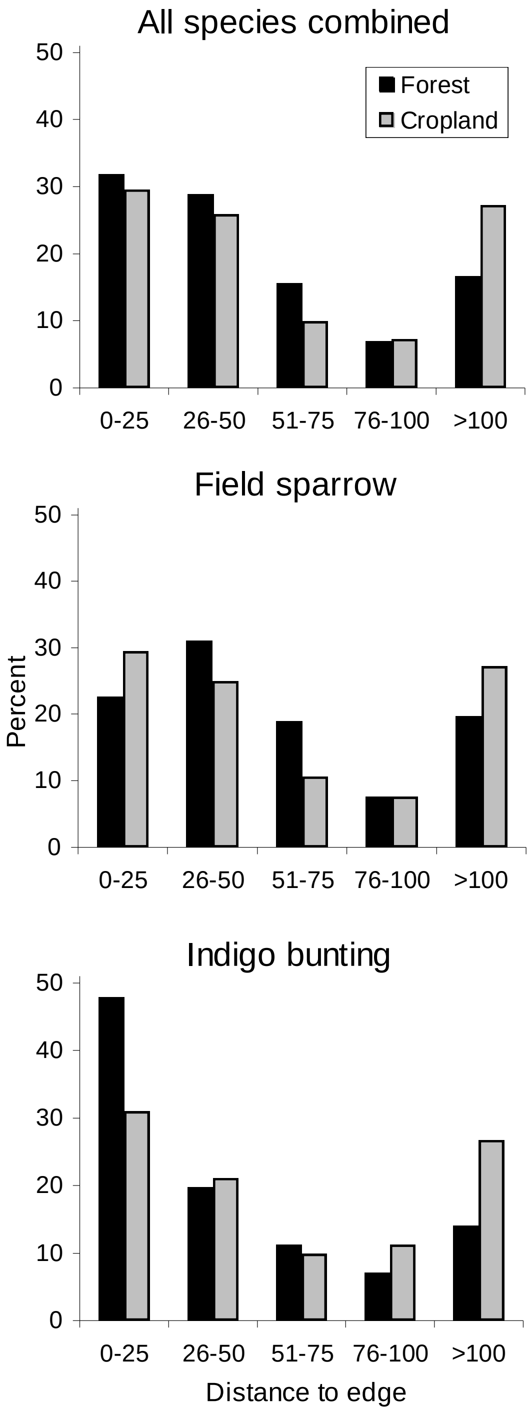

Figure 1. Distribution of shrubland bird nests relative to mature forest and cropland habitat edges in early successional forested riparian buffers in North Carolina, USA, 2007 and 2008.

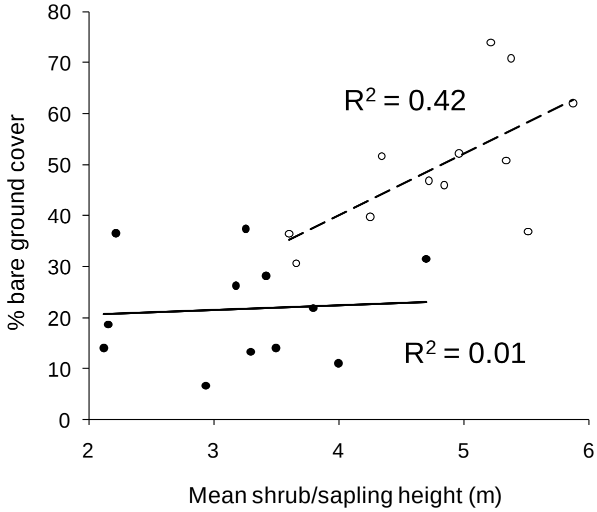

Figure 2. Linear relationship and correlation coefficient (R^2) between within-patch estimates of mean shrub/sapling height and % bare ground cover in 2007 (filled dots and solid line) and 2008 (open dots and dashed line) for 12 early successional forested riparian buffers in North Carolina, USA.

Table 2. Effective sample size (*n*) and estimates of daily nest predation for shrubland birds in early successional forested riparian buffers in North Carolina, USA, 2007 and 2008. Yearly estimates are calculated from the between-year effects model (Daily nest predation = Year), while the overall estimate is calculated from the constant predation model.

Species	*n*	Daily nest predation (± SE)		
		2007	2008	Overall
All species combined	2827	0.041 ± 0.005	0.058 ± 0.006	0.049 ± 0.004
Field sparrow	1188	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

Table 3. Model selection results showing best models (ΔAIC ≤ 2) and 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 % agriculture cover within 2.5 km (PctAg). The all species combined data set includes nests of field sparrow (*Spizella pusilla*), indigo bunting (*Passerina cyanea*), blue grosbeak (*Passerina caerulea*), yellow-breasted chat (*Icteria virens*), and prairie warbler (*Dendroica discolor*).

Analysis Model description	ΔAIC [a]	w_i	- 2*Log Likelihood
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 with standard error 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 % agriculture cover within 2.5 km (PctAg). All species combined includes nests of field sparrow (*Spizella pusilla*), indigo bunting (*Passerina cyanea*), blue grosbeak (*Passerina caerulea*), yellow-breasted chat (*Icteria virens*), and prairie warbler (*Dendroica discolor*).

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

[a] Indicates strong evidence of a covariate effect, where confidence interval does not overlap zero.

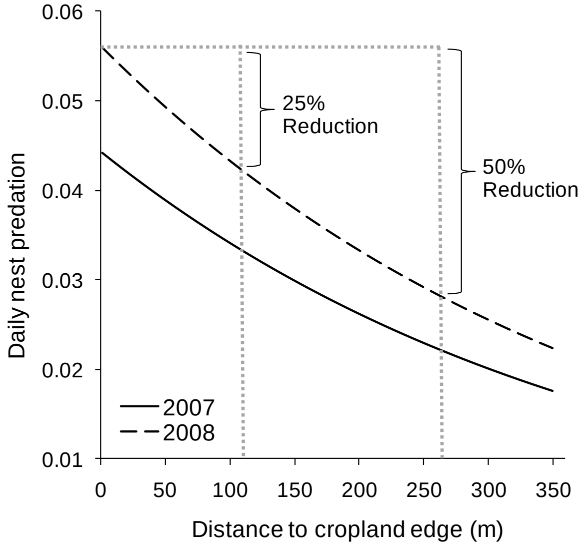

Figure 3. Predicted daily nest predation at varying distances from the cropland edge for five shrubland bird species in early-successional forested riparian buffers in North Carolina, USA, 2007 and 2008. Predictions are based on estimates from the model (daily nest predation = Year + DE Crop + SSHgt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

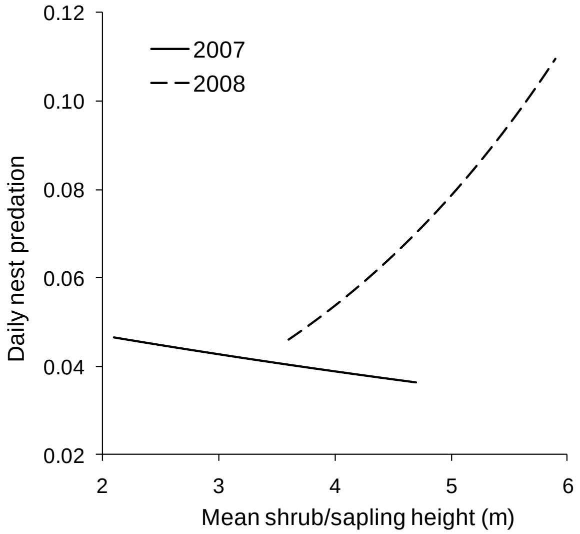

Figure 4. Predicted daily nest predation for five shrubland bird species in early-successional forested riparian buffer patches with varying mean shrub/sapling height (SSHgt) in North Carolina, USA, 2007 and 2008. Predictions are based on the model (daily nest predation = Year + DE Crop + SSHgt + Year*SSHgt),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

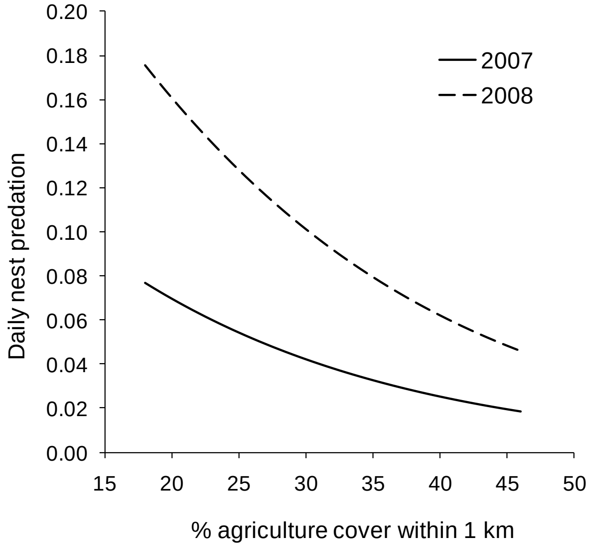

Figure 5. Predicted daily nest predation with varying % agricultural cover within 2.5 km of a patch (PctAg) for field sparrows (*Spizella pusilla*) in early-successional forested riparian buffers in North Carolina, USA, 2007 and 2008. Predictions are based on the model (daily nest predation = Year + PctAg).