



## Landscape effects mediate breeding bird abundance in midwestern forests

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### Abstract

We examine the influence of both local habitat and landscape variables on avian species abundance at forested study sites situated within fragmented and contiguous landscapes. The study was conducted over a six year period (1991–1996) at 10 study sites equally divided between the heavily forested Missouri Ozarks and forest fragments in central Missouri. We found greater species richness and diversity in the fragments, but there was a higher percentage of Neotropical migrants in the Ozarks. We found significant differences in the mean number of birds detected between the central Missouri fragments and the unfragmented Ozarks for 15 (63%) of 24 focal species. We used stepwise regression to determine which of 12 local vegetation variables and 4 landscape variables (forest cover, core area, edge density, and mean patch size) accounted for the greatest amount of variation in abundance for 24 bird species. Seven species (29%) were most sensitive to local vegetation variables, while 16 species (67%) responded most strongly to one of four landscape variables. Landscape variables are significant predictors of abundance for many bird species; resource managers should consider multiple measures of landscape sensitivity when making bird population management decisions.

### Introduction

Traditionally ecologists and wildlife managers have attempted to determine relationships between the occurrence (or abundance) of species and local habitat (or patch) characteristics because of the broad implications of these relationships to both ecological theory and biodiversity management (Cody 1985; Verner et al. 1986). Wildlife habitat relationships and habitat suitability indices have been statistically modeled for a variety of taxa (Blenden et al. 1986; Murphy and Wilcox 1986) especially birds (reviewed in Verner et al. 1986; Morrison et al. 1992), to predict the occurrence and abundance of species within a habitat, as well as to rank appropriate habitat for a species (Fish and Wildlife Service 1980). Models are typically based on attributes within the patch (e.g. vegetation

traits), so that care must be exercised when interpreting data beyond the scale of the patch (Bolger et al. 1996). Species-area curves have also been employed to determine relationships between overall patch size and the number of species present, especially in island (or island-like) systems (MacArthur and Wilson 1967). An underlying assumption for many of these approaches is that the relationship between the habitat patch and species occurrence (or abundance) will be similar, regardless of the landscape context.

However, ecologists are increasingly examining ecological patterns and processes at a landscape scale to understand the distribution and abundance of organisms contained within the habitat patches that compose the landscape (Forman and Godron 1986; Flather and Sauer 1996; Bolger et al. 1997). This approach is necessary because species' responses to a

habitat patch may change with attributes of the landscape. Species interactions and responses may vary for species within patches that adjoin different patch types (e.g. edge effects, Paton 1994); for species in habitat patches of similar composition, but of differing patch sizes or distributions (e.g. habitat fragmentation effects, Robinson et al. 1995); for species requiring source-sink dynamics among patches in a landscape (e.g. meta-populations, Pulliam 1988); and for species in habitat patches of similar composition but located within different landscape matrices (e.g. forest patches within clearcuts, monocultures, or contiguously forested matrices [Renjifo 1999]).

Certain organisms, or suites of organisms, may be more or less resilient to landscape perturbations (e.g. fragmentation) or landscape characteristics (such as the amount of core habitat). A species' resilience or sensitivity to changes in the landscape may be related to its degree of habitat specialization so that habitat generalists are less affected by change than habitat specialists. Similarly, species which require multiple habitat types to complete their life cycle may be less resilient to change. Neotropical migratory birds require spatially disjunct habitats for different phases of their life cycle (e.g. breeding and wintering activities). Recently these birds were found to be more 'sensitive' to landscape structure on the breeding grounds than birds with other migratory tendencies in the eastern United States (Flather and Sauer 1996). These trends are of particular concern because many populations of Neotropical migrants appear to be declining across North America (Robbins et al. 1989; Terborgh 1989).

The evidence for population declines in Neotropical migrant birds has come principally from the Breeding Bird Survey (BBS), a continent-wide compilation of roadside censuses. Although this may be a powerful method for detecting regional or national population trends, attempts to explain population declines of migrants detected by BBS data have been complicated by a variety of factors. These include disagreement about which models are appropriate for analyzing the data (Thomas 1996), problems with interpreting data when these patterns may be the result of a complex pattern of regional population declines and increases (James et al. 1996), and the failure to incorporate detailed vegetation information and possible long-term changes in vegetation when interpreting census results (James et al. 1992).

The absence of detailed habitat information at three scales limits the extent that census data can be used to interpret population patterns or trends. At the

very local scale of breeding habitat, census data must be considered with regard to specific habitat patch characteristics of the study sites because habitat differences can affect nest site selection and territory establishment by species (Robbins et al. 1989). Population trends may be the result of either natural or anthropogenic changes in habitat, but without vegetation data observers are unable to discriminate between possible causes of increases or declines in bird populations. At the landscape scale, information on the size, number, and distribution of habitat patches may be required to interpret patterns in species abundance; moreover, many of these landscape-associated factors may interact or covary with each other. For example, the degree of habitat fragmentation in the landscape influences the distribution of habitat patches, which may be important to avian population dynamics (Freemark et al. 1995; Robinson et al. 1995; Kessler et al. 1992). Studies have shown strong relationships between habitat composition of the landscape and avian abundance (Bolger et al. 1997) or reproductive success (Donovan et al. 1995a; Robinson et al. 1995). Habitat fragmentation also increases edge habitat while reducing core habitat (Faaborg et al. 1995), resulting in decreased food availability (Burke and Nol 1998) and increased nest predation (Paton 1994) and brood parasitism (Robinson et al. 1995). Finally, at the regional level, the fact that some local bird populations persist despite apparently low reproductive rates within habitat patches, suggests that many migrants may exhibit regional source-sink dynamics (Donovan et al. 1995b; Robinson et al. 1995); therefore, understanding population variation at the local patch and landscape levels also requires knowledge of regional demography and regional dispersal patterns (Pulliam 1988; Donovan et al. 1995a, b; Robinson et al. 1995).

In this study we examined relationships between species abundance and patch characteristics for sites with similar vegetation features, but different landscape attributes. We used vegetation and landscape composition data to understand avian abundance patterns over a six-year period (1991–1996) for ten study sites equally divided between the unfragmented Missouri Ozarks and the forest fragments in Central Missouri. We analyzed: (a) patterns of relative avian abundance, species richness, and diversity in fragmented and unfragmented landscapes; (b) vegetation and landscape measures within and between the fragmented and unfragmented regions; and (c) the relative importance of vegetation and landscape characteristics on avian abundance patterns, especially for species

with different migratory tendencies. We also noted species showing significant local population increases or declines and discuss possible reasons for these changes. We conclude with suggestions about what our findings mean to migratory bird management.

## Study site and methods

### *Study sites*

Data were collected at ten study sites in mature oak-hickory forest (> 40 years old) in Missouri (Figure 1). Five sites were situated within forest fragments (340–880 ha in area) in Central Missouri, and five sites were situated in relatively continuous forest (18,000–30,125 ha in area) in the Missouri Ozarks. All sites were selected to minimize variability in forest structure and composition; detailed measurements from a prior study on a subset of the fragmented sites showed them to be structurally very similar (Wenny et al. 1993). Within each study site we established a sampling grid with 15 census points, 150 m apart. Points were situated at least 70 m from the edge of fragments to reduce edge effects (Paton 1994). While the Ozark study sites represent a smaller percentage of the surrounding forest than the fragmented sites, there is generally greater habitat homogeneity throughout the Ozarks so that the Ozark study sites are representative of the surrounding forest. Ozark sites are described in detail in Kabrick et al. (1997) and fragmented study sites are described in Donovan (1994).

### *Vegetation variables*

Twelve variables describing local vegetation structure were measured according to the BBIRD protocol (Montana Cooperative Wildlife Research Unit [MCWRU] 1994) at each of the census points at all sites in 1995. We used a 5 m radius circle as the vegetation plot and recorded: (a) the number of living stems in three size classes based on stem diameter at breast height (< 2 cm, 2–5 cm, and 5–10 cm dbh); (b) organic litter depth at 12 points, 2 m apart, along perpendicular axes of the circle; (c) percent canopy cover as estimated with an ocular tube; (d) estimated percentage of downed logs; and (e) estimated percentage of forbs < 50 cm off the ground). In addition, within a 11.3 m radius circle, we counted all snags, pine stems, and the number of trees in each of three size classes (10–20 cm, 20–50 cm, and > 50 cm dbh).

We sampled one to three non-overlapping vegetation plots for each bird census point and averaged the values for each variable. We then calculated mean values of these variables for each study site across all fifteen points within a site.

### *Landscape variables*

Four landscape statistics were measured within a 10 km radius circle of each of the ten sites using Landsat imagery and an existing GIS database (Donovan 1994). A 10 km radius circle was chosen because it best explains the distribution of cowbirds in our study area (Donovan et al. 1999) and encompasses the average distances moved by female cowbirds during the breeding season (Thompson 1994). Landscape measures included (a) MEANPAT which measured the mean size (ha) of forested patches, (b) COREINDX which measured the percentage of core area (i.e. the amount of forest > 250 m from any edge), (c) FORCOV which measured the percentage of forest, and (d) EDGEDENS which measured edge density or meters of edge per hectare (m/ha). All four landscape variables were highly correlated (Pearson correlation coefficients ranged from 0.90 to 0.97,  $P < 0.001$ ); however, each landscape variable measured a unique attribute of the landscape (see Discussion).

### *Point counts*

Birds were censused using the point count methodology outlined in the BBIRD field protocol (MCWRU 1994). Observers recorded all bird species seen or heard within 50 m of the bird census points during a 10 min period. One limitation of most point count data is that not all birds detected are breeding species and some birds detected are more typically found in adjacent habitat. We attempted to control for this problem by limiting point counts to a 50 m radius and situating points at least 70 m from the forest edge.

Sites were visited at least three times each year between 20 May and 15 June, but two Ozark sites were not surveyed in 1991 or 1992 (DRC and CCC) and one Central Missouri fragment was not surveyed in 1991 (ASH). To reduce the effects of observer bias, 3–5 observers were rotated between sites each year, but some observers censused in multiple years. Observers used different paths within a site on each visit to vary the order in which points were censused and to minimize any effects of time of day on count results. No counts were conducted on days when visibility was poor, or in windy or rainy conditions. We calculated the average

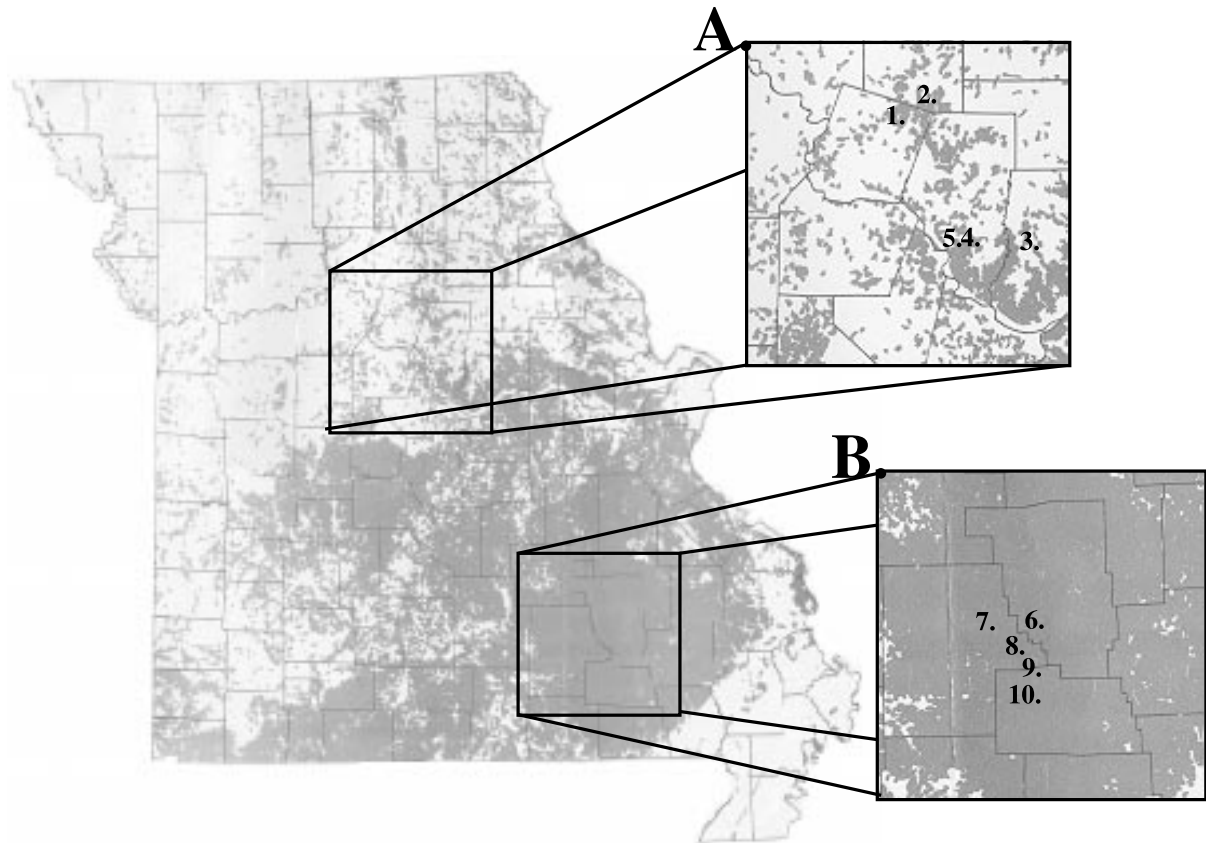


Figure 1. Location of ten study sites in (A) Central Missouri fragments: (1) Hungry Mother Wildlife Area, (2) Bennitt Wildlife Area, (3) Fulton, (4) Ashland, (5) Ashland Lake; and (B) Missouri Ozarks: (6) Deer Run, (7) Carr's Creek, (8) Cardareva, (9) Peck Ranch A, (10) Peck Ranch B. Shaded area corresponds to forest cover.

number of detections of each species at each census point for each year. We then calculated mean values of these variables for each study site across all fifteen points within a site.

#### Statistical analyses

The statistical package SAS (SAS Institute Inc. 1990) was used to perform various statistical tests described in Sokal and Rohlf (1981). A probability of Type I error of 0.05 or less was accepted as significant (unless otherwise noted) but greater values are shown for descriptive purposes. All variables were tested for normality using the Wilkes–Shapiro test and nonparametric tests were used when necessary. For comparisons of avian abundances between the two regions and for the analyses of vegetation structure and landscape effects on avian abundance, we focused on 24 species which bred consistently in both regions. We excluded irruptive breeders, passage migrants, species not ad-

equately sampled by standard point counts, species occurring in only one region, and species which were only detected during one year of the six year study from these analyses.

We compared mean species abundances between the Central Missouri fragments and the unfragmented Ozarks using Mann–Whitney *U*-tests for all 24 focal bird species. These tests entailed 24 planned comparisons (for each of the 24 focal bird species) between the two landscapes so we decreased the experiment-wise level of alpha to 0.0021 (Bonferroni correction) in order to reduce the probability of committing a Type I error (Sokal and Rohlf 1981).

We compared vegetation variables between the fragmented Central Missouri fragments and the contiguous Ozarks regions with the *a priori* expectation that the vegetation composition would be *similar* between regions (all study sites were chosen based on their similar vegetation characteristics). We made

comparisons between regions for each of the 12 vegetation variables using Mann–Whitney *U*-tests. We did not use multivariate techniques when comparing vegetation measures among sites because variable reduction or combination can make results difficult to interpret. The derived components from such analyses are artificial variates which may maximize explained variance, but they are not designed for interpretability (Stevens 1992). Additionally, as we expected sites to be similar, we wanted to determine the precise source of any differences that were found. Because we expected the null hypothesis to be true (i.e. no difference in vegetation characteristics between the regions) we wanted to reduce the probability of committing a Type II error (falsely accepting a null hypothesis), so we did not perform a Bonferroni adjustment on alpha when comparing vegetation variables.

We also expected *a priori* that the landscape measures would *differ* between regions (as per our study design) because five sites were within a contiguous forest matrix and five sites were within a fragmented forest matrix. We made comparisons between regions using a Mann–Whitney *U*-test for each of the four landscape measures; however, for these four planned comparisons we expected to find differences and we used a Bonferroni correction to decrease the probability of committing a Type I to 0.0125 for each test.

To determine trends in species abundance in each region, we performed a repeated measures ANOVA to examine the effect of a year on mean species abundance for each species in each region (Ozarks and Central Missouri fragments). We decreased the experimentwise level of alpha to 0.0021 in order to reduce the probability of committing a Type I error. When a significant year effect was found for a species, we used post-hoc contrast analyses (Rosenthal and Rosnow 1985) to determine if the year effect was due to a population increase, a population decrease, or general annual variability during the six years of the study. We only report results for species in which the significant year effect also indicated a significant increasing or decreasing trend.

We used stepwise multiple regression models to determine which of 12 vegetation variables and four landscape variables accounted for the greatest amount of variation in species abundance for 24 species. Vegetation variables were included in the regressions as means per site to provide an overall picture of the characteristics of a site within a certain landscape (fragmented or unfragmented), although there may

be some vegetational variability within a site that is masked by the mean. Stepwise multiple regression identifies which variables explain the greatest amount of variation in species abundance; the first variable to enter the stepwise model accounts for the greatest variability. A variable may be removed if variables are highly correlated, but this occurred in only two models and in each case the variable was not the first to enter the model and it had an  $r^2$  less than 0.03. Only variables that made significant contributions to the overall model were kept ( $P < 0.05$ ). After first employing the stepwise procedure to identify significant variables, we analyzed each overall model again using multiple regression.

#### *Bird species diversity*

To compare diversity and evenness between landscapes we calculated the Shannon diversity index (*H*) and the Shannon evenness index (*J*) for each landscape. We chose this diversity index to compare landscapes because it meets the criteria of having index values at each classification level which sum to the index value for all classification levels (Hunter 1990), and we used the natural logarithm in our calculations. We also ranked each species' proportional abundance to compare the frequency of birds with different migratory tendencies (Neotropical migrant versus resident/short distance migrant) in each landscape.

## **Results**

#### *Habitat parameters*

All ten study sites were selected because they have generally similar vegetation characteristics despite lying within a larger matrix of two different landscapes (Table 1). All sites support mature oak-hickory forest and have similar measures of canopy cover, stems < 2 cm dbh, stems > 20 cm dbh, leaf litter depth, and downed logs. Nonetheless, vegetation differences were found between regions. Much of this difference is because the Ozark sites are at a higher elevation, have greater topographic relief, and are at a slightly more southern latitude than the Central Missouri sites. The boundaries of the Ozark study plots did not generally encompass the riparian habitats found in lower elevations of the Central Missouri sites. In addition, the Ozark sites have more pine stems (no pine occurs naturally in Central Missouri), nearly twice as many

Table 1. Landscape and vegetation characteristics of ten study sites with comparisons between regions. Values for vegetation characteristics are means across n plots measured per site.

Site <sup>a</sup>	HUM	RBE	ASH	ALA	FUL	Cen. Missouri <sup>b</sup>	PRE	CCC	CAU	DRC	Ozarks <sup>b</sup>	U <sup>c</sup>
Landscape												
FORCOV	35.6	38.2	43.2	43.5	21.4	36.4 (9.02)	95.6	96.5	95.9	95.3	90.2	94.7 (2.55)
MEANPAT	620.8	631.6	1508.3	1519.4	231.0	902.2 (581.22)	18000.0	29150.0	30125.0	29950.0	28350.0	27115.0 (5144.10)
EDGEDENS	10.1	10.7	9.2	9.1	7.0	9.2 (1.42)	2.6	2.1	2.1	2.6	4.6	2.8 (1.04)
COREINDEX	7.0	8.3	12.1	12.4	3.4	8.6 (3.77)	73.6	79.6	78.9	76.2	66.0	74.9 (5.48)
Vegetation												
Plots	30	30	30	26	30	146	30	30	29	30	149	
Pine stems	0	0	0	0	0	0	1.7	1.0	1.4	1.1	0.3	1.1 (0.51)
Snags	1.0	0.4	0.7	0.5	0.4	0.6 (0.24)	1.5	0.7	1.0	1.4	1.0	1.1 (0.33)
Stems <2 cm	26.7	38.1	17.1	19.0	26.9	25.8 (8.29)	20.2	15.8	17.0	14.0	19.4	17.3 (2.56)
2–5 cm	10.6	8.6	6.6	6.8	4.2	7.4 (2.39)	3.1	4.3	3.9	5.2	4.9	4.3 (0.82)
5–10 cm	3.7	2.9	3.5	3.6	1.7	3.0 (0.83)	2.7	4.4	3.5	3.8	3.8	3.7 (0.63)
10–20 cm	3.9	3.3	5.4	4.3	9.1	5.2 (2.32)	8.0	8.8	13.4	15.8	8.6	10.9 (3.48)
20–50 cm	6.2	6.3	7.8	6.7	7.5	6.9 (0.73)	7.8	6.1	5.8	6.4	6.3	6.5 (0.76)
>50 cm	0.8	1.5	1.0	1.2	0.3	1.0 (0.44)	0.6	0.7	0.7	0.6	0.4	0.6 (0.13)
Total stems	51.9	60.6	41.3	41.5	49.8	49.2 (8.05)	42.4	40.1	44.3	45.8	43.5	43.2 (2.14)
Canopy cover	96.2	93.9	93.5	99.6	96.6	96.0 (2.45)	96.5	98.0	96.4	100.0	98.2	97.3 (1.31)
Litter depth	2.5	2.3	1.7	2.2	2.4	2.2 (0.32)	2.2	2.2	2.7	3.0	3.2	2.7 (0.47)
Downed logs	4.3	2.9	2.1	3.6	5.5	3.7 (1.31)	4.5	3.4	7.6	4.0	5.1	4.9 (1.60)
Forbs	25.0	31.3	16.7	60.8	70.2	40.8 (23.34)	8.6	12.1	13.0	18.6	16.2	13.7 (3.83)

<sup>a</sup>Site abbreviations: HUM=Hungry Mother; RBE=Rudolph Bennitt Wildlife Area; ASH=Ashland; ALA=Ashland Lake; FUL=Fullton; PRE=Peck Ranch East; RBE=Peck Ranch West; CCC=Carr's Creek; CAU=Cardareva; DRC=Deer Run Creek.

<sup>b</sup>Central Missouri and Ozarks columns show means (SD) calculated across all five sites per region.

<sup>c</sup>Comparisons between Central Missouri and Ozarks based on Mann–Whitney U-test, df=1. \*P<0.05, \*\*P<0.009.

snags, and more large stems (10–20 cm dbh). The Central Missouri sites have significantly more small stems (2–5 cm dbh) and forbs. However, the greatest differences between Central Missouri and Ozark sites were among landscape variables, as per our study design. The Ozarks differed significantly from the Central Missouri sites in all the landscape measures, as the latter is a fragmented forest region with lower amounts of forest cover, smaller forest patches, lower core indices, and greater edge density.

We found some variation in landscape and vegetation parameters within regions as well (Table 1). However, the variation in vegetation measurements in both regions is distributed in such a manner that no site is particularly unusual in a large number of vegetation measures. Within the Central Missouri fragments, the forest tracts vary in size from 340 ha to 880 ha so that some landscape measures vary (e.g. mean patch size within 10 km radius); however all fragmented sites have similar amounts of edge density and percent core area (Table 1). The lack of forest fragmentation within the Ozarks results in less variation among landscape measures for these sites.

#### *Bird species richness*

We detected 74 species of birds in point counts among both regions over the six year course of this investigation. Twenty-five species were considered irruptive breeders, passage migrants, or inadequately sampled by point counts, and were excluded from any further analyses. Of the remaining 49 breeding species, 36 species were detected in the Ozarks, of which 26 (70%) occurred in all years, while four (11%) were detected in only one year. The total number of species per year in the unfragmented Ozark sites varied from a low of 28 in 1992 to a high of 32 in 1991, 1994, and 1995. In the Ozarks, 25 (68%) species were Neotropical migrants and 11 (30%) were permanent resident species. One short-distance migrant was encountered on the Ozark study sites. Three species found in the Ozarks were not present at the Central Missouri sites (Appendix 1).

We found greater species richness in the fragmented Central Missouri region, although there was less annual consistency in species composition. A total of 47 species were detected, of which 31 (66%) occurred in all years, and 5 (11%) were encountered in only one year. The number of species detected in Central Missouri varied among years, ranging from 35 in 1994 and 1996 to 41 in 1992. Of the species

sampled by point counts at Central Missouri sites, 29 (62%) were Neotropical migrants, 6 (13%) were short-distance migrants, and 12 (26%) were permanent residents. Thirteen species found on Central Missouri sites were not present on the Ozark sites (Appendix 1).

#### *Species abundances*

We found significant differences in the mean number of birds detected between the Central Missouri fragments and the unfragmented Ozarks for 15 (63%) of the 24 focal species (Figure 2, Appendix 1). We found significantly higher abundances of seven species in the Ozarks, all Neotropical migrants (Acadian Flycatcher,  $U=46.5$ ,  $P<0.001$ ; Black-and-white Warbler,  $U=171.0$ ,  $P<0.001$ ; Blue-gray Gnatcatcher,  $U=141.0$ ,  $P<0.001$ ; Red-eyed Vireo,  $U=20.0$ ,  $P<0.001$ ; Scarlet Tanager,  $U=69.5$ ,  $P<0.001$ ; Worm-eating Warbler,  $U=185.5$ ,  $P=0.001$ ; and Yellow-throated Vireo,  $U=120.0$ ,  $P<0.001$ ). In contrast, of the eight species we found to have significantly higher abundances in the Central Missouri fragments, only four were Neotropical migrants (Eastern Wood-Pewee,  $U=625.0$ ,  $P<0.001$ ; Great Crested Flycatcher,  $U=631.0$ ,  $P<0.001$ ; Kentucky Warbler,  $U=670.0$ ,  $P<0.001$ ), and five were permanent residents or short-distance migrants (Brown-headed Cowbird,  $U=730.0$ ,  $P<0.001$ ; Blue Jay,  $U=688.5$ ,  $P<0.001$ ; Northern Cardinal,  $U=729.0$ ,  $P<0.001$ ; Red-bellied Woodpecker,  $U=628.0$ ,  $P<0.001$ ; and Tufted Titmouse,  $U=670.0$ ,  $P<0.001$ ). The most abundant species in the fragments was the Brown-headed Cowbird, whereas the most abundant species in the Ozarks was the Red-eyed Vireo.

#### *Species diversity*

The Shannon diversity index was greater in the fragments ( $H=2.87$ ) than in the contiguous Ozarks ( $H=2.64$ ). Evenness was also greater in the fragments ( $J=0.90$ ) than the Ozarks ( $J=0.83$ ), although both evenness values are relatively high (evenness indices range from zero to one) indicating species equitability.

The ranking of species by their proportional abundances indicates that the most abundant species in the Ozarks tend to consist of Neotropical migrants (87.5%), whereas in the fragments the abundantly occurring species are evenly divided between Neotropical migrants and residents/short distance migrants (Figure 3). In the Ozarks the species composition included fewer Neotropical migrants (and more residents or short distance migrants) as rank category

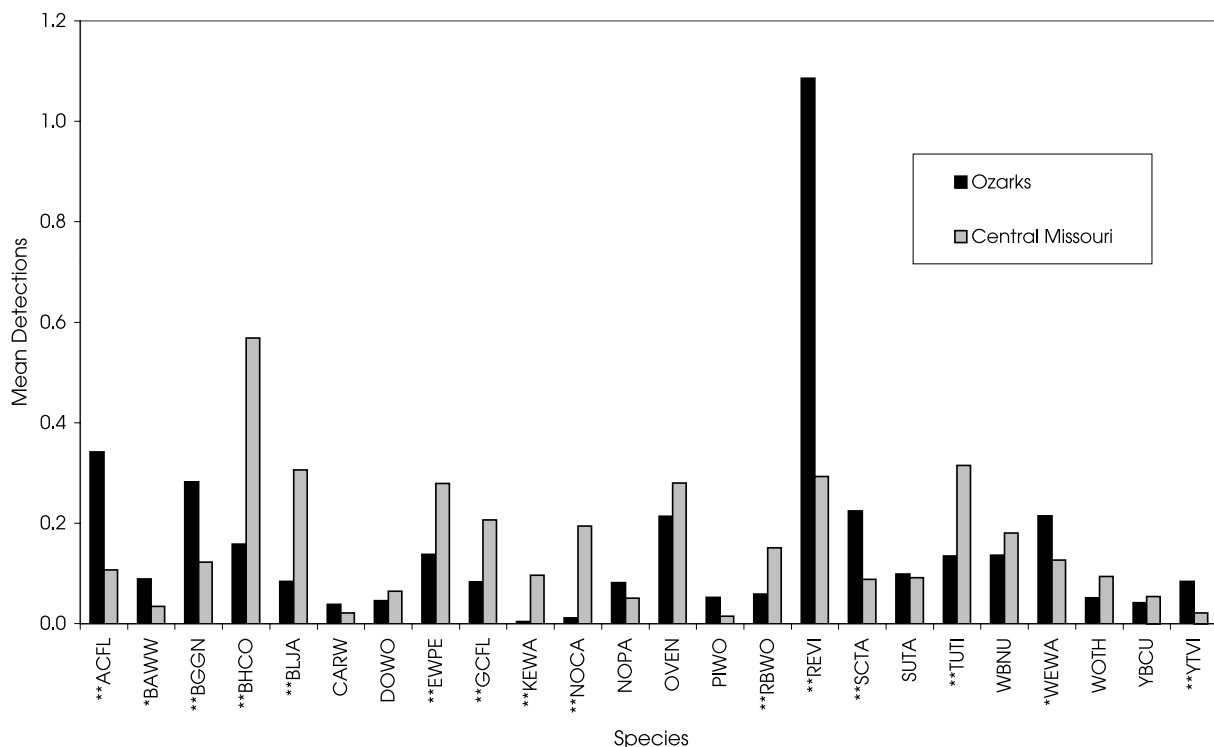


Figure 2. Differences in abundances (mean detections) between regions for 24 species of birds found in Central Missouri forest fragments and unfragmented Missouri Ozark forests based on the Mann–Whitney *U*-test. \* $P < 0.0021$ , \*\* $P < 0.001$ .

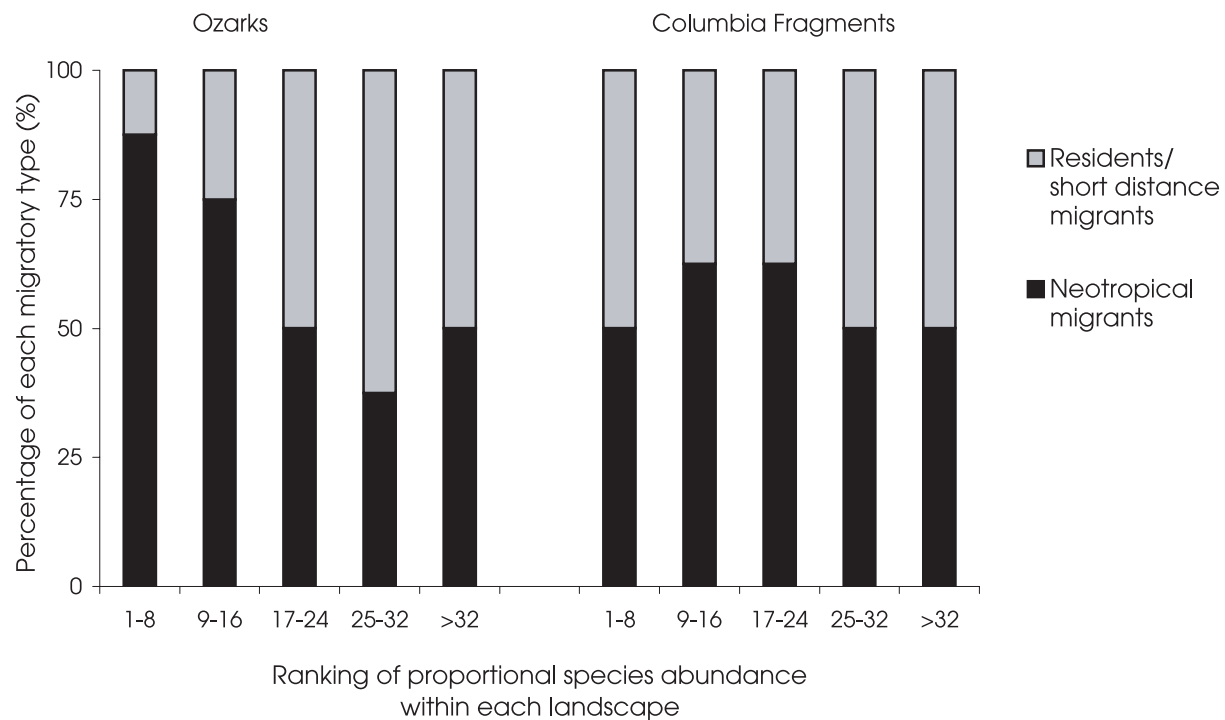


Figure 3. Ranking of species proportional abundance for birds with different migratory tendencies within each landscape. Species rankings are divided into categories ranging from proportionately most common to proportionately most rare within each landscape.



increased (and species became proportionately less abundant). In the fragments there were approximately equal percentages of Neotropical migrants and residents/short distance migrants in all rank categories including abundant and rare species.

#### *Population trends*

During the six-year period, we detected significant year effects for eight of the 24 focal species breeding in one of the regions. However, seven of these significant year effects were due to annual variability in bird numbers (including above average numbers of bird detections in 1992) and were not due to overall population increases or decreases. *Post-hoc* comparisons revealed that only the significant year effect for the Blue Jay ( $F_{1,8}=11.4$ ,  $P<0.01$ ) was associated with a significant declining population trend over the six year period. The decline was only detected in the central Missouri fragments, although the mean detection rate for Blue Jays over the six year period was greater in the fragments than the contiguous Ozarks (Figure 2). There was no significant year effect or population trend for Blue Jays in the Ozarks.

#### *Environmental correlates of bird abundance*

Of the 24 breeding bird species analyzed, 23 (96%) exhibited one or more significant correlations with the landscape or vegetation variables in our stepwise multiple regression (Table 2). We refer to a species as being sensitive to a particular vegetation or landscape variable when that variable is the first to enter the stepwise multiple regression model, accounting for the greatest amount of variation in abundance for that particular species. Only the Yellow-billed Cuckoo was not sensitive to any of the landscape or vegetation variables in the stepwise regression.

Sixteen species (67%) were most sensitive to one of the landscape variables (Table 2). For each of these landscape sensitive species, the first landscape variable had an  $r^2>0.50$  and the overall model had an  $r^2>0.62$ . Among the landscape sensitive species, four species responded most strongly to the edge density variable. The Blue-gray Gnatcatcher had a negative association, while the Brown-headed Cowbird, Blue Jay, and Eastern Wood-Pewee had positive associations with edge density. Three species responded most strongly to the forest cover variable; the Pileated Woodpecker had a positive association and the Kentucky Warbler and Northern Cardinal had negative associations with this variable. Six species responded

most strongly to the mean patch size variable. The Acadian Flycatcher, Red-eyed Vireo, Scarlet Tanager, and Yellow-throated Vireo all had positive associations with mean patch size, while the Great Crested Flycatcher and Tufted Titmouse had negative associations. Finally, three species responded most strongly to the core index variable. The Carolina Wren and Northern Parula had positive associations with core index, while the Red-bellied Woodpecker had a negative association with this variable.

Seven bird species (29%) were most sensitive to one of the vegetation variables. For every vegetation sensitive species, the first vegetation variable had an  $r^2>0.38$ , and the overall model had an  $r^2>0.47$ . Of the seven species that were most sensitive to a vegetation variable, four species were most sensitive to a single vegetation variable: the Black-and-White Warbler was positively associated with pine density, the Worm-eating Warbler was negatively associated with forb density, the Downy Woodpecker was negatively associated with stems in the 5–10 cm category, and the White-breasted Nuthatch was negatively associated with stems in the 10–20 cm category. Three additional species were most sensitive to a vegetation variable, but were also associated with other variables. The Ovenbird showed a positive association with density of stems less than 2 cm and a negative association with large trees; the Summer Tanager was negatively associated with litter depth and positively associated with snags; and the Wood Thrush was positively associated with stems less than 2 cm, number of logs, and stems greater than 50 cm.

## **Discussion**

### *Bird species richness and abundance*

Both fragmented and unfragmented oak-hickory forest supported over 30 species of breeding birds. The unfragmented Ozarks supported a greater percentage of Neotropical migrants and contained only one short distance migrant, while the Central Missouri fragments supported more short distance migrants and bird species associated with shrub habitats and openings (e.g. Blue Jays) which were not detected, or occurred in low numbers, in the Ozarks. The lack of short distance migrants in the Ozarks may however be an 'artifact' of the habitat, as most forest breeding birds are either Neotropical migrant birds or permanent residents; short distance migrants tend to breed in heterogeneous habitats (e.g. Blue Jay).

Table 2. Results of stepwise multiple regression of landscape and vegetation effects on birds breeding in fragmented forests in Central Missouri and unfragmented Ozark forests. All variables that contributed significantly to the regression model for a given species are shown in their order of importance. Table includes the coefficient and partial  $r^2$  for each variable in the model, as well as the significance level and  $r^2$  for the overall model.

Bird species	First variable	Coefficient	Partial $r^2$	Second variable	Coefficient	Partial $r^2$	Third variable	Coefficient	Partial $r^2$	Fourth variable	Coefficient	Partial $r^2$	Model $r^2$	Model $P$
Landscape sensitive species														
BGGN	EDGEDENS	-0.02350	0.63										0.63	0.0059
BHCO	EDGEDENS	0.06155	0.85	STEMS<2	0.0176	0.09	LITDEP	-0.1754	0.03	CANOPY	0.0239	0.02	0.99	0.0001
BLJA	EDGEDENS	0.39667	0.71	LOGS	0.0438	0.21							0.92	0.0041
EWPE	EDGEDENS	0.02261	0.84										0.84	0.0002
KEWA	FORCOV	-0.00896	0.67	COREINDX	0.0067	0.19	STEMS<2	0.0040	0.10	SNAGS	0.0427	0.03	0.99	0.0001
NOCA	FORCOV	-0.00558	0.86	STEMS>50	-0.1108	0.09	STEMPINE	0.0604	0.03	FORBS	-0.00114	0.02	0.99	0.0012
PIWO	FORCOV	0.00068	0.87										0.87	0.0001
ACFL	MEANPATC	0.00002	0.74	STEM10-20	-0.0317	0.14	LOGS	0.0372	0.08				0.97	0.0001
GCFL	MEANPATC	-0.000003	0.71	LITDEP	-0.0901	0.15							0.86	0.001
REVI	MEANPATC	0.00003	0.95										0.95	0.0001
SCTA	MEANPATC	0.000005	0.72										0.72	0.002
TUTI	MEANPATC	-0.000006	0.88	STEMS<2	0.0046	0.06							0.94	0.0001
YTVI	MEANPATC	0.01919	0.63										0.63	0.0064
CARW	COREINDX	0.00271	0.51	STEM5-10	0.0184	0.16	FORCOV	-0.0023	0.16	MEANPATC	-0.000002	0.12	0.96	0.0014
NOPA	COREINDX	0.00034	0.85										0.85	0.0001
RBWO	COREINDX	-0.00141	0.83										0.83	0.0003
Vegetation sensitive species														
BAWW	STEMPINE	0.04535	0.51										0.51	0.0213
DOWO	STEM5-10	-0.01958	0.47										0.47	0.0288
OVEN	STEMS<2	0.0124	0.39	STEM20-50	-0.1124	0.32							0.70	0.014
SUTA	LITDEP	0.06035	0.38	SNAGS	0.0487	0.32							0.71	0.0134
WBNU	STEM10-20	-0.0089	0.66										0.66	0.0041
WEWA	FORBS	-0.002	0.50										0.50	0.0224
WOTH	STEMS<2	0.0034	0.47	LOGS	0.02267	0.23	STEMS>50	0.07209	0.19				0.89	0.0025

We found greater diversity and number of species in the Central Missouri fragments than we did in the unfragmented Ozarks. Our point count data support the finding that disturbance and fragmentation may increase local species diversity (Faaborg 1980; Noss 1983; but see Faaborg et al. 1995). These data suggest that such processes may increase the number of niches, habitats, or microhabitats available in a community. For example, fragmentation may increase the amount of edge habitat which may be valuable for some species (e.g. Blue Jay, Northern Cardinal), depending on their habitat preferences, life history traits, and dispersal capabilities. Disturbance may also provide an opportunity for generalist species (e.g. Great Crested Flycatcher, Red-bellied Woodpecker) to become established, as well as species that prefer open or brushy habitats but which may also venture into forested habitats (e.g. Brown-headed Cowbird, Northern Cardinal).

#### *Effects of vegetation characteristics on avian distribution*

In this study, vegetation variables were significantly correlated with the abundance of eight species. Despite the overall similarity of the mature oak-hickory forest across the ten study sites, differences were present which created distinct microhabitats. These microhabitats contributed to some of the differences in avian abundances between regions. For example, Black-and-white Warblers were associated with the density of pine trees (which are not naturally found in Central Missouri), and differences in abundance of Worm-eating Warblers may be partially ascribed to the relative scarcity of steep wooded slopes in the Central Missouri sites.

Other differences in bird abundances may be attributed to microhabitat differences, but these differences may be more difficult to detect without more detailed studies of habitat selection. For example, several species (Downy Woodpecker, White-breasted Nuthatch) were most sensitive to a single vegetation variable (e.g. number of trees with small stems, forb density), but these variables may themselves be indicators of other microhabitat conditions (e.g. forest age or canopy gaps) which we did not directly measure or are masked by other vegetation variables.

Results for the ground-nesting Ovenbird, which responded to two different vegetation variables (a positive association with density of stems less than 2 cm and a negative association with large trees), may be an

effect of the averaging of vegetation measures across a site, thereby losing critical microhabitat selection data. Previous work suggests Ovenbirds prefer habitats with large trees and high canopy closure (Van Horn and Donovan 1994), however measures of ground cover vary widely among studies (Van Horn and Donovan 1994).

The ground-foraging Wood Thrush, which also responded to multiple vegetation variables (positive association with stems less than 2 cm, logs, and stems greater than 50 cm), may suggest a requirement for second growth forest or a developed understory within a mature forest setting. This is consistent with Hoover and Brittingham's (1998) finding that Wood Thrush selected nest sites with a high density of trees, higher canopy, and higher density of shrubs than randomly selected points. Further autecological research is needed to clarify some of these habitat relationships.

#### *Effects of landscape characteristics on avian distribution*

In this study, landscape variables were significant predictors of abundance for many species. Landscape variables explained the greatest amount of variation in species abundance for 67% of the species analyzed, including nine Neotropical migrants. Moreover, most of the landscape sensitive species responded to a single landscape variable and this variable explained greater than 50% of the species variation in abundance. Eight landscape sensitive species were also associated with vegetation variables, but these variables typically explained no more than 10% of the variance.

While the four landscape measures were all highly correlated, the fact that many species were found to be sensitive to single measures suggests that there are some meaningful biological associations between bird abundance and particular landscape characteristics. Despite the correlations, the landscape measures were not measuring the same characteristics of the landscape. For example, the amount of forest cover in a landscape can vary independent of the amount of edge habitat in a landscape, depending on the size, number and distribution of forest patches; moreover, two landscapes with equivalent amounts of forest cover may differ in all other landscape measures (edge density, core index, or mean patch size) depending on the patch arrangement (Forman and Godron 1986).

It appears from this study that some Missouri breeding birds respond to different attributes of the

fragmented landscape, depending on the species. For example, a suite of species, including Red-eyed Vireo, Scarlet Tanager, Yellow-throated Vireo, and Pileated Woodpecker appear to be forest interior species by responding positively to forest core area or the mean size of forest patches. But another set of forest species seems unaffected by the level of forest fragmentation which we studied. These species, including Eastern Wood-Pewee, Red-bellied Woodpecker, Great Crested Flycatcher, and Tufted Titmouse, may be more abundant in fragmented forests, assuming that the forest fragments are large enough to include an average territory size. Such a pattern has also been found for some Neotropical migrants wintering in forest fragments (Wunderle and Latta; in press).

Not all landscape sensitive species favored interior forest habitat. Not surprisingly, Brown-headed Cowbird and Blue Jay were more abundant in edge-dominated sites. Additionally, a single species (Carolina Wren) was associated with multiple landscape variables, supporting the idea that this species is a habitat generalist (breeding in open woods as well as dense undergrowth) with a widespread distribution in Missouri (Jacobs and Wilson 1997; Haggerty and Morton 1995).

Some apparently landscape sensitive species may require further study to clarify habitat associations and landscape sensitivity. Similarly, species that require riparian areas, bottomland habitats, or steep slopes (Acadian Flycatcher, Kentucky Warbler, Worm-eating Warbler), which may vary within and between regions, may show up as being sensitive to fragment size in this study. Although we did not expect to find abundance differences resulting from latitudinal variation of the fragmented and unfragmented sites, this could partially explain differences in abundance of Acadian Flycatcher, which is near the northwestern limit of its distribution.

#### *Population trends*

Over the six-year period we found the Blue Jay (a year round resident or short distance migrant), declining in the Central Missouri fragments. We detected no significant population trends in the Missouri Ozarks for the Blue Jay, or any of the other focal species. Our results are in contrast to results from the Breeding Bird Survey (BBS). Using the 'Estimating Equation Results Trend Methodology' from the BBS for the Missouri region over the same 6-year period as well as over the 30-year period 1966–1996 (Sauer et al.

1997), there were no significant trends in abundance for the Blue Jay over the 6- and 30-year periods. These differences in trends may occur because of the small number of BBS routes in Missouri, and because BBS routes generally include multiple habitat types; only one BBS route appears to include contiguous Ozark forests, and one route appears near our Central Missouri fragments, but each of these Missouri routes includes other habitat types as well. These results emphasize the fact that large-scale studies such as the BBS may mask population dynamics occurring on a smaller, more local scale (Brawn and Robinson 1996). However, longer term data are required to determine if these trends persist.

#### *Study limitations*

Interpretation of the results of our point counts is limited by a variety of factors. The detection of a species at a site does not necessarily indicate successful pairing, and differences in abundance of a species between regions may not be correlated with their breeding productivity. Recent work during the breeding season has shown strong relationships between habitat composition at the landscape level and species abundance (Bolger et al. 1997), as well as reproductive success (Donovan et al. 1999; Robinson et al. 1995). Indeed, higher rates of nest predation and brood parasitism are associated with increased fragmentation and edges (Donovan et al. 1995a, 1997; Robinson et al. 1995) which reduce bird breeding success. Additionally, Burke and Nol (1998) found decreased food supply at edges. All these factors may explain why reduced pairing success has been observed in small fragments and on forest edges (Villard et al. 1993; Van Horn et al. 1995; Burke and Nol 1998).

Subsets of the same study sites in this investigation have been used to show that several species of birds experience poorer breeding or pairing performance in the Central Missouri fragments than conspecifics in the Ozarks. Porneluzi and Faaborg (1999) found reduced season-long productivity of breeding Ovenbird pairs in the fragments. Moreover, paired males that failed to raise young almost never returned to the fragments. Gibbs and Faaborg (1980) also found reduced pairing success for Ovenbirds and Kentucky Warblers in some of these same fragments. Donovan et al. (1995a) and Robinson et al. (1995) found that Ovenbird, Wood Thrush, Red-eyed Vireo, and Worm-eating Warbler had greater breeding productivity in the Ozarks than in the Central Missouri fragments. Other

breeding species may have similar patterns. Because of the negative effects mentioned above, Central Missouri fragments often consist of sink populations of birds in which reproduction does not exceed mortality (Donovan 1995a; Porneluzi and Faaborg 1999). The fact that local populations persist despite apparently low reproductive rates has suggested that many of these species may exhibit regional source-sink dynamics, such that explaining population variation locally requires knowledge of landscape composition, regional demography, and patterns of dispersal.

Finally, care must be taken in interpreting results of the stepwise regression. While our regression models cannot be interpreted as cause and effect, they can demonstrate the relative importance of each of the variables included in the models. As previously mentioned, one of the problems inherent in this approach is that models say nothing about habitat selection *per se*, only statistically what accounted for the greatest observed variation. Habitat heterogeneity and the precise habitat features selected by a species may be masked by averaging vegetation measures and by the modeling process. But this statistical technique does provide an important first means of assessing variation in species abundance at various levels and provides a big picture of site characteristics. We expect extensive detailed studies of each species would reveal finer mechanisms of habitat selection or territory establishment. Including these other variables in subsequent models may demonstrate that species abundances are associated with other factors, although these unmeasured variables may also be correlated with a variable we did measure. More detailed analyses of habitat selection cues are needed, including intraspecific studies which elucidate habitat selection in both fragmented and unfragmented regions.

#### *Management implications*

While diversity and abundance indices are useful in making management decisions, it should be clear that not all diversity is necessarily desirable. Increased diversity is not universally 'good' (Faaborg 1980; Noss 1983) and the types of bird species present must be evaluated. For example, while we found lower overall diversity in the unfragmented Ozarks, the majority of Neotropical migrants and forest dwelling species were found at greater abundances in these sites. We encountered more edge associated or generalist species on the fragments, indeed the Brown-headed Cowbird was the most abundant species in the fragments. The habitat

generalist or edge associated species occurred despite our attempts to minimize such effects by censusing similar forest types at points greater than 70 m from the forest edge. To successfully preserve and manage for forest dwelling species, managers must realize that while a large number of Neotropical migratory birds are more abundant in large contiguous forest tracts, these areas may naturally support a lower diversity of species relative to more disturbed or fragmented sites. The birds in disturbed or fragmented areas may also experience reduced reproductive success (Robinson et al. 1995).

Our data make clear that managers should consider both vegetational characteristics and landscape measures when managing for bird populations. For some species contiguous forest tracts may be required for nesting, but for other species, small forest fragments or small specialized habitats may be sufficient to support breeding populations. Simple correlations between the numbers of birds at a census point and the vegetative structure around that point have limited value if not put into a local and regional habitat context. In addition to the habitat patch preferences and natural history traits of an organism (or suite of organisms), landscape features must be considered in conservation and management activities. Reserve design and planning should assess the potential influence of the surrounding landscape on the proposed reserve (or reserve network), as well as the actual biotic composition of the proposed reserve. Moreover, it may be necessary to consider multiple landscape measures to assess a species' landscape sensitivity. Differences in sensitivity to vegetation and landscape characteristics emphasize the difficulty in managing for a broad variety of species, and underscore the fact that management for multiple species involves trade-offs (Liu et al. 1995).

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## Appendix 1.

Species codes, common names, scientific names, mean number of detections per region (Central Missouri and Ozarks), and migratory status for each bird species.

Code	Species common name	Scientific name	Cen. Missouri	Ozarks	Mig. status <sup>a</sup>
ACFL	Acadian Flycatcher	<i>Empidonax virescens</i>	0.107	0.341	N
AMGO	American Goldfinch	<i>Carduelis tristis</i>	0.011	0	R
AMRE	American Redstart	<i>Setophaga ruticilla</i>	0.021	0.002	N
AMRO	American Robin	<i>Turdus migratorius</i>	0.007	0	S
BAOR	Baltimore Oriole	<i>Icterus galbula</i>	0.005	0	N
BAWW	Black-and-white Warbler	<i>Mniotilta varia</i>	0.034	0.089	N
BCCH	Black-capped Chickadee	<i>Poecile atricapillus</i>	0.038	0.003	R
BGGN	Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	0.123	0.282	N
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>	0.569	0.159	S
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	0.306	0.084	R
BRTH	Brown Thrasher	<i>Toxostoma rufum</i>	0.004	0	S
BWWA	Blue-winged Warbler	<i>Vermivora pinus</i>	0.038	0.008	N
CACH	Carolina Chickadee	<i>Poecile carolinensis</i>	0	0.001	R
CARW	Carolina Wren	<i>Thryothorus ludovicianus</i>	0.021	0.038	R
CEWA	Cerulean Warbler	<i>Dendroica cerulea</i>	0.013	0.017	N
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	0.001	0	N
DOWO	Downy Woodpecker	<i>Picoides pubescens</i>	0.064	0.046	R
EAPH	Eastern Phoebe	<i>Sayornis phoebe</i>	0.003	0	N
EATO	Eastern Towhee	<i>Pipilo erythrophthalmus</i>	0.066	0	S
EWPE	Eastern Wood-Pewee	<i>Contopus virens</i>	0.279	0.138	N
GCFL	Great Crested Flycatcher	<i>Myiarchus crinitus</i>	0.207	0.083	N
GRCA	Gray Catbird	<i>Dumetella carolinensis</i>	0.014	0	N
HAWO	Hairy Woodpecker	<i>Picoides villosus</i>	0.022	0.013	R
HOWA	Hooded Warbler	<i>Wilsonia citrina</i>	0	0.001	N
HOWR	House Wren	<i>Troglodytes aedon</i>	0.001	0	N
INBU	Indigo Bunting	<i>Passerina cyanea</i>	0.034	0.025	N
KEWA	Kentucky Warbler	<i>Oporornis formosus</i>	0.096	0.004	N
LOWA	Louisiana Waterthrush	<i>Seiurus motacilla</i>	0.058	0.002	N
MODO	Mourning Dove	<i>Zenaidura macroura</i>	0.005	0	R
NOCA	Northern Cardinal	<i>Cardinalis cardinalis</i>	0.194	0.012	R
NOFL	Northern Flicker	<i>Colaptes auratus</i>	0.003	0	S
NOPA	Northern Parula	<i>Parula americana</i>	0.051	0.081	N
OROR	Orchard Oriole	<i>Icterus spurius</i>	0.001	0	N
OVEN	Ovenbird	<i>Seiurus aurocapillus</i>	0.280	0.214	N
PIWA	Pine Warbler	<i>Dendroica pinus</i>	0	0.057	N
PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>	0.015	0.052	R
RBGR	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	0.081	0.001	N
RBWO	Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	0.151	0.059	R
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	0.293	1.086	N
RHWO	Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	0.004	0	R
SCTA	Scarlet Tanager	<i>Piranga olivacea</i>	0.088	0.225	N
SUTA	Summer Tanager	<i>Piranga rubra</i>	0.091	0.099	N
TUTI	Tufted Titmouse	<i>Baeolophus bicolor</i>	0.315	0.135	R
WBNU	White-breasted Nuthatch	<i>Sitta carolinensis</i>	0.180	0.136	R
WEWA	Worm-eating Warbler	<i>Helmitheros vermivorus</i>	0.127	0.215	N
WOTH	Wood Thrush	<i>Hylocichla mustelina</i>	0.094	0.051	N
YBCU	Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	0.054	0.042	N
YTVI	Yellow-throated Vireo	<i>Vireo flavifrons</i>	0.021	0.084	N
YTWA	Yellow-throated Warbler	<i>Dendroica dominica</i>	0.001	0.085	N

<sup>a</sup>Migratory status: N=Neotropical migrant; S=short distance migrant; R=year-round resident.