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Songbird Use of Regenerating Forest, Glade, and Edge Habitat Types

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Abstract

Population numbers of many bird species associated with early-successional or disturbance-dependent habitat types are declining. We used an information-theoretic approach to evaluate hypotheses concerning factors affecting breeding bird densities in different early-successional habitat types. We studied shrubland bird communities in 3- to 5-year-old regenerating forest ($n = 3$), glade ($n = 3$), and forest-pasture edge ($n = 3$) habitat types in the predominantly forested Missouri Ozarks in 1997–1999. We monitored 8 bird species using spot mapping and total mapping techniques, searched for and monitored nests, and measured vegetation structure within nested circular plots. In evaluating breeding densities in these habitat types, we compared support for a global model with year, habitat type, and a habitat type \times year interaction to several reduced models and a null model with only an intercept, and we used model-averaged coefficients to evaluate effect size. We found support for the effects of habitat type on breeding densities of prairie warbler (*Dendroica discolor*) and yellow-breasted chat (*Icteria virens*); the effects of habitat type and year on densities of blue-winged warbler (*Vermivora pinus*), eastern towhee (*Pipilo erythrophthalmus*), and field sparrow (*Spizella pusilla*); the effect of year on densities of indigo bunting (*Passerina cyanea*) and northern cardinal (*Cardinalis cardinalis*); and no effects on densities of white-eyed vireo (*Vireo griseus*). The effect size of habitat type on breeding densities varied among species and indicated important species-specific differences in habitat use. Most shrubland bird species used both glades and regenerating forests more than forest-pasture edge sites, and breeding densities of some species were higher in regenerating forests than in glades. For some species, patterns in reproductive success (reported as interval nest success) mirrored observed patterns in breeding densities. However, substantial variation existed among species with respect to patterns in habitat use and nest success. Conservation planning for the persistence of birds requiring early-successional habitat types should consider the ephemeral nature of these areas and the potential contribution from young, regenerating forest. (JOURNAL OF WILDLIFE MANAGEMENT 70(1):180–188; 2006)

Key words

disturbance-dependent birds, early-successional habitats, forest edge, forest management, glade, habitat use, migrant birds, Missouri Ozarks, reproductive success, shrubland songbirds, young forest

Population numbers of many bird species occupying habitat types maintained by periodic disturbance (e.g., shrubland, shrub-scrub, early-successional, disturbance-dependent) are declining (Brawn et al. 2001, Sauer et al. 2005). Whereas only 12% of woodland-breeding species are declining in Missouri, 50% of grassland- and 38% of shrubland-breeding bird species exhibit significant negative population trends in the state (Sauer et al. 2005). Missouri's shrubland songbird community includes prairie warbler, yellow-breasted chat, indigo bunting, field sparrow, northern cardinal, white-eyed vireo, blue-winged warbler, and eastern towhee, and half of these species are declining in number in the state (i.e., prairie warbler, field sparrow, northern cardinal, eastern towhee; Sauer et al. 2005). Additionally, some of these shrubland species are regional and national conservation priorities: 2 species are identified as priority species in the Ozark-Ouachitas physiographic area (prairie warbler and field sparrow; Fitzgerald and Pashley 2000), and the prairie warbler is identified as a Partners in Flight Watchlist species (Fitzgerald and Pashley 2000).

In the Midwest, shrubland birds occur in early-successional vegetation communities dominated by grasses and shrubs, including primary natural communities and old fields. These communities require intermittent disturbance to maintain their

early-successional characteristics. Without disturbance, the vegetation succeeds to subsequent seral stages and becomes less suitable for many shrubland songbirds. While primary natural communities (particularly glades) and old fields provide habitat for shrubland birds, the quantity and quality of these sites are a consequence of natural disturbances (e.g., fire and wind) as well as land-management and restoration activities of public and private landowners.

Many shrubland bird species also use regenerating forests resulting from timber harvest or other major disturbance to forests. Even-aged management (i.e., clearcut, seed tree, and shelterwood regeneration methods) creates young stands that provide habitat for shrubland birds for several years, depending on site quality and similar factors (Annand and Thompson 1997, Brawn et al. 2001, Faaborg 2002). Some species, however, do not use the small habitat patches created by uneven-aged management (Thompson et al. 1992, Annand and Thompson 1997). Changes in silvicultural prescriptions resulting from social and political influences (e.g., reduced clearcutting) may reduce the future availability of these even-aged habitat types (Askins 2001, Trani et al. 2001).

Understanding habitat use of shrubland birds across habitat types is essential to conservation efforts because these species are linked to ephemeral, disturbance-dependent vegetation communities largely mediated by land-management activities. Although the vegetation attributes of natural and managed shrubland communities are similar in many ways, important differences

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exist that may affect breeding-bird species richness and abundance, including disturbance frequency and vegetation density and diversity (Brawn et al. 2001). All early-successional habitat types result from disturbance, although the intervals vary between disturbances. Young forests resulting from forest management are ephemeral and thus may be suitable for shrubland birds for only a few years (Thompson and DeGraaf 2001). Regenerating oak forests on xeric sites (e.g., in U.S. central hardwood forests) may be suitable for 10 or more years, whereas more productive sites (e.g., northern hardwoods) may reach canopy closure in as few as 5 years (Thompson and DeGraaf 2001). Other shrubland natural communities remain in early-successional stages for multiple reasons (including shallow soils, xeric conditions, and periodic fire) and thus for longer periods than do regenerating forest sites. More permanent environments show a more constant level of quality and may be preferable to more dynamic, ephemeral environments for maximization of fitness (Southwood 1977). Thus, relative frequency of disturbance and the related degree of stability of vegetation communities may affect bird species richness and abundance in disturbed habitat types.

In addition to disturbance-dependent communities, some shrubland birds use forest edges for breeding. The increased light exposure in forest edges result in the well-developed understory vegetation that attracts shrubland birds. Avian species richness is often elevated near forest edges because edges can attract both forest and shrubland species (e.g., Strelke and Dickson 1980, Chasko and Gates 1982).

We conducted a comprehensive study of shrubland-bird demography from 1997 to 1999 in 3 habitat types (glade, regenerating forest, forest-pasture edge) in the Missouri Ozarks to better understand patterns of habitat use and reproductive success in natural and anthropogenically created shrubland communities. Our primary goals were to determine habitat-specific demography and identify potential population limiting factors. In this component of the project, we compared avian- and vegetation-community characteristics in 3 shrubland habitat types. We hypothesized that breeding bird densities would be affected by habitat type, year, habitat type and year, or an interaction by habitat type and year. We used an information-theoretic approach and compared support among models representing these hypotheses and a null model with no effects. Based on previous studies, we also predicted: 1) bird densities are higher in regenerating forests and glades than in forest-pasture edges, and 2) bird densities are different between glades and regenerating forests due to differences in vegetation composition and density and the ecological processes affecting these habitat types. Because density alone is not necessarily a good indicator of habitat quality (Van Horne 1983, Vickery et al. 1992, Brawn and Robinson 1996), we also report estimates of interval nest success by species and habitat type for comparison to density estimates. A comprehensive manuscript on factors affecting productivity is currently in preparation.

Methods

Study Area

We conducted our study on the Rolla-Houston Ranger District of the Mark Twain National Forest in Laclede and Pulaski counties

in the Ozarks of southern Missouri, USA. This geographic area is characterized by oak-hickory forest (*Quercus-Carya* spp.), hills of steep to moderate slopes, and moderate to heavy forest cover (e.g., 68% forested near the study sites; Woodward et al. 2001). Public forests are managed by both even-aged and uneven-aged silvicultural systems.

We selected 3 study sites in each of the following 3 habitat types: 3- to 5-year-old regenerating forest, dolomite glades, and forest-pasture edge. We studied these habitat types because they are potentially important to breeding shrubland birds; glades are a naturally occurring shrubland vegetation community; and the availability of these habitat types, especially the regenerating forests, is affected by forest-management activities.

The regenerating forest stands resulted from clearcut timber harvest in 1994, occurred on rocky ridge-top or upper-slope sites, and were 4.2, 5.0, and 5.1 ha in size (in 1997, we sampled only 1.6 ha of the smallest site). The preharvest forest canopy was oak-hickory. Residual canopy trees remained from the previous stand and occurred singly or in small groupings. Tree regeneration was primarily oaks and hickories from stump sprouts and advanced tree reproduction. Other woody plant species present included sassafras (*Sassafras albidum*), blackberry and black raspberry (*Rubus* spp.), fragrant sumac (*Rhus aromatica*), grape (*Vitis* spp.), dogwood (*Cornus* spp.), black cherry (*Prunus serotina*), and downy serviceberry (*Amelanchier arborea*). Each site was heterogeneous and dissected by logging roads and skidder trails that created a matrix of shrubland intersected by grassy openings. Dead tree tops and branches left behind by the logging operation provided vertical structure for climbing vine species.

Glades are natural, fire-maintained shrublands that occur on shallow, rocky soils as isolated openings within an oak-hickory forest matrix and cover approximately 162,000 ha in Missouri, primarily in the southern part of the state (Nelson 1985). The vegetation structure of Ozark glades varies with fire frequency. Frequent burning (every 3–4 years) results in communities dominated by grasses with sparse shrub cover. Moderate burn frequencies (7–10 years) result in a patchier matrix of grass and shrub cover. Infrequent fire results in sites dominated by thick stands of eastern red cedar (*Juniperus virginiana*). The dolomite glades considered in this study were burned at a moderate frequency and were 2.5, 5.7, and 12.1 ha in size (in 1997, we sampled only 5.3 ha of the largest site). The dominant grasses were bluestems (e.g., little bluestem [*Schizachyrium scoparium*]) and Indiangrass (*Sorghastrum nutans*), and the dominant shrub species was fragrant sumac. The dominant tree species were red cedar, oaks, and shortleaf pine (*Pinus echinata*). Each glade contained large dolomite outcrops and 1 or more small waterways supporting dense stands of various woody species. Standing and downed dead wood were common and widespread throughout glade sites.

Forest-pasture edge occurred at the abrupt ecotone of mature oak-hickory forest and an open, grass-dominated grazing allotment. Fescue (*Festuca* spp.), bluestems, bunchgrasses, and mixed forbs characterized allotments. Each allotment also contained scattered clumps of woody species; however, we selected allotments with minimal woody cover to reduce the occurrence of potential habitat away from the edge. We defined edge sites as a

30-m band on either side of the edge. Edge sites were 3.4, 3.6, and 5.1 ha in size.

Bird Densities and Nest Success

We surveyed avian communities using a combination of total-mapping and spot-mapping techniques (Verner 1985, Ryder 1986, Ralph et al. 1993, Wunderle 1994) from approximately 1 May to 15 August in 1997, 1998, and 1999. We marked individuals of 3 species (prairie warbler, yellow-breasted chat, indigo bunting) with unique combinations of numbered aluminum, fade-resistant color bands (Fink 2003; animal handling protocol approved by the University of Missouri Animal Care and Use Committee). We used the total-mapping approach for these 3 species; this technique is the optimal census technique for intensive demographic research because it permits identification of all territorial individuals, precise estimation of densities, and monitoring of changes of territories and territory holders throughout the breeding season (Verner 1985, Wunderle 1994). We monitored the remaining shrubland-breeding species with spot-mapping techniques (after Ryder 1986, Ralph et al. 1993, Wunderle 1994).

We counted birds during a minimum of 15 visits to each site in each breeding season. We recorded bird locations and behaviors (e.g., singing, calling, counter-singing) on sections of modified, enlarged U.S. Geological Survey topographic maps using topographic relief, important physical features (e.g., old roads, creeks, rock ledges), and marked site boundaries as location guides (Ralph et al. 1993). We trained all observers to recognize the 8 bird species of interest and familiarized them with the sites and site maps. We transferred bird sightings to species location maps and delineated territories of marked and unmarked birds using standard techniques (described by Verner and Milne 1990). One observer (ADF) compiled the bird locations and delineated territories to minimize interpretation bias (Verner 1985). We converted the number of territories per site to territories per ha for data analyses.

We conducted extensive searches of each site to locate as many nests as possible. We located nests using behavioral observation (Ralph et al. 1993, Martin et al. 1997) and systematic searches. We considered nests to be active if we observed at least 1 host egg in the nest and confirmed parental attendance of the nest; nests abandoned or lost during the building stage or before a host egg was observed were excluded from all analyses. We checked nests by direct visual observation every 1–3 days, depending on nest stage; we checked nests more frequently in the late incubation and nestling stages to better estimate hatching and fledging, respectively. We recorded egg number, nestling number, evidence of parasitism and predation, and parental activity (e.g., singing, calling, scolding, etc.). We considered nests successful if they fledged host young. We assumed a nest fledged if the young it contained were almost fully feathered the day before the nest was found empty, the nest cup showed evidence of young having perched on the edge (Ralph et al. 1993), and the behavior of parents indicated the presence of fledglings. We critically assessed permutations of these criteria; in ambiguous cases, we used conservative estimates of fledging (i.e., if fledging could not be concluded with confidence, we classified nests as outcome unknown).

Vegetation Measurements

We measured vegetation structure and composition to provide a quantitative description of the vegetation in each habitat. We sampled vegetation using nested circular plots in late July and August 1997–1999. We randomly selected sampling-plot locations at an approximate density of 2 per ha (6 locations in the smallest site, 26 in the largest site, 300 total over the 3-year study). We measured diameter at breast height (dbh) of all woody species ≥ 1.3 m in height and dbh ≥ 0.5 cm on 0.01-ha plots. We counted all woody stems ≥ 50 cm in height and dbh < 0.5 cm on 0.001-ha plots. We calculated stem densities in 4 size classes: shrub stems (height ≥ 50 cm and dbh < 0.5 cm), $0.5 \leq \text{dbh} < 3$ cm, $3 \leq \text{dbh} < 10$ cm, and dbh ≥ 10 cm. Mean dbh was calculated for all stems ≥ 0.5 cm dbh. We estimated percent ground cover in woody, forb, grass, litter, and substrate (soil, rock, and water combined) using 4 1-m² quadrats following methods modified from Daubenmire (1959), and we assessed vegetation height and density using 4 visual obstruction readings (after Robel et al. 1969). We estimated canopy cover by averaging 2 spherical densiometer readings taken at each plot's center. We measured the heights of 3 randomly selected dominant trees in both the residual tree canopy and regeneration subcanopy using a clinometer and meter tape. We first calculated means of all vegetation variables for each site (i.e., across years) and then calculated means and SEs for each habitat using the site means.

Data Analysis

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate hypotheses concerning factors affecting breeding densities. We modeled breeding density using mixed linear models with year as a repeated measure. We specified compound symmetry as the covariance structure for the repeated measure of year and defined the error term by nesting sites within habitat type (PROC MIXED; Littell et al. 1996). Our set of a priori candidate models included 1) a global model with year, habitat type, and habitat type \times year interaction; 2) reduced models with habitat type and year alone and in combination; and 3) a null model with no effects (Table 1). Year and habitat type were categorical variables. Levels of year were 1997, 1998, and 1999; 1999 was treated as the reference category. Levels of habitat type were edge, regenerating forest, and glade; glade was treated as the reference category. Each coefficient for a category level represented the increase or decrease (if positive or negative, respectively) in territories/ha for the category level of interest compared to the reference category.

We compared support for the models by ranking models from most supported to least supported using Akaike's Information Criterion for small sample sizes (AIC_c; Burnham and Anderson 2002). We evaluated the goodness-of-fit of the global model by comparing it to the null model with a likelihood-ratio test. We assumed that any reduced models ranked higher by model selection would have equal or better fit than the global model (Burnham and Anderson 2002). We did not modify AIC_c for overdispersion because overdispersion factors ranged from 0.08 to 16 and were < 5 (Burnham and Anderson 2002) for half the models, our study sites were independent habitat patches, and our model was conservative because we treated each year's count as a repeated measure in the model.

We considered model-selection uncertainty by calculating a

Table 1. A priori candidate models explaining breeding bird density (territories/ha) for 8 species in the Missouri Ozarks, USA, 1997–1999. Models are general linear models with year as a repeated measure; number of parameters (K) includes the intercept, covariance terms, and each explanatory variable. Models with a lower ΔAIC_c and a greater Akaike weight (w_i) have more substantial support.

Model	K	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
		Blue-winged warbler		Eastern towhee		Field sparrow		Indigo bunting	
Null	3	11.82	0.00	8.45	0.01	9.00	0.01	2.37	0.17
Year	5	8.85	0.01	0.50	0.43	3.88	0.11	0.00	0.55
Habitat type	5	1.74	0.29	6.73	0.02	3.89	0.11	3.37	0.10
Habitat, year	7	0.00	0.69	0.00	0.55	0.00	0.77	2.23	0.18
Habitat, year, habitat \times year	11	18.49	0.00	17.18	0.00	16.89	0.00	19.30	0.00
		Northern cardinal		Prairie warbler		White-eyed vireo		Yellow-breasted chat	
Null	3	1.51	0.21	2.93	0.16	0.00	0.76	6.21	0.04
Year	5	0.00	0.44	5.54	0.04	3.50	0.13	9.53	0.01
Habitat type	5	1.96	0.16	0.00	0.69	4.18	0.09	0.00	0.86
Habitat, year	7	1.67	0.19	3.83	0.10	8.91	0.01	4.55	0.09
Habitat, year, habitat \times year	11	18.32	0.00	18.21	0.00	26.77	0.00	19.44	0.00

model-averaged coefficient and an unconditional 95% confidence interval (CI) for each explanatory variable (Burnham and Anderson 2002). We calculated model-averaged coefficients as the sum of coefficients multiplied by AIC_c weights (w_i) from their respective model (Burnham and Anderson 2002). We used zero for a coefficient when a model did not contain the explanatory variable, so averaged coefficients represented the contribution of the explanatory variable across the entire set of candidate models (Burnham and Anderson 2002). We only interpret coefficients with confidence intervals that do not include zero because model-averaged coefficients that deviate greatly from zero and whose confidence intervals do not include zero represent large and well-supported effects. Because habitat-type and year effects were indicated for most species, we calculated mean density and SE for each species in each habitat type and year, as well as mean density by species and habitat type across the 3 years of the study.

We estimated interval nesting success and confidence intervals using the general methods of Mayfield (Mayfield 1961, 1975) with program MICROMORT (Heisey and Fuller 1985). When events occurred between nest checks, we used the midpoint between visits as the event date (Martin et al. 1997, Manolis et al. 2000). We pooled observation days across nest stage and year to produce estimates by species and habitats; we are preparing a more detailed manuscript that examines temporal, nest-site, and habitat effects on productivity. Interval nest success estimates were based on interval lengths of 22 days for blue-winged warbler, field sparrow, and yellow-breasted chat; 25 days for eastern towhee and white-eyed vireo; 24 days for northern cardinal and prairie warbler; and 23 days for indigo bunting (Fink 2003). We qualitatively compared the pattern of nest success among habitat types to the pattern of densities among habitat types; a more detailed, model-based approach to determining factors affecting productivity is in preparation.

Results

Support for habitat-type and year effects varied among species; however, the best-supported model included habitat type for 5 of the 8 species (Table 1). The model with habitat type had the most support for prairie warbler and yellow-breasted chat. The model with habitat type and year had the most support for blue-winged

warbler, eastern towhee, and field sparrow. The model with year had the most support for indigo bunting and northern cardinal. The null model with no effects had the most support for white-eyed vireo (Table 1).

Model-averaged coefficients indicated some general and some species-specific responses to year and habitat type (Table 2). Lower confidence limits of the coefficient for the 1997 level of year were >0 for blue-winged warbler, eastern towhee, field sparrow, and indigo bunting, indicating these species were more abundant in 1997 than 1999, the reference category (Table 2). The upper confidence limit of the coefficient for the edge level of habitat was <0 for blue-winged warbler, prairie warbler, and yellow-breasted chat, indicating they were less abundant in edge than glades, the reference category (Table 2). There were, on average, 0.38 more field sparrow territories/ha in edge than glades, and 0.42 more yellow-breasted chat territories/ha in regenerating forests than glades (Table 2). Patterns in mean densities among habitat types and years followed effects indicated by the model coefficients and results of model selection (Fig. 1; Appendix 1).

We located and monitored 389 nests of the 8 bird species for a total of 4,453.5 observation days: 55 prairie warbler nests (623.5 observation days), 92 yellow-breasted chat nests (1,053 observation days), 117 indigo bunting nests (1,390.5 observation days), 59 field sparrow nests (555.5 observation days), 28 northern cardinal nests (301.5 observation days), 22 white-eyed vireo nests (315 observation days), 10 eastern towhee nests (106 observation days), and 6 blue-winged warbler nests (108.5 observation days). Field sparrow, indigo bunting, northern cardinal, and white-eyed vireo were the only species for which we found nests in edge. Interval nest success ranged from 0.16 (eastern towhee in regenerating forest; Fig. 1) to 0.69 (blue-winged warbler in regenerating forest; Fig. 1). Interval nest success did not reach its greatest level for any species in the edge habitat type, and for 5 of the 8 species, it was greatest in regenerating forest (Fig. 1).

The vegetation community characteristics differed among habitat types (Table 3). Regenerating forest sites had more woody vegetation as was evidenced by the higher shrub stem and small stem densities, higher visual-obstruction measurements, and greater percentage of woody ground cover (Table 3). Glades exhibited more grass and forb ground cover than regenerating

Table 2. Model-averaged parameter estimates (coefficients and 95% confidence intervals) from 5 models explaining density of breeding songbirds (territories/ha) in the Missouri Ozarks, USA, 1997–1999. Estimates are unconditional in that they take into account model-selection uncertainty.

Variable	Parameter estimate	Parameter estimate	Parameter estimate	Parameter estimate
	Blue-winged warbler	Eastern towhee	Field sparrow	Indigo bunting
Intercept	0.37 (0.22, 0.51)	0.05 (−0.01, 0.22)	0.20 (−0.02, 0.43)	0.94 (0.51, 1.38)
Year–1997	0.15 (0.01, 0.29)	0.18 (0.08, 0.27)	0.24 (0.08, 0.38)	0.22 (0.01, 0.43)
Year–1998	0.03 (−0.07, 0.14)	0.04 (0.05, 0.23)	0.14 (−0.00, 0.27)	0.19 (−0.01, 0.39)
Habitat–regeneration	−0.09 (−0.22, 0.04)	0.08 (−0.04, 0.20)	0.17 (−0.02, 0.35)	0.17 (−0.14, 0.49)
Habitat–edge	−0.37 (−0.50, −0.24)	−0.06 (−0.16, 0.05)	0.38 (0.18, 0.59)	−0.00 (−0.17, 0.17)
	Northern cardinal	Prairie warbler	White-eyed vireo	Yellow-breasted chat
Intercept	0.32 (0.13, 1.39)	0.92 (0.44, 1.39)	0.42 (0.22, 0.63)	0.53 (0.22, 0.83)
Year–1997	0.11 (−0.01, 0.23)	0.22 (−0.03, 0.07)	0.01 (−0.02, 0.04)	0.01 (−0.01, 0.02)
Year–1998	0.05 (−0.03, 0.15)	0.03 (−0.03, 0.08)	0.01 (−0.02, 0.05)	0.01 (−0.02, 0.04)
Habitat–regeneration	−0.02 (−0.06, 0.11)	−0.01 (−0.45, 0.44)	0.01 (−0.04, 0.05)	0.42 (0.01, 0.82)
Habitat–edge	0.09 (−0.06, 0.24)	−0.69 (−1.23, −0.15)	−0.02 (−0.07, 0.04)	−0.51 (−0.91, −0.10)

forests. The remaining vegetation measures were similar between the 2 habitat types (Table 3). The combination of forest and pasture at edge sites resulted in, on average, high densities of large trees and high grass and forb ground cover (Table 3). Edge sites also were characterized by tall, relatively closed tree canopies (Table 3). For most measured vegetation characteristics, glade values were between edges and regenerating forests (e.g., woody, forb, and grass ground cover; small and large stem density; mean dbh; Table 3); thus, these sites provided a mix of dense regrowth, open-grassland, and closed-forest characteristics.

Discussion

We found strong support for our hypothesis of habitat-type and year effects on breeding bird densities. Both habitat type and year

were in the best-supported model, either alone or together, for 5 of the 8 species. In only the white-eyed vireo was the null model the best supported. There was some model-selection uncertainty for all species; however, in all but the northern cardinal, the best-supported model had a $w_i > 0.50$. This model-selection uncertainty was expressed to some extent in wide unconditional confidence intervals surrounding model-averaged coefficients; nevertheless, 4 species had coefficients for regenerating forest or edge habitat types that did not overlap zero. In addition, 4 other species had habitat-type coefficients that overlapped zero by ≤ 0.05 , which suggests additional effects, especially since we had only 3 replicates of each habitat type because we treated year as a repeated measure. These habitat-type effects suggest densities of blue-winged warbler, eastern towhee, prairie warbler, and yellow-

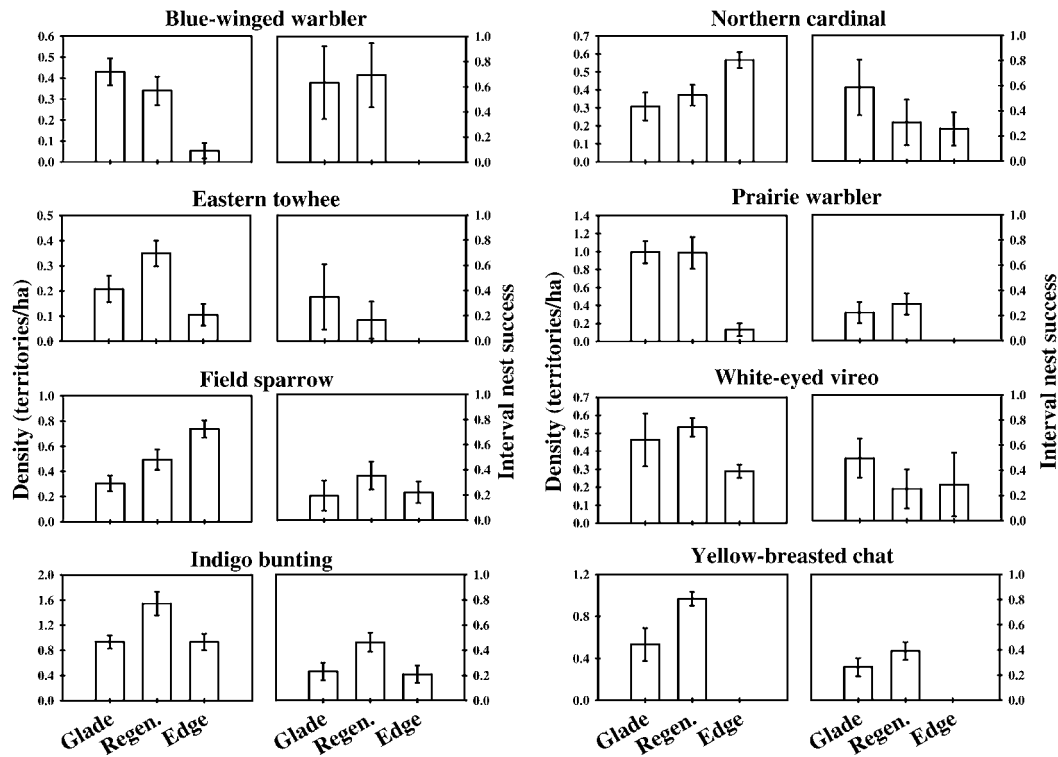


Figure 1. Mean number of territories/ha (\pm SE; left column) and interval nest success (\pm SE; right column) of 8 bird species in 3 habitat types in the Missouri Ozarks, USA, 1997–1999.

Table 3. Mean vegetation structure in 3 shrubland habitat types in the Missouri Ozarks, USA, 1997–1999. Shrub stem and tree densities are reported as numbers of stems per 0.001-ha and 0.01-ha plot, respectively.

Vegetation variable	Glade <i>n</i> = 3		Regeneration <i>n</i> = 3		Edge <i>n</i> = 3	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Shrub stem density	35.36	10.89	62.44	7.06	15.57	3.01
Tree density $0.5 \leq \text{dbh} < 3$ cm	26.97	8.83	107.11	18.00	10.39	2.96
Tree density $3 \leq \text{dbh} < 10$ cm	4.77	1.19	4.58	0.80	6.00	0.95
Tree density ≥ 10 cm dbh	1.64	0.35	0.26	0.22	3.25	0.68
Mean dbh	3.57	0.40	1.54	0.23	3.95	0.82
Number of shrub species	5.25	1.10	6.95	0.26	2.73	0.33
Canopy height (m)	6.31	0.27	3.16	0.45	7.54	1.02
Subcanopy height (m)	2.35	0.20	2.78	0.07	1.45	0.06
Visual obstruction (cm)	87.64	9.97	135.78	4.15	58.20	1.47
Canopy cover (%)	31.62	3.84	27.79	3.48	40.56	0.55
Woody ground cover (%)	22.07	2.64	41.78	2.03	14.93	2.42
Forb ground cover (%)	16.39	2.32	7.84	1.06	17.88	4.03
Grass ground cover (%)	23.88	2.33	8.12	1.37	28.24	4.25
Litter ground cover (%)	30.54	1.67	40.36	2.49	36.12	2.53
Substrate ground cover (%)	2.39	0.39	0.69	0.08	1.35	0.43

breasted chat were lower in edges than glades; densities of blue-winged warbler were lower in regenerating forests than glades; and densities of eastern towhee, field sparrow, and yellow-breasted chat were greater in regenerating forests than glades. Because eastern towhee, prairie warbler, and yellow-breasted chat had similar or greater densities in regenerating forests than glades, we also can infer that their densities were greater in regenerating forests than edges.

Field sparrows, and possibly northern cardinals, were the only species more abundant in edge than in glades, and indigo buntings had similar densities in edges and glades. Field sparrows likely were associated with the grassland habitat adjacent to the forest, and cardinals more likely were associated with the adjacent forest. These habitat associations are similar to those in other geographic locations (e.g., Johnston and Odum 1956, Best 1979).

Edge habitat, however, is often unfavorable for birds. Some breeding birds at or near forest edges experience elevated rates of nest predation and parasitism (reviewed by Paton 1994, Chalfoun et al. 2002), and this even includes some shrubland birds (Woodward et al. 2001). Although these edge effects are influenced by landscape context (Donovan et al. 1997), increased predation and parasitism may affect bird habitat use, reproductive success, and site fidelity.

At least 4 species (blue-winged warbler, eastern towhee, prairie warbler, yellow-breasted chat) were more abundant in both glades and regenerating forests than edges. The yellow-breasted chat was not observed in the edge habitat type, and prairie and blue-winged warblers occurred at very low densities. A single unpaired territorial male blue-winged warbler was observed at each of 2 edge sites in 1997; no blue-winged warblers were observed at edge sites in 1998 or 1999. Unpaired territorial male prairie warblers were recorded at 1 edge study site possessing more woody cover in the adjacent grassland than the other edge sites and thus may have provided sufficient structure to induce settlement and territory establishment for these birds. The low densities or absence of these species from edges supports the idea that some disturbance-dependent species depend on patches of appropriate habitat and are not edge species.

All 8 species occurred in the regenerating forest habitat type, and at least 3 were most abundant there. Higher breeding densities of some species in regenerating forests probably were linked to the density of woody vegetation. Regenerating forest had greater vegetation diversity and density resulting from disturbance and rapid growth of vegetation following clearcutting. A primary tenet of biological diversity research is that increased vegetation density and diversity result in increased animal species richness due to the diversity of available niches (Hutchinson 1959; reviewed by Schluter and Ricklefs 1993, Huston 1994). Numerous studies have demonstrated the positive correlation between vegetation structural diversity and avian species richness (e.g., MacArthur and MacArthur 1961, Conner et al. 1983, Rice et al. 1984, Merrill et al. 1998, Schulte and Niemi 1998). Vegetation structure may be more diverse in space and time in postharvest regenerating forests compared to more stable, less dynamic natural communities, and thus bird species richness and abundance may differ in these habitat types.

All 8 species also occurred in the glade habitat type, blue-winged warblers were more abundant in glades than regenerating forests, and several species were more abundant in glades than edges. Glades, like regenerating forests, also have diverse habitat structure resulting from periodic fire, shallow soils, and rock outcrops. Glades had more grass and forb cover and less woody cover than regenerating forests. Blue-winged warblers may have been most abundant in glades because they nest directly in grass or forb cover, whereas most of the other species build nests in woody cover (Gill et al. 2001).

Although the densities of birds differed among habitat types, differences in habitat quality should not be inferred from density alone (Van Horne 1983, Vickery et al. 1992, Brawn and Robinson 1996). Our observed values of nesting success were not directly related to the pattern in densities; however, most species had their greatest abundance and greatest nesting success in habitat types other than edge. Field sparrow and northern cardinal were the exception to this pattern: they reached their greatest density in edge and had low nesting success there.

Management Implications

Our observation that species breed at different densities in these 3 habitat types has important management implications. Natural shrubland habitats like glades continue to provide important habitat for shrubland birds; however, similar and sometimes greater densities of shrubland birds occur in regenerating forests created through timber-management activities. Whereas shrubland songbirds are sometimes referred to as edge species, we observed that several species did not breed in forest-pasture edges, and we suggest that the edge habitat type was not optimum habitat for any species studied, a conclusion further supported by our observed patterns in nest success. Thus, effective management strategies for these songbird species populations—many of which are declining in numbers—must seek to incorporate natural shrubland areas already present on the landscape, evaluate the potential contribution of regenerating forests, and acknowledge that edges present in the natural and modified landscape matrix are insufficient sources of habitat for these species.

Continued management of glade habitats (i.e., controlled burning, mowing, grazing, cedar felling) is important to the conservation of shrubland bird species in the midwestern United States. Additionally, restoration of glades that have not received management attention—namely through the control of dominant woody species like eastern red cedar—can set back succession to a shrub-dominated seral stage (Askins 1998) and, in so doing, benefit shrubland songbird species as well as nonavian species that also may be management priorities (e.g., tarantulas [*Aphonopelma hentzi*]; Janowski-Bell 2001). While our results support the importance of active glade management, clearly, natural habitats whose occurrence depends on a variety of biological and physical conditions (e.g., periodic fire and shallow, rocky soils) may be difficult to add or restore to the landscape. Thus, managers in areas where shrubland songbirds are considered a conservation priority should consider timber management as a way to create habitat useful to these species.

Provision of regenerating forest habitat is somewhat easier and can be accomplished through commercial timber harvest at no cost or even profit to the landowner, although it too comes with unique management challenges. This habitat type could be important in maintaining shrubland bird populations in some areas, and our results indicate that a unit of regenerating forest can provide habitat for more individuals of some species (e.g., yellow-breasted

chat, indigo bunting, eastern towhee) than a unit of either glade or edge habitat. Management of regenerating forests requires planning because the length of time the habitat is suitable for shrubland birds varies and depends on local (e.g., site quality) and regional (e.g., climate) factors (reviewed in Thompson and DeGraaf 2001). In the Ozarks, regenerating stands are suitable for shrubland bird occupancy for approximately 10–15 years (Thompson and Dessecker 1997); some high-quality sites (as in soil conditions, slope, aspect, etc.) may maintain shrubland bird populations for less time, and poor sites may be suitable for longer. In contrast, because glade sites succeed to more closed canopy eastern red cedar stands at a slower rate, an unmanaged glade site could remain suitable for 30 years or more (Chambers 1994). Further, the effects of forest fragmentation on wildlife species require that managers carefully consider and balance the establishment of regenerating forest stands with the needs for habitat quantity and quality by species requiring later seral stages.

In addition to important differences in abundance of breeding birds in these 3 habitat types, we also observed important differences in nesting success. These results provide further support for a careful interpretation of breeding densities. While a simple gauge of the success of management activities is the estimation of avian abundance, greater abundance does not always equate to greater productivity, and, thus, improved evaluations of management effectiveness should incorporate estimates of reproductive success.

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Appendix 1. Mean number of territories/ha, standard error (SE), and 95% confidence intervals [(lower confidence limit, upper confidence limit); truncated at zero to avoid negative densities] of 8 bird species in 3 habitat types in the Missouri Ozarks, USA, 1997–1999.

Species	Glade			Regeneration			Edge		
	\bar{x}	SE	95% CI	\bar{x}	SE	95% CI	\bar{x}	SE	95% CI
Blue-winged warbler									
1997	0.565	0.187	(0, 1.37)	0.475	0.079	(0.14, 0.81)	0.163	0.086	(0, 0.53)
1998	0.363	0.023	(0.26, 0.46)	0.346	0.129	(0, 0.90)	0	0	
1999	0.363	0.023	(0.26, 0.46)	0.199	0.116	(0, 0.70)	0	0	
All years	0.430	0.054	(0.20, 0.66)	0.340	0.065	(0.06, 0.62)	0.054	0.029	(0, 0.18)
Eastern towhee									
1997	0.319	0.073	(0.00, 0.63)	0.410	0.126	(0, 0.95)	0.159	0.083	(0, 0.52)
1998	0.249	0.079	(0, 0.59)	0.358	0.084	(0, 0.72)	0.159	0.083	(0, 0.52)
1999	0.055	0.055	(0, 0.29)	0.279	0.063	(0.01, 0.55)	0	0	
All years	0.208	0.047	(0.01, 0.41)	0.349	0.078	(0.01, 0.68)	0.106	0.055	(0, 0.34)
Field sparrow									
1997	0.440	0.064	(0.17, 0.71)	0.607	0.014	(0.55, 0.67)	0.867	0.168	(0.14, 1.59)
1998	0.363	0.023	(0.26, 0.46)	0.541	0.160	(0, 1.23)	0.672	0.085	(0.31, 1.04)
1999	0.110	0.110	(0, 0.58)	0.330	0.173	(0, 1.08)	0.672	0.085	(0.31, 1.04)
All years	0.304	0.053	(0.08, 0.53)	0.493	0.106	(0.03, 0.95)	0.737	0.076	(0.41, 1.06)
Indigo bunting									
1997	1.079	0.191	(0.25, 1.90)	1.701	0.418	(0, 3.50)	0.965	0.259	(0, 2.08)
1998	0.916	0.158	(0.24, 1.60)	1.587	0.414	(0, 3.37)	1.124	0.195	(0.28, 1.96)
1999	0.803	0.214	(0, 1.73)	1.334	0.169	(0.61, 2.06)	0.708	0.236	(0, 1.72)
All years	0.933	0.168	(0.21, 1.66)	1.541	0.307	(0.22, 2.86)	0.932	0.228	(0, 1.91)
Northern cardinal									
1997	0.455	0.189	(0, 1.27)	0.477	0.141	(0, 1.08)	0.579	0.009	(0.54, 0.62)
1998	0.277	0.069	(0, 0.57)	0.357	0.082	(0.00, 0.71)	0.607	0.130	(0.05, 1.17)
1999	0.191	0.119	(0, 0.70)	0.279	0.063	(0.01, 0.55)	0.513	0.060	(0.25, 0.77)
All years	0.308	0.126	(0, 0.85)	0.371	0.057	(0.13, 0.61)	0.566	0.058	(0.32, 0.81)
Prairie warbler									
1997	1.204	0.286	(0, 2.43)	0.933	0.315	(0, 2.29)	0.097	0.097	(0, 0.52)
1998	0.975	0.126	(0.43, 1.52)	1.146	0.433	(0, 3.01)	0.195	0.195	(0, 1.03)
1999	0.803	0.214	(0, 1.73)	0.883	0.261	(0, 2.01)	0.097	0.097	(0, 0.52)
All years	0.994	0.155	(0.33, 1.66)	0.987	0.331	(0, 2.41)	0.130	0.130	(0, 0.69)
White-eyed vireo									
1997	0.460	0.241	(0, 1.50)	0.605	0.110	(0.13, 1.08)	0.257	0.030	(0.13, 0.39)
1998	0.491	0.374	(0, 2.10)	0.570	0.095	(0.16, 0.98)	0.350	0.109	(0, 0.82)
1999	0.437	0.237	(0, 1.46)	0.423	0.027	(0.31, 0.54)	0.257	0.030	(0.13, 0.39)
All years	0.463	0.146	(0.13, 0.80)	0.533	0.041	(0.36, 0.71)	0.288	0.051	(0.07, 0.51)
Yellow-breasted chat									
1997	0.616	0.314	(0, 1.97)	0.869	0.159	(0.18, 1.55)	0	0	
1998	0.573	0.356	(0, 2.10)	1.124	0.060	(0.86, 1.38)	0	0	
1999	0.410	0.236	(0, 1.42)	0.912	0.055	(0.67, 1.15)	0	0	
All years	0.533	0.281	(0, 1.74)	0.968	0.072	(0.66, 1.28)	0	0	