

INFLUENCE OF PATCH SIZE AND SHAPE ON OCCUPANCY BY SHRUBLAND BIRDS

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Abstract. Populations of many shrubland bird species are declining in the eastern United States. Efforts to restore shrubland and early-successional forest may help to ameliorate these declines. However, uncertainty remains about how the size and shape of habitat patches and the surrounding habitat matrix affect patch occupancy by shrubland passerines. Our objectives were to determine if shrubland birds avoid small or irregularly shaped habitat patches and to identify minimum area requirements for area-sensitive species. Additionally, we sought to determine if the proportion of mature forest cover in the landscape influences patch occupancy. We surveyed 35 individual habitat patches in 2007 and 43 in 2008 for the presence of eight shrubland birds. Then, we modeled the probability of five of these species occupying an individual patch relative to patch area, patch shape, and percent forest cover within 1 km of the patch. We documented evidence of area sensitivity for the Yellow-breasted Chat (*Icteria virens*) and Prairie Warbler (*Setophaga discolor*) and estimated their minimum area requirements at 2.3 and 1.1 ha, respectively. The Blue Grosbeak (*Passerina caerulea*) also was area-sensitive in irregularly shaped patches. Predicted patch-occupancy probability was >0.9 in patches ≥5.5 ha for all area-sensitive species. Patch shape alone and proportion of forest cover were not important predictors of occupancy for these 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, occupancy modeling, Prairie Warbler, shrubland birds, Yellow-breasted Chat.

Influencia del Tamaño y la Forma del Parche en el Nivel de Ocupación por Parte de Aves de Matorral

Resumen. Las poblaciones de muchas especies de aves de matorral están disminuyendo en el este de Estados Unidos. Los esfuerzos para restaurar el matorral y el bosque en estadios sucesionales tempranos pueden ayudar a mejorar estas disminuciones. Sin embargo, se desconoce cómo el tamaño y la forma de los parches de hábitat y de la matriz de hábitat circundante afectan el nivel de ocupación de los parches por parte de los paserinos de matorral. Nuestros objetivos fueron determinar si las aves de matorral evitan los parches de hábitat pequeños y de forma irregular e identificar los requerimientos de área mínima para las especies sensibles al área. Adicionalmente, hemos tratado de determinar si la proporción de cobertura de bosque maduro en el paisaje influencia el nivel de ocupación de los parches. Inspeccionamos 35 parches de hábitat individuales en 2007 y 43 en 2008 para evaluar la presencia de ocho especies de aves de matorral. Luego, modelamos la probabilidad de que cinco de estas especies ocupen un parche individual con relación al área del parche, la forma del parche y el porcentaje de cobertura del bosque dentro de 1 km del parche. Documentamos la sensibilidad que pueden presentar *Icteria virens* y *Setophaga discolor* al tamaño del parche y estimamos sus requerimientos de área mínima en 2.3 y 1.1 ha, respectivamente. *Passerina caerulea* también fue una especie sensible al tamaño del parche en los parches de forma irregular. La probabilidad predicha de ocupación de los parches fue >0.9 en los parches ≥5.5 ha para todas las especies sensibles al tamaño del parche. La forma del parche por separado y la proporción de la cobertura del bosque no fueron variables predictivas importantes del nivel de ocupación de estas aves de matorral. Los matorrales restaurados y los bosque en estadios sucesionales tempranos inmersos en paisajes agrícolas pueden brindar hábitat a muchas especies de aves de matorral, pero los parches deberían ser >5 ha para maximizar la diversidad de aves de matorral.

INTRODUCTION

Numbers of many wildlife species associated with disturbance-dependent habitats have declined as a consequence of habitat loss in North America (Askins 1993, Dessecker and McAuley 2001, Hunter et al. 2001, Litvaitis 2001). In the eastern

United States, 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 agriculture (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

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(hereafter referred to as shrubland birds; Brawn et al. 2001, Hunter et al. 2001). Some shrubland birds, such as the Prairie Warbler (*Setophaga discolor*), are now considered high-priority species for conservation 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 U. S., where a large percentage of land is privately owned, several federal and state conservation programs and initiatives focus on habitat restoration on private land. The programs have various goals, including erosion reduction, water-quality improvement, and wildlife-habitat restoration, but most focus on converting cultivated agricultural land back to natural vegetation. In 2008, over 1.5 million ha in the United States were enrolled in federal programs that create shrubland and early-successional forest during all or part of their enrollment period (Farm Service Agency 2008). Enrollments most often are applied to single crop fields, so vegetation is restored as discrete habitat patches. The design of these restored habitat patches varies to fit the objectives of individual programs and landowners. Consequently, the size and shape of restored patches of early-successional and shrubland habitat can vary considerably. Improved understanding of the effects of patch area and shape on shrubland birds' habitat use would help ensure that restored patches are appropriately designed.

A patch's area influences whether some bird species will occupy it (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 in eastern North America. Although several studies have examined shrubland bird abundance in relation to patch size (Rudnicki and Hunter 1993, Lanham and Gynnn 1998, Kremetz and Christie 2000, Lehnen and Rodewald 2009), results have been inconsistent. Studies of shrubland bird abundance have shown evidence of area sensitivity, particularly in very small habitat patches. Some shrubland bird species were completely absent from patches <1 ha (Annand and Thompson 1997, Robinson and Robinson 1999, Costello et al. 2000, Moorman and Gynnn 2001), while only a few species, such as the Yellow-breasted Chat (*Icteria virens*), appeared area-sensitive in studies of larger patches (Lanham and Gynnn 1998, Gram et al. 2003, Rodewald and Vitz 2005, Askins et al. 2007, Chandler et al. 2009, Lehnen and Rodewald 2009).

A patch's shape also may influence whether a bird occupies it, particularly if the patch is small and the species tends to avoid habitat edges (Helzer and Jelsinki 1999). Little is known about the effect of patch shape on shrubland bird occupancy, but considerable evidence suggests many shrubland birds avoid habitat edges (Schlossberg and King 2008). On

the basis of their meta-analysis, Schlossberg and King (2008) recommend that shrubland bird conservation focus on providing large habitat patches and avoiding irregularly shaped patches. Though this finding is useful, more specific estimation of minimum patch-size requirements, especially for various patch shapes, is needed for shrubland birds.

Features in the surrounding landscape matrix also are likely to influence birds' use of individual patches (Lanham and Gynnn 1998, Gascon et al. 1999, Norton et al. 2000). Variation in the composition of various habitat types in the landscapes surrounding a habitat patch can explain a large proportion of the variation in communities of grassland and forest birds (Bakker et al. 2002), but studies of landscape effects on shrubland birds are few and the results are mixed. Mitchell et al. (2001) found the occurrence of some shrubland birds in managed forests in the southeastern U.S. to be related to landscape-scale habitat features, but the abundance of shrubland birds in clearcuts and beaver (*Castor canadensis*) meadows in the northeastern U.S. is 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 birds' habitat use, especially in agricultural landscapes.

Most studies of shrubland bird occupancy and abundance have not accounted for variation in species' detectability, an important potential source of bias in estimates based on bird counts (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 birds' occupancy of patches of restored early-successional forest and shrubland. Our overall objectives were (1) to detect and model patterns of area sensitivity and edge avoidance by shrubland birds, (2) to determine minimum area requirements for area-sensitive species, and (3) to determine if landscape composition influences shrubland bird occupancy.

METHODS

STUDY SITES

We studied restored patches of early-successional forest 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). The patches were enrolled in North Carolina's Conservation Reserve Enhancement Program (CREP), a state and federal cooperative incentive program aimed at reducing erosion, improving water quality, and restoring wildlife habitat in environmentally sensitive areas. Landscapes in this region are a mosaic of forest and cultivated

land, though there is noticeable local variation in percentages of these two land-cover types. Landscapes within 1 km of our study patches averaged 50% (SE = 14) mature forest, 38% (SE = 10) agricultural land, 11% (SE = 8) other (includes grassland, shrubland, early-successional forest, barren, open water, and developed). The dominant forest types are 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 are corn, soybeans, cotton, and tobacco.

In 2007, we surveyed 35 patches of restored early-successional forest for the occurrence of eight focal shrubland birds: the White-eyed Vireo (*Vireo griseus*), Prairie Warbler, Common Yellowthroat (*Geothlypis trichas*), Yellow-breasted Chat (*Icteria virens*), Eastern Towhee (*Pipilo erythrophthalmus*), Field Sparrow (*Spizella pusilla*), Blue Grosbeak (*Passerina caerulea*), and Indigo Bunting (*Passerina cyanea*). 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 patches studied ranged in size from 0.3 to 24.9 ha (mean = 6.1, SE = 5.7). A comparison of these 43 patches to 100 patches of CREP habitat randomly selected 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 arrangements for planting of hardwoods and pines. In all patches, loblolly pine (*Pinus taeda*) had been planted in rows, generally in a 3 × 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 patch's total area. Several other plants grew naturally into the patches after planting, but the distribution

and density of these plants within a single patch depended on the existing seed bank, surrounding vegetation, and previous management. The most common other plants were broomsedge bluestem (*Andropogon virginicus*), introduced cool-season grasses, eastern baccharis (*Baccharis halimifolia*), sapling sweetgum (*Liquidambar styraciflua*), blackberry (*Rubus* spp.), wax myrtle (*Morella cerifera*), and dogfennel (*Eupatorium capillifolium*). 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.

BIRD-OCCUPANCY SAMPLING

We sampled each habitat patch along a single straight-line transect 150 m long to determine presence or absence of all eight focal species. For each patch, we determined the start point and direction of the transect randomly, with the constraint that the transect line be completely within the patch. Our 150-m-long transect was sized to fit within our smallest and most linear patches. 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 patch. Because many of our focal species that maintained a territory inside the patch characteristically perched on tall trees at the edge of the patch to sing or foraged at the edge of cultivated fields, we considered observations in the first 10 m of adjacent habitat types as within the habitat patch. In all patches we sampled from transects of the same length and for the same duration (mean ± SE = 20 ± 1 min) because occurrence data sampled proportional to patch area can falsely indicate area sensitivity (Haila 1986, Horn et al. 2000). 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

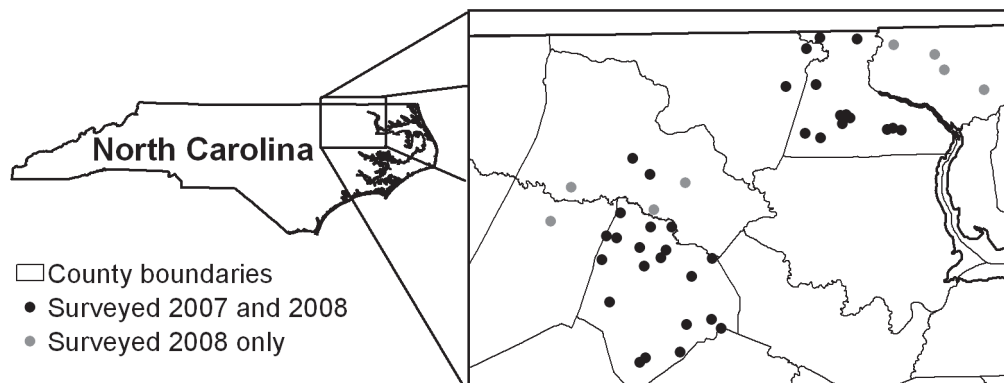


FIGURE 1. Location of 43 patches of early-successional forested riparian buffer habitat surveyed for occurrence of shrubland birds in North Carolina, 2007–2008.

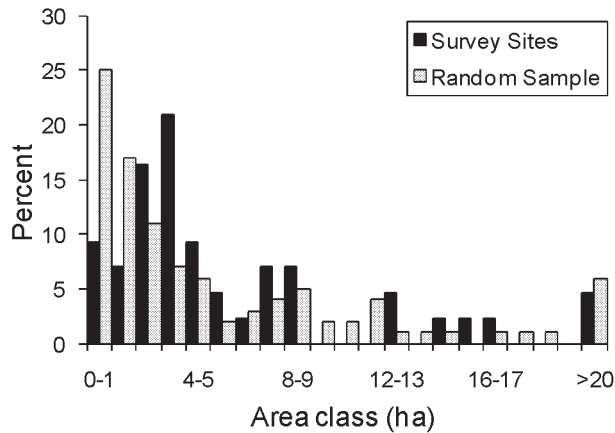


FIGURE 2. Histogram showing percentage of total habitat patches in 1-ha area classes for survey sites ($n = 43$) and randomly selected habitat patches ($n = 100$) in North Carolina, 2007-2008.

and 15 June. Within a year, the same two observers sampled all patches, but the observers in 2007 differed from those in 2008. All surveys were conducted from sunrise until 09:00 EST and only in the absence of high winds and rain.

PATCH CHARACTERISTICS

To measure the size and shape of our habitat patches, we delineated the perimeters of individual patches with spatially referenced aerial photo data, then calculated patch size and perimeter with ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA). We calculated each patch's shape index, which is a measure of the deviation in the perimeter of a given patch from the perimeter of a circular patch of the same area: $\text{shape index} = \text{perimeter} / [2\sqrt{(\pi \times \text{area})}]$. Our use of this metric avoids the high correlation between a standard perimeter-area ratio metric and area, which is useful for distinguishing 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 the shape of a patch becomes more irregular (Fig. 3).

We measured the proportion of mature forest within 1 km of each habitat patch in ArcGIS 9.2 with cover-type data from the most recent National Landcover Dataset, 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 (Saab 1999). We pooled four vegetation types, evergreen forest, deciduous forest, mixed forest, and woody wetlands, as mature forest (see Homer et al. 2004 for all cover types). We used percent mature forest as our landscape variable in occupancy modeling for two reasons: (1) most of our focal bird species do not breed in mature forest and thus may not readily colonize shrubland patches isolated in landscapes with high cover of inhospitable mature forest (Andren 1994, Dunning et al. 1995) and (2) mature forest is classified from Landsat imagery with much higher accuracy than is early-seral forest (Sader et al. 1991).

STATISTICAL ANALYSES

We used an independent double-observer approach for bird sampling because it allowed for estimation of each observer's probability of detecting 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) is 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-min count period (Nichols et al. 2009). We used the program PRESENCE 2.0 (Hines 2006) to analyze our occupancy data, which allowed us to compare models by Akaike's information criterion (AIC) (Burnham and Anderson 2002). This information-theoretic approach

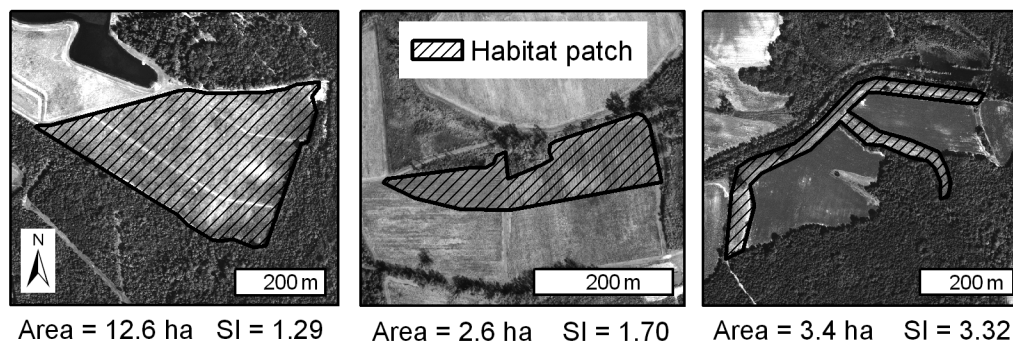


FIGURE 3. Examples of area and shape index (SI) of three early-successional forested riparian buffer habitat patches surveyed for bird occurrence in North Carolina, 2007-2008. Base maps are 2003 ortho-photo images and hatched lines indicate habitat patch edges.

allowed us to assess the influence of covariates on occupancy and detection probability by examining the evidence from a set of competing models (Burnham and Anderson 2002). Because our data were collected over 2 years, we used multi-season models (with year as season) in PRESENCE, which estimate rates of colonization (γ) and local extinction (ϵ) in the two seasons. For models that include covariates, PRESENCE also estimates individual patch occupancy, which is defined as the probability a species will occupy a given patch. We used the original parameterization of the multi-season models of Mackenzie et al. (2006), 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 covariates' effects over all years of data, allowed us to determine if the patterns observed were consistent in both years. Although we did not survey eight of the 43 patches in 2007, missing observations are acceptable and accommodated in multi-season models (MacKenzie et al. 2006:195).

We developed a model set based on a priori hypotheses that patch occupancy of eight scrub-successional birds may be affected by patch area, shape index, and/or landscape composition. We first fit the data to a baseline model in which occupancy was constant across all patches and did not vary with any patch-specific covariates [denoted as $\psi(\cdot)$, Table 1, model 1]. Next, we modeled occupancy relative to area and hypothesized that if a species is area-sensitive, its occupancy of smaller patches should be reduced (i.e., a positive effect of area; Table 1, model 2). We then modeled occupancy relative to shape index and hypothesized that occupancy of irregularly shaped patches by species that avoid edges should be reduced (i.e., a negative relationship with shape index; Table 1,

TABLE 1. Model set and number of model parameters (K) for multi-season occupancy modeling of shrubland birds in North Carolina, 2007–2008. For each species, occupancy (ψ) 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 [$p(\cdot)$ in models 1–10] or allowed to vary by observer [$p(\text{obs})$ in models 11–20]. Parameters for colonization (γ) and local extinction (ϵ) were left constant in all models.

Model	K
(1) $\psi(\cdot) \gamma(\cdot) \epsilon(\cdot) p(\cdot)$	4
(2) $\psi(\text{area}) \gamma(\cdot) \epsilon(\cdot) p(\cdot)$	5
(3) $\psi(\text{SI}) \gamma(\cdot) \epsilon(\cdot) p(\cdot)$	5
(4) $\psi(\% \text{ forest}) \gamma(\cdot) \epsilon(\cdot) p(\cdot)$	5
(5) $\psi(\text{area} + \text{SI} + \text{area} * \text{SI}) \gamma(\cdot) \epsilon(\cdot) p(\cdot)$	7
(6) $\psi(\text{area} + \text{SI}) \gamma(\cdot) \epsilon(\cdot) p(\cdot)$	6
(7) $\psi(\text{area} + \% \text{ forest}) \gamma(\cdot) \epsilon(\cdot) p(\cdot)$	6
(8) $\psi(\text{SI} + \% \text{ forest}) \gamma(\cdot) \epsilon(\cdot) p(\cdot)$	6
(9) $\psi(\text{area} + \text{SI} + \% \text{ forest}) \gamma(\cdot) \epsilon(\cdot) p(\cdot)$	7
(10) $\psi(\text{area} + \text{SI} + \text{area} \times \text{SI} + \% \text{ forest}) \gamma(\cdot) \epsilon(\cdot) p(\cdot)$	8
(11–20) Models 1–10, but with $p(\text{obs})$	Original + 3

model 3). Next, we modeled the effect of percent forest cover within 1 km and hypothesized that occupancy should be lower in patches surrounded by high percent forest cover (Table 1, model 4). We also hypothesized that area sensitivity may be more pronounced in patches with a high shape index, so we modeled an interaction between area and shape index (Table 1, model 5). Finally, we modeled the covariates in various combinations (Table 1, models 6–10).

We also hypothesized that detection probability (p) may differ by observer for some species, because of variation in observers' level of experience, hearing ability, or judgment of distance to observed birds. To examine this effect, we ran the same 10 models described above but allowed p to vary for each of the four observers [denoted $p(\text{obs})$; Table 1, models 11–20]. We left parameters for colonization (γ) and local extinction (ϵ) constant in all models because we did not expect them to vary for any species relative to any of the measured covariates, which were the same in the 2 years, but rather we expected them 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 modeled estimates of covariates' effects. First, we examined whether the best models in the set explained the data better than constant-occupancy models [i.e., $\psi(\cdot)$...]. Next, we identified which covariates were consistently included in the best models in the set. The final and most critical evidence, however, was the estimates of covariates' effects and their standard errors (hereafter, "beta estimates" or "betas"). Instead of reporting beta estimates from a single best model, we report 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 the models containing that covariate, weighted by each model's Akaike weight (Burnham and Anderson 2002:150–167). We calculated 95% confidence intervals for each model-averaged estimate (95% CI = estimate $\pm$ 1.96 $\times$ standard error). We considered estimates whose confidence interval did not overlap zero to provide strong evidence of a covariate's effect. Covariates whose confidence intervals were nearly centered on zero provided little evidence of such an effect.

For species that showed strong evidence of a covariate's effect, we graphed individual estimates of patch occupancy and their 95% confidence intervals with respect to that covariate. 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's predictions to identify the area at which we would expect the point estimate of patch occupancy to be equal to 0.5. We suggest this value as a minimum-area requirement because we 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 term the “optimal area value,” the area at which the model estimated the occupancy of the patch to be equal to 0.9. This value provided a minimum area for greater certainty that a species occupies a given patch.

RESULTS

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

Occupancy was high for the Common Yellowthroat, Field Sparrow, and Indigo Bunting (Table 2). Because these three species occupied nearly all the patches, we excluded them from the model-selection analysis. Occupancy estimates for all species were similar in the 2 years, the greatest differences being 0.15 and 0.16 for the White-eyed Vireo and Yellow-breasted Chat, respectively (Table 2). The probability of detection of all species was relatively high (Table 2), 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 [... $p(\text{obs})$]; Table 3].

Patch area was a good predictor of patch occupancy for two species, the 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 3). 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 4, Fig. 4). Patch area was consistently in the best models for the Prairie Warbler as well (Table 3), and the confidence interval of the model-averaged estimate of beta for patch area only slightly overlapped zero, indicating moderately strong evidence of a

TABLE 2. Patch occupancy (ψ) and detection probability (p) during the breeding season for eight species of shrubland birds in patches of early-successional forested riparian buffer habitat ($n = 35$ in 2007 and $n = 43$ in 2008) in North Carolina. Estimates are from the model with occupancy and detection probability constant, $\psi(\cdot) \gamma(\cdot) \epsilon(\cdot) p(\cdot)$.

Species	ψ (SE)		p (SE)
	2007	2008	
White-eyed Vireo	0.54 (0.09)	0.69 (0.08)	0.77 (0.05)
Prairie Warbler	0.82 (0.07)	0.74 (0.07)	0.98 (0.01)
Common Yellowthroat	0.97 (0.03)	0.88 (0.22)	1.00 (0.00)
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)
Field Sparrow	0.97 (0.03)	0.86 (0.18)	0.96 (0.10)
Blue Grosbeak	0.79 (0.08)	0.69 (0.07)	0.83 (0.04)
Indigo Bunting	0.97 (0.03)	0.95 (0.06)	1.00 (0.00)

patch-area effect (Table 4, Fig. 4). For the Yellow-breasted Chat, we estimated a minimum-area requirement (where individual patch occupancy probability = 0.5) of 2.3 ha and an optimal area value (where individual patch occupancy probability = 0.9) of 4.4 ha. For the Prairie Warbler, we estimated

TABLE 3. Top models ($\Delta\text{AIC} < 2$) and best constant-occupancy model [$\psi(\cdot) \dots$] for patch occupancy of five species of scrub-successional birds in patches of early-successional forested riparian buffer habitat in North Carolina, 2007–2008. Colonization (γ) and local extinction (ϵ) were constant in all models and are omitted from the models' descriptions.

Species and model	ΔAIC^a	w_i	$-2(\log \text{likelihood})$
White-eyed Vireo			
$\psi(\text{area}) p(\text{obs})$	0.00	0.28	159.66
$\psi(\text{area} + \text{SI}) p(\text{obs})$	1.01	0.17	158.67
$\psi(\cdot) p(\text{obs})$	1.95	0.11	163.61
$\psi(\text{area} + \% \text{ forest}) p(\text{obs})$	2.00	0.10	159.66
$\psi(\text{area} + \text{SI} + \text{area} \times \text{SI}) p(\text{obs})$	2.00	0.10	157.66
Prairie Warbler			
$\psi(\text{area}) p(\text{obs})$	0.00	0.24	85.02
$\psi(\text{area} + \text{SI}) p(\text{obs})$	0.66	0.17	83.68
$\psi(\text{area} + \% \text{ forest}) p(\text{obs})$	1.60	0.11	84.63
$\psi(\text{area} + \text{SI} + \% \text{ forest}) p(\text{obs})$	1.93	0.09	82.95
$\psi(\cdot) p(\text{obs})$	4.26	0.03	91.28
Yellow-breasted Chat			
$\psi(\text{area} + \text{SI}) p(\text{obs})$	0.00	0.20	94.06
$\psi(\text{area} + \text{SI}) p(\cdot)$	0.63	0.15	100.69
$\psi(\text{area} + \text{SI} + \% \text{ forest}) p(\text{obs})$	1.19	0.11	93.25
$\psi(\text{area}) p(\text{obs})$	1.23	0.11	97.29
$\psi(\text{area}) p(\cdot)$	1.75	0.08	103.81
$\psi(\text{area} + \text{SI} + \% \text{ forest}) p(\cdot)$	1.80	0.08	99.86
$\psi(\text{area} + \% \text{ forest}) p(\text{obs})$	1.86	0.08	95.92
$\psi(\cdot) p(\text{obs})$	12.88	0.00	110.94
Eastern Towhee			
$\psi(\text{area}) p(\text{obs})$	0.00	0.33	132.07
$\psi(\text{area} + \% \text{ forest}) p(\text{obs})$	1.80	0.13	131.87
$\psi(\text{area} + \text{SI}) p(\text{obs})$	1.99	0.12	132.06
$\psi(\cdot) p(\text{obs})$	2.57	0.09	136.64
Blue Grosbeak			
$\psi(\cdot) p(\text{obs})$	0.00	0.24	158.74
$\psi(\text{area} + \text{SI} + \text{area} \times \text{SI}) p(\text{obs})$	0.09	0.23	152.82
$\psi(\% \text{ forest}) p(\text{obs})$	1.57	0.11	158.31
$\psi(\text{SI}) p(\text{obs})$	1.72	0.11	158.45
$\psi(\text{area} + \text{SI} + \text{area} \times \text{SI} + \% \text{ forest}) p(\text{obs})$	1.86	0.09	152.59
$\psi(\text{area}) p(\text{obs})$	2.00	0.09	158.74

^aMinimum AIC = 159.66 for the White-eyed Vireo; 101.02 for the Prairie Warbler; 112.06 for the Yellow-breasted Chat; 148.07 for the Eastern Towhee; 172.74 for the Blue Grosbeak.

a minimum-area requirement of 1.1 ha and an optimal area value of 5.5 ha (Fig. 4). Although area appeared consistently in the best models for the Eastern Towhee and White-eyed Vireo, 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 3 and 4).

For the Blue Grosbeak, patch occupancy also appeared unrelated to patch area when the covariate was considered alone, but the model with an interaction of area and shape index received support nearly equal to that of the best model in the set (Table 3). The model-averaged beta estimate of the effect of the area–shape index interaction on Blue Grosbeak occupancy was strongly positive (Table 4). The positive effect

TABLE 4. Model-averaged beta estimates, standard error, and 95% confidence intervals of effects of covariates on occupancy of patches of early-successional forested riparian buffer habitat by five shrubland bird species in North Carolina, 2007–2008. Estimates and confidence intervals are on the logit scale.

Species	β (SE)	95% C.I.
Area		
White-eyed Vireo	1.48 (2.06)	–2.56, 5.51
Prairie Warbler	2.75 (1.54)	–0.27, 5.51
Yellow-breasted Chat	6.09 (2.37)	1.44, 10.74 ^a
Eastern Towhee	1.98 (1.64)	–1.23, 5.20
Blue Grosbeak	–6.54 (5.04)	–16.41, 3.34
Shape index		
White-eyed Vireo	–0.22 (2.41)	–4.94, 4.51
Prairie Warbler	–0.51 (1.96)	–4.36, 3.34
Yellow-breasted Chat	–0.84 (1.43)	–3.65, 1.97
Eastern Towhee	0.03 (1.98)	–3.84, 3.91
Blue Grosbeak	–1.16 (2.32)	–5.70, 3.38
Area–shape index interaction		
White-eyed Vireo	–2.96 (1.85)	–6.59, 0.67
Prairie Warbler	–0.81 (2.00)	–4.72, 3.11
Yellow-breasted Chat	0.18 (4.28)	–8.21, 8.58
Eastern Towhee	1.14 (2.88)	–4.50, 6.79
Blue Grosbeak	12.10 (1.36)	9.43, 14.77 ^a
Percent forest within 1 km		
White-eyed Vireo	–0.05 (3.00)	–5.93, 5.83
Prairie Warbler	0.32 (1.93)	–3.46, 4.10
Yellow-breasted Chat	–0.49 (1.46)	–3.36, 2.37
Eastern Towhee	–0.28 (2.18)	–4.55, 3.99
Blue Grosbeak	–0.25 (2.88)	–5.88, 5.39

^a95% confidence interval does not include zero; indicates strong evidence for covariate effect.

of area on individual patch occupancy was more pronounced in patches with a high shape index (3.3) than in those with the mean shape index of 1.8. In patches where shape index = 3.3, the Blue Grosbeak's minimum area requirement and optimal area value were 2.8 and 4.1 ha, respectively (Fig. 5).

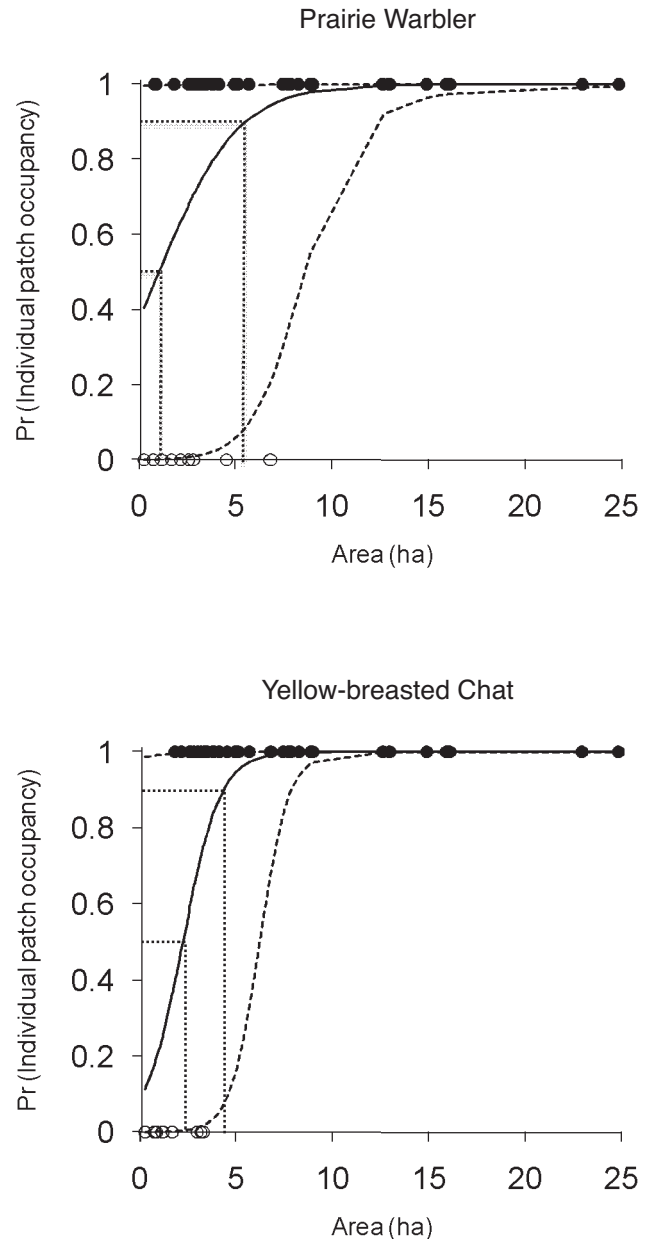


FIGURE 4. Individual patch occupancy estimates (solid lines) and 95% confidence intervals (dotted lines) relative to patch area, and occurrence data (closed dots = present, open dots = absent) for the Prairie Warbler (*Setophaga discolor*) and Yellow-breasted Chat (*Icteria virens*) in early-successional forested riparian buffer habitat patches in North Carolina, 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 the program PRESENCE with the multi-season model $\psi(\text{area}) \gamma(\cdot) \epsilon(\cdot) p(\text{obs})$.

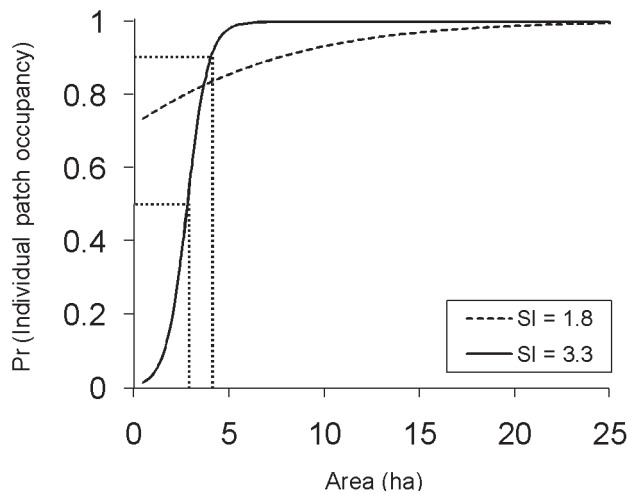


FIGURE 5. Predicted individual patch occupancy estimates relative to patch area at two shape index values for the Blue Grosbeak in early-successional forested riparian buffer habitat patches in North Carolina, 2007–2008. Shape index values represent the mean (1.8) and an extreme high (3.3) from our sample of patches. Occupancy estimates were calculated using beta estimates from the area-shape index interaction occupancy model, $\psi(\text{area} + \text{SI} + \text{area} \times \text{SI}) \gamma(\cdot) \varepsilon(\cdot) p(\cdot)$.

We found 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 3 and 4).

DISCUSSION

Among the factors we considered, patch area had the most significant influence on patch occupancy of shrubland birds. Two of our eight focal species, the Yellow-breasted Chat and Prairie Warbler, were area-sensitive; their occupancy of our smallest patches was low. Also, the Blue Grosbeak was area-sensitive in very linear, irregularly shaped patches. Similar patterns of absence from patches <1 ha have been observed for the Yellow-breasted Chat, Prairie Warbler, Field Sparrow, and Eastern Towhee (Annand and Thompson 1997, Robinson and Robinson 1999, Moorman and Gynn 2001, Alterman et al. 2005). Other studies have shown that although the abundance of some shrubland bird species, particularly the Yellow-breasted Chat and Eastern Towhee, may increase with increasing patch area, 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 of at least 0.8 ha. Our study is the first to identify minimum-area requirements for shrubland birds in eastern North America based on detailed analyses of occurrence data, and it indicates that the Yellow-breasted Chat and Prairie

Warbler require patches of at least 2.3 and 1.1 ha, respectively. If patches are linear or irregularly shaped, the Blue Grosbeak may require as much as 3 ha. When habitat for shrubland birds is created, however, patches ≥ 5.5 ha may be preferable because the probability that all three area-sensitive species would occupy patches of this size was higher.

For some shrubland birds, the proximate cause of area sensitivity may be edge avoidance in small or very linear patches that are almost entirely edge habitat (Schlossberg and King 2008). The ultimate causes of edge avoidance by shrubland birds remain uncertain, though some potential mechanisms have been investigated. Edge-avoidance behavior and birds' use of small patches of early-successional habitat do 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 birds' 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, Riddle and Moorman 2010), including at cropland edges in our study area (Shake et al. 2011). Other studies elsewhere, however, have found that nest success does not decline at mature forest–shrubland edges (Woodward et al. 2001, Moorman et al. 2002) and that productivity of breeding is not lower in smaller patches (Lehnen and Rodewald 2009, Krementz and Christie 2000). Detailed studies of the demographics (e.g., 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 the Field Sparrow, Indigo Bunting, Prairie Warbler, and Yellow-breasted Chat should decrease in irregularly shaped patches with a high shape index, we discovered no strong evidence that shape index alone influences patch occupancy of these species. Although shrubland birds may be less abundant in irregularly shaped patches (Schlossberg and King 2008), edge effects may not preclude occupancy of a patch, provided that the patch meets minimum area requirements. Also, our habitat patches may not have been sufficiently narrow or irregularly shaped to preclude occupancy. Our most linear patch was, on average, approximately 30 m wide and occupied by all of our focal species. In contrast, the Field Sparrow and Prairie Warbler are absent from early-successional field borders <3 m wide in this region (J. Riddle, pers. obs.).

Percent forest cover in landscapes surrounding habitat patches did not appear to influence shrubland birds' patch occupancy. Similarly, Askins et al. (2007) documented no response in abundance of shrubland-specialist birds to landscape composition within 1 km of patches of clearcut forest in Connecticut. Shrubs may occupy patches regardless of the extent of forest cover in the surrounding landscape, because, as Askins et al. (2007) suggested, they may be adapted to colonize patches of ephemeral habitat isolated in forested landscapes. Historically, some disturbances that maintained shrubland in the eastern

United States, such as beavers, wind, and fires, were small and isolated in a heavily forested matrix (Askins 2001). The small size of these historical disturbances may partially explain why at least five of our focal species were not area-sensitive. These species may be well adapted to colonizing historically small patches created by disturbance and are therefore not particularly sensitive to patch size.

Birds are closely linked to habitat structure and composition, so features of shrubland patches may affect occupancy (MacArthur and MacArthur 1961, Wiens and Rotenberry 1981). We did not measure the influence of patch vegetation on bird occupancy, and the characteristics of the restored patches we studied were likely different from those other types of shrubland communities in eastern North America (e.g., regenerating logged forest). However, the avian species using the patches in our study were the same as those in regenerating logged forest and abandoned agricultural fields in the southeastern United States (Krementz and Christie 2000, Whitehead et al. 2002). Additionally, similar findings of area sensitivity or edge avoidance by the Prairie Warbler and Yellow-breasted Chat in other regions suggest our results apply to other shrubland types and other regions (Annand and Thompson 1997, Robinson and Robinson 1999, Moorman and Guynn 2001, Alterman et al. 2005, Schlossberg and King 2008).

CONSERVATION IMPLICATIONS

Compared to area-sensitive forest- and grassland-breeding passerines, which may require habitat patches >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), shrubland-breeding passerines occupy relatively small habitat patches in landscapes with varying amounts of forest and agricultural cover. However, because of evidence of area sensitivity, edge avoidance, and decreased nest survival near agricultural edges, we suggest 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, Lehen and Rodewald 2009, Shake et al. 2011). Although several shrubland bird species occupied nearly all of our study sites, we recommend that patches should be >5 ha to ensure habitat use by the entire community of shrubland birds we considered. Because this recommendation is designed only to ensure that species will occupy a patch and does not consider a patch's ability to support a high density and productive breeding by shrubland birds, it is likely patches may need to be even larger. In fact, patches of restored habitat adjacent to cropland may need to be as wide as 250 m (e.g., a square of 6.3 ha) to significantly reduce shrubland birds' risk of nest predation (Shake et al. 2011).

The evidence suggesting that shrubland bird occupancy is insensitive to variation in landscape composition has two important implications. First, the patterns of minimum patch area we observed are more likely to be consistent with other

regions where landscape composition varies within a range similar to ours (24–81% forest cover). This suggests our recommendations for minimum patch area for shrubland birds are applicable to a broad geographic region with significant landscape variation, unlike those for grassland birds in North America (Bakker et al. 2002). Second, the lack of a landscape influence is encouraging for habitat-restoration programs in highly agricultural landscapes that are targeted at conservation of shrubland birds. The overall high rates of occupancy we found 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 and minimize negative edge effects.

Most types of shrubland in the eastern U.S., including restored habitats, are ephemeral and will transition to mature successional stages. In the absence of many natural agents of disturbance, active management is necessary to retard or restart forest succession to maintain shrubland habitats. For restoration programs aimed at creating shrubland, this will require flexible regulations that allow landowners to use regenerative management practices such as timber harvest or, in some regions, prescribed fire. The maintenance of many restored habitats enrolled in incentive-based conservation programs, especially those in short-term agreements, is also requisite on continued federal and state funding of these programs. Other studies have highlighted the importance of these programs for wildlife conservation in the United States (Dunn et al. 1993, Hohman and Halloum 2000, Gray and Teels 2006, Veech 2006, Herkert 2009). Our study reconfirms these programs' importance and underscores their potential for providing habitat for declining shrubland birds.

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LITERATURE CITED

- ALTERMAN, L. E., J. C. BEDNARZ, AND R. E. THILL. 2005. Use of group-selection and see-tree cuts by three early-successional migratory species in Arkansas. *Wilson Bulletin* 117:353–363.
- AMBUEL, B., AND S. A. TEMPLE. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* 64:1057–1068.
- ANDRÉN, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat—a review. *Oikos* 71:355–366.
- ANNAND, E. M., AND F. R. THOMPSON, III. 1997. Forest bird response to regeneration practices in central hardwood forests. *Journal of Wildlife Management* 61:159–171.

- ASKINS, R. A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. *Current Ornithology* 11:1–34.
- ASKINS, R. A. 2001. Sustaining biological diversity in early successional communities: the challenge of managing unpopular habitats. *Wildlife Society Bulletin* 29:407–412.
- ASKINS, R. A., M. PHILBRICK, AND D. SUGENO. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. *Biological Conservation* 39:129–152.
- ASKINS, R. A., B. ZUCKERBERG, AND L. NOVAK. 2007. Do the size and landscape context of forest openings influence the abundance and breeding success of shrubland songbirds in southern New England? *Forest Ecology and Management* 250:137–147.
- BAKKER, K. K., D. E. NAUGLE, AND K. F. HIGGINS. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. *Conservation Biology* 16:1638–1646.
- BOULINIER, T., J. D. NICHOLS, J. E. HINES, J. R. SAUER, C. H. FLATHER, AND K. H. POLLOCK. 2001. Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology* 82:1159–1169.
- BRAWN, J. D., S. K. ROBINSON, F. R. THOMPSON III. 2001. The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics* 32:251–276.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.
- CHANDLER, R. B., D. I. KING, AND S. DEStEFANO. 2009. Scrub-shrub bird habitat associations at multiple scales in beaver meadows in Massachusetts. *Auk* 126:186–197.
- CHAMPLIN, T. B., J. C. KILGO, AND C. E. MOORMAN. 2009. Food abundance does not determine bird use of early-successional habitat. *Ecology* 90:1586–1594.
- COSTELLO, C. A., M. YAMASAKI, P. J. PERKINS, W. B. LEAK, AND C. D. NEEFUS. 2000. Songbird response to group selection harvests and clearcuts in a New Hampshire northern hardwood forest. *Forest Ecology and Management* 127:41–54.
- DEGRAAF, R. M., AND M. YAMASAKI. 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. *Forest Ecology and Management* 185:179–191.
- DESSECKER, D. R., AND D. G. MCAULEY. 2001. Importance of early-successional habitat to Ruffed Grouse and American Woodcock. *Wildlife Society Bulletin* 29:456–465.
- DUNN, C. P., F. STEARNS, G. R. GUNTENSPERGEN, AND D. M. SHARPE. 1993. Ecological benefits of the Conservation Reserve Program. *Conservation Biology* 7:132–139.
- DUNNING, J. B. JR., R. BORGELLA JR., K. CLEMENTS, AND G. K. MEFFE. 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conservation Biology* 9:542–550.
- FARM SERVICE AGENCY. 2008. Conservation Reserve Program summary and enrollment statistics, FY 2008. Farm Service Agency, United States Department of Agriculture, Washington, DC.
- FREEMARK, K. E., AND B. COLLINS. 1992. Landscape ecology of birds breeding in temperate forest fragments, p. 443–454. *In* J. M. Hagan III, and D. W. Johnston [EDS.], *Ecology and conservation of neotropical migrant landbirds*. Smithsonian Institution Press, Washington, DC.
- GASCON, C., T. E. LOVEJOY, R. O. BIERREGAARD, J. R. MALCOLM, P. C. STOUFFER, H. L. VASCONCELOS, W. F. LAURANCE, B. ZIMMERMAN, M. TOCHER, AND S. BORGES. 1999. Matrix habitat and species richness in tropical forest remnants. *Biological Conservation* 91:223–229.
- GRAM, W. K., P. A. PORNELUZI, R. L. CLAWSON, J. FAABORG, AND S. C. RICHTER. 2003. Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests. *Conservation Biology* 17:1324–1337.
- GRAY, R. L., AND B. M. TEELS. 2006. Wildlife and fish conservation through the Farm Bill. *Wildlife Society Bulletin* 34:906–913.
- HAILA, Y. 1986. North European land birds in forest fragments: evidence for area effects?, p. 315–319. *In* J. Verner, M. Morrison, and C. J. Ralph [EDS.], *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, WI.
- HELZER, C. J., AND D. E. JELSINKI. 1999. The relative importance of patch area and perimeter–area ratio to grassland breeding birds. *Ecological Applications* 9:1448–1458.
- HERKERT, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological Applications* 4:461–471.
- HERKERT, J. R. 2009. Response of bird populations to farmland set-aside programs. *Conservation Biology* 23:1036–1040.
- HINES, J. E. [ONLINE]. 2006. PRESENCE2—Software to estimate patch occupancy and related parameters. <<http://www.mbr-pwrc.usgs.gov/software/presence.html>> (1 September 2008).
- HOHMAN, W. L., AND D. J. HALLOUM. 2000. A comprehensive review of farm bill contributions to wildlife conservation, 1985–2000. *Wildlife Habitat Management Institute Technical Report*. U.S. Department of Agriculture, Natural Resources Conservation Service, Washington, DC.
- HOMER, C., C. HUANG, L. YANG, B. WYLIE, AND M. COAN. 2004. Development of a 2001 national land-cover database for the United States. *Photogrammetric Engineering and Remote Sensing* 70:829–840.
- HORN, D. J., R. J. FLETCHER JR., AND R. R. KOFORD. 2000. Detecting area sensitivity: a comment on previous studies. *American Midland Naturalist* 144:28–35.
- HUNTER, W. C., D. A. BUEHLER, R. A. CANTEBURY, AND J. L. CANTERBURY. 2001. Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin* 29:440–455.
- KING, D. I., AND B. E. BYERS. 2002. An evaluation of powerline rights-of-way as habitat for early-successional shrubland birds. *Wildlife Society Bulletin* 30:868–874.
- KREMENTZ, D. G., AND J. S. CHRISTIE. 2000. Clearcut stand size and scrub-successional bird assemblages. *Auk* 117:913–924.
- LANHAM, J. D., AND D. C. GUYNN JR. 1998. Habitat–area relationships of shrub-scrub birds in South Carolina. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 52:222–231.
- LEHNEN, S. E., AND A. D. RODEWALD. 2009. Investigating area-sensitivity in shrubland birds: responses to patch size in a forested landscape. *Forest Ecology and Management* 257:2308–2316.
- LITVAITUS, J. A. 2001. Importance of early-successional habitats to mammals in eastern forests. *Wildlife Society Bulletin* 29:466–473.
- LORIMER, C. G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. *Wildlife Society Bulletin* 29:425–439.
- MACARTHUR, R. H., AND J. W. MACARTHUR. 1961. On bird species diversity. *Ecology* 42:594–598.
- MACKENZIE, D. I., J. D. NICHOLS, G. B. LACHMAN, S. DROEGE, J. A. ROYLE, AND C. A. LANGTIMM. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- MACKENZIE, D. I., J. D. NICHOLS, J. A. ROYLE, K. H. POLLOCK, L. L. BAILEY, AND J. E. HINES. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Amsterdam.
- MITCHELL, M. S., R. A. LANCIA, AND J. A. GERWIN. 2001. Using landscape-level data to predict the distribution of birds on a managed forest: effects of scale. *Ecological Applications* 11:1692–1708.

- MOORMAN, C. E., AND D. C. GUYNN JR. 2001. Effects of group-selection opening size on breeding bird habitat use in a bottomland forest. *Ecological Applications* 11:1680–1691.
- MOORMAN, C. E., D. C. GUYNN JR., AND J. C. KILGO. 2002. Hooded Warbler nesting success adjacent to group-selection and clearcut edges in a southeastern bottomland forest. *Condor* 104:366–377.
- NICHOLS, J. D., J. E. HINES, J. R. SAUER, F. W. FALLON, J. E. FALLON, AND P. J. HEGGLUND. 2000. A double-observer approach for estimating detection probability and abundance from point counts. *Auk* 117:393–408.
- NICHOLS, J. D., L. THOMAS, AND P. B. CONN. 2009. Inferences about landbird abundance from point counts, p. 201–235. *In* D. L. Thompson, E. G. Cooch, and M. J. Conroy [EDS.], *Environmental and ecological statistics*, vol. 3: modeling demographic processes in marked populations. Springer-Verlag, New York.
- NORTON, M. R., S. J. HANNON, AND F. K. A. SCHMIEGELOW. 2000. Fragments are not islands: patch vs. landscape perspectives on songbird presence and abundance in a harvested boreal forest. *Ecography* 23:209–223.
- RICH, T. D., C. J. BEARDMORE, H. BERLANGA, P. J. BLANCHER, M. S. W. BRADSTREET, G. S. BUTCHER, D. W. DEMAREST, E. H. DUNN, W. C. HUNTER, E. E. IÑIGO-ELIAS, J. A. KENNEDY, A. M. MARTELL, A. O. PANJABI, D. N. PASHLEY, K. V. ROSENBERG, C. M. RUSTAY, J. S. WENDT, AND T. S. WILL. 2004. Partners in Flight North American landbird conservation plan. Cornell Lab of Ornithology, Ithaca, NY.
- RIDDLE, J. D., AND C. E. MOORMAN [ONLINE]. 2010. The importance of agriculture-dominated landscapes and lack of field border effect for early-succession songbirds. *Avian Conservation and Ecology* 5(2):9. <<http://www.ace-eco.org/vol5/iss2/art9/>>.
- ROBBINS, C. S., D. K. DAWSON, AND B. A. DOWELL. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildlife Monographs* 103.
- ROBINSON, W. D., AND S. K. ROBINSON. 1999. Effects of selective logging on forest bird populations in a fragmented landscape. *Conservation Biology* 13:58–66.
- RODEWALD, A. D., AND A. C. VITZ. 2005. Edge- and area-sensitivity of shrubland birds. *Journal of Wildlife Management* 69:681–688.
- RUDNICKY, T. C., AND M. L. HUNTER JR. 1993. Reversing the fragmentation perspective: effects of clearcut size on bird species richness in Maine. *Ecological Applications* 3:357–366.
- SAAB, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications* 9:135–151.
- SADER, S. A., G. V. N. POWELL, AND J. H. RAPPOLE. 1991. Migratory bird habitat monitoring through remote sensing. *International Journal of Remote Sensing* 12:363–372.
- SCHLOSSBERG, S., AND D. I. KING. 2008. Are shrubland birds edge specialists? *Ecological Applications* 18:1325–1330.
- SHAKE, C. S., C. E. MOORMAN, AND M. R. BURCHELL. 2011. Cropland edge, forest succession, and landscape affect shrubland bird nest predation. *Journal of Wildlife Management* 75:825–835.
- SUAREZ, A. V., K. F. PFENNING, AND S. K. ROBINSON. 1997. Nesting success of a disturbance dependent songbird on different kinds of edges. *Conservation Biology* 11:928–935.
- THOMPSON, F. R. III, AND R. M. DEGRAAF. 2001. Conservation approaches for woody, early-successional communities in the eastern United States. *Wildlife Society Bulletin* 29:493–494.
- VEECH, J. A., 2006. A comparison of landscapes occupied by increasing and decreasing populations of grassland birds. *Conservation Biology* 20:1422–1432.
- VICKERY, P. D., M. L. HUNTER JR., AND S. M. MELVIN. 1994. Effects of habitat area on the distribution of grassland birds in Maine. *Conservation Biology* 8:1087–1097.
- WARNER, R. E. 1994. Agricultural land use and grassland habitat in Illinois: future shock for midwestern birds? *Conservation Biology* 8:147–156.
- WHITEHEAD, M. A., S. H. SCHWEITZER, AND W. POST. 2002. Cowbird/host interactions in a southeastern old-field: a recent contact area? *Journal of Field Ornithology* 73:379–386.
- WIENS, J. A., AND J. T. ROTENBERRY. 1981. Habitat associations and community structure of birds in shrubsteppe environments. *Ecological Monographs* 51:21–42.
- WOODWARD, A. A., A. D. FINK, AND F. R. THOMPSON III. 2001. Edge effects and ecological traps: effects on shrubland birds in Missouri. *Journal of Wildlife Management* 65:668–675.