

RESPONSE OF BIRD SPECIES DENSITIES TO HABITAT STRUCTURE AND FIRE HISTORY ALONG A MIDWESTERN OPEN-FOREST GRADIENT

Author(s): RALPH GRUNDEL and NOEL B. PAVLOVIC

Source: The Condor, 109(4):734-749.

Published By: Cooper Ornithological Society

DOI: [http://dx.doi.org/10.1650/0010-5422\(2007\)109\[734:ROBSDT\]2.0.CO;2](http://dx.doi.org/10.1650/0010-5422(2007)109[734:ROBSDT]2.0.CO;2)

URL: [http://www.bioone.org/doi/](http://www.bioone.org/doi/full/10.1650/0010-5422%282007%29109%5B734%3AROBSDT%5D2.0.CO%3B2)

[full/10.1650/0010-5422%282007%29109%5B734%3AROBSDT%5D2.0.CO%3B2](http://www.bioone.org/doi/full/10.1650/0010-5422%282007%29109%5B734%3AROBSDT%5D2.0.CO%3B2)

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

RESPONSE OF BIRD SPECIES DENSITIES TO HABITAT STRUCTURE AND FIRE HISTORY ALONG A MIDWESTERN OPEN-FOREST GRADIENT

RALPH GRUNDEL AND NOEL B. PAVLOVIC

U.S. Geological Survey, Great Lakes Science Center, 1100 North Mineral Springs Road, Porter, IN 46304

Abstract. Oak savannas were historically common but are currently rare in the Midwestern United States. We assessed possible associations of bird species with savannas and other threatened habitats in the region by relating fire frequency and vegetation characteristics to seasonal densities of 72 bird species distributed across an open-forest gradient in northwestern Indiana. About one-third of the species did not exhibit statistically significant relationships with any combination of seven vegetation characteristics that included vegetation cover in five vertical strata, dead tree density, and tree height. For 40% of the remaining species, models best predicting species density incorporated tree density. Therefore, management based solely on manipulating tree density may not be an adequate strategy for managing bird populations along this open-forest gradient. Few species exhibited sharp peaks in predicted density under habitat conditions expected in restored savannas, suggesting that few savanna specialists occur among Midwestern bird species. When fire frequency, measured over fifteen years, was added to vegetation characteristics as a predictor of species density, it was incorporated into models for about one-quarter of species, suggesting that fire may modify habitat characteristics in ways that are important for birds but not captured by the structural habitat variables measured. Among those species, similar numbers had peaks in predicted density at low, intermediate, or high fire frequency. For species suggested by previous studies to have a preference for oak savannas along the open-forest gradient, estimated density was maximized at an average fire return interval of about one fire every three years.

Key words: *bird density, fire frequency, nonparametric multiplicative regression, oak savanna, restoration, seasonal effects, tree density.*

Respuestas de las Densidades de Especies de Aves a la Estructura del Hábitat y a la Historia de Fuego a lo Largo de un Gradiente de Bosque Abierto del Medio Oeste

Resumen. Las sabanas de roble fueron históricamente comunes en el Medio Oeste de Estados Unidos pero actualmente son raras en esta región. Evaluamos las posibles asociaciones de especies de aves con sabanas y otros ambientes amenazados en esta región, relacionando la frecuencia de fuego y las características de la vegetación con las densidades estacionales de 72 especies de aves distribuidas a lo largo de un gradiente de bosque abierto en el noroeste de Indiana. Cerca de un tercio de las especies no exhibieron relaciones estadísticamente significativas con ninguna de las combinaciones de siete características de la vegetación, que incluyeron la cobertura de la vegetación en cinco estratos verticales, la densidad de árboles muertos y la altura de los árboles. Para el 40% de las especies remanentes, los modelos que mejor predijeron la densidad de especies incorporaron la densidad de árboles. Por lo tanto, el manejo basado exclusivamente en la manipulación de la densidad de árboles no sería una estrategia adecuada para el manejo de las poblaciones de aves a lo largo de este gradiente de bosque abierto. Pocas especies exhibieron picos marcados en las predicciones de densidad bajo las condiciones de hábitat esperadas en las sabanas restauradas, sugiriendo que son pocas las especies de aves especialistas de sabana que existen en el Medio Oeste. La frecuencia de fuego, medida durante más de quince años, sumada a las características de la vegetación como variable que predice la densidad de especies, fue incorporada en los modelos para alrededor de un cuarto de las especies. Esto sugiere que el fuego puede modificar características del hábitat que son importantes para las aves, pero estas modificaciones no estuvieron reflejadas por las variables de estructura del hábitat medidas en este estudio. Entre las especies especialistas de sabana, un número similar de especies presentó picos de densidad predicha a frecuencias de fuego baja, intermedia y alta. Según estudios anteriores, para las especies que prefieren sabanas de roble a lo largo de un gradiente de bosque abierto, la densidad

estimada fue máxima a un intervalo promedio de retorno de fuego de aproximadamente un fuego cada tres años.

INTRODUCTION

Of the world's major terrestrial biomes, temperate grasslands, shrublands, and savannas are of special conservation concern because a high percentage of their historic area has been converted to human use and a low percentage is protected for conservation (Hoekstra et al. 2005). In the Midwestern United States and Canada, prairies, savannas, and forests historically occurred within a large transition zone of >10 million ha located between deciduous and coniferous forests to the east and north and prairies to the west (Anderson 1998). The rate of conversion of savannas and prairies to human use in this region has been very high (Nuzzo 1986), even compared to global trends.

The loss of Midwestern savannas and prairies, and negative Breeding Bird Survey trends shown by many prairie, savanna, and disturbance-dependent bird species in the region (Sauer et al. 2005), has motivated planning for savanna and prairie conservation and restoration (Leach and Ross 1995, Brawn et al. 2001) and has highlighted the need for improved description of how bird abundances relate to key habitat and management parameters in the transition zone (Thogmartin et al. 2004). Across prairie-savanna-forest gradients, understanding use of vegetation strata by bird species, and the effects of fire frequency on habitat use, can help forecast how species might respond to different approaches to savanna restoration (Artman et al. 2005, Hartung and Brawn 2005). Previous work has addressed such forecasting by defining habitats and then examining differences in avian density among habitats (Brawn 2006, Grundel and Pavlovic 2007). However, it is also important to examine species responses to continuous gradients, because defining habitats precisely, especially ecotonal habitats like savannas, can be problematic (Leach and Ross 1995). Additionally, fire, both in its promotion and suppression, was historically, and is currently, the primary agent for restoration and maintenance of habitats along the prairie-forest continuum. Effective management of birds along this continuum requires improved understanding of where, when, and how often fires should burn (Artman

et al. 2005). Although research has compared the relative benefits to birds of burned and unburned forest sites (Davis et al. 2000, Brawn 2006), or examined the effects of fire on overall community composition (Grundel and Pavlovic 2007), we generally lack information on expected species-specific responses to continuous gradients of fire frequency. Put in broad perspective, the Midwestern prairie-forest transition zone historically represented an east-west gradient of generally decreasing woody vegetation density, increasing grassland cover, and increasing precipitation variability (Anderson 1998), likely associated with gradients of fire frequency that yielded a mosaic of grasslands, savannas, woodlands, scrublands, and forests. Therefore, if we wish to understand how savanna restoration might affect habitat use by birds, it is important to document how individual species respond to these gradients of woody vegetation cover, herbaceous cover, and fire frequency historically present in the transition zone.

We took advantage of a confluence of habitat types in northwestern Indiana to examine the effects of such gradients on bird densities. The climatic influence of Lake Michigan, sandy soils, and the meeting of more eastern- and more western-centered floras in northwestern Indiana produced nearly the entire range of transition zone habitats (Cowles 1899, Bacone et al. 1980). We examined the distributions of individual bird species in relation to the resulting gradients of woody and herbaceous vegetation density and fire frequency in northwestern Indiana.

METHODS

SURVEY LOCATIONS

A primary goal of this study was to understand how densities of individual bird species varied with habitat differences along an open-forest gradient in northwestern Indiana. This gradient represents both pre-European settlement distribution of habitats within the grassland-forest transition zone of the Midwest United States and alterations in the structure of savanna habitat that have arisen due to human disturbances, such as tree removal and soil

disruption (Wilcox et al. 2005) and changes in fire frequency over the past century (Anderson 1998). Along this gradient, we documented bird densities at 102 survey points from April 1998 to October 2002 at Indiana Dunes National Lakeshore (41°38'N, 87°09'W; $n = 75$ points; 6000 ha), Tefft Savanna Nature Preserve and Jasper-Pulaski Fish and Wildlife Area (41°10'N, 86°58'W; $n = 24$ points; 3250 ha; Dancey 1991), and Hoosier Prairie Nature Preserve (41°31'N, 87°27'W; $n = 3$ points; 225 ha). Birds were surveyed during the breeding season, spring and fall migrations, and over winter (Grundel and Pavlovic 2007).

HABITAT ASSESSMENT

We selected bird survey points to span a gradient of tree density. Sites for counting birds were delimited so that the density of smaller (<10 cm dbh) or larger (>10 cm dbh) woody vegetation around each point was relatively uniform. Birds were surveyed and vegetation cover was measured within the delimited area. Vegetation sampling was done during the first summer and fall of this study. Vegetation cover was measured in six 0.05 ha circular plots around each bird survey point and average vegetation cover within 100 m of the survey point was then estimated by inverse distance weighting interpolation of cover values from these six plots using ArcGIS version 9.0 (ESRI, Inc., Redlands, California). Fires occurring at the study sites from 1983 to 2002 were mapped at the time of the fires. These fire data were used to determine the number of equivalent times that a 100 m radius area around a survey point burned within one year of a bird survey (fires yr^{-1}), an indicator of recent fire activity, and within 15 years of a survey (fires 15 yr^{-1}). We refer to these variables as fire frequency 1 and fire frequency 15, respectively. Fire frequency 15 provides a longer-term perspective on fire frequency and represents both the longest interval for which detailed fire histories were available and corresponds to the approximate time before the start of this study when prescribed burning for management began at these sites.

Vegetation cover was measured within five vertical strata in each plot along with density of dead trees and average tree height. The seven habitat variables were: (1) Bare ground (%). At 100 points per plot (Elzinga et al. 1998), we

classified ground cover as either bare ground, vegetation <0.3 m tall, or litter and then converted to percentage of occurrence of these three categories, (2) Low ground vegetation (%). At four points per plot, percent vertical cover 0.3–1 m tall was measured using a 1 m² frame, divided into one hundred sections. This percentage was averaged with the percentage vegetation cover <0.3 m tall to estimate cover of low ground vegetation. Litter cover was highly correlated with low ground vegetation ($r = -0.82$) and was not used as a separate predictor of bird density, (3) High ground vegetation (%). Percent vertical cover of vegetation 1–2 m tall was measured with the 1 m² frame, (4) Within the 25.2 m diameter plot, numbers of living woody shrubs, sprouts, saplings, or small trees 2.5–10 cm dbh (shrub density; shrubs ha^{-1}), (5) living trees >10 cm dbh (tree density; trees ha^{-1}), and (6) dead woody stems >2.5 cm dbh (dead tree density; dead trees ha^{-1}) were determined by total counts, and (7) Tree height (m). Four quadrants were defined around each survey point. The height of the tree nearest to the survey point within each quadrant was measured and the average height of the four trees calculated.

BIRD COUNTS

At each survey point, birds were counted for 5 min. Points were separated by 0.2–61 km. Although points that were closest to each other could have similar fire histories, points with high and low fire frequencies were also often near to each other. Bird counts took place from approximately one hour after sunrise through midmorning if wind speed was <20 kph and, for winter counts, under conditions of minimal snow cover and temperature above -5°C . Distance from bird to observer was estimated after observers were trained in distance estimation. We counted birds during spring migration (15 April–20 May), the breeding season (1 June–15 July), fall migration (1 September–15 October), and winter (15 November–15 March). Each point was surveyed 48 times. From April 1998 to April 2001, each point was visited three times during each season, except two visits during winter 2001. After winter 2001, winter visits were discontinued and the numbers of spring, breeding, and fall visits were three, two, and three in the fourth year and two, one, and two during the fifth year of the study.

We used distance sampling to convert raw counts to an estimate of species density (Buckland et al. 2001, Thomas et al. 2004). Six conventional distance-sampling models (uniform + cosine, uniform + simple polynomial, half normal + cosine, half normal + Hermite polynomial, hazard rate + cosine, and hazard rate + simple polynomial) were fit for each species, and one model was selected based on Akaike's information criterion (AIC) and on the fit of the model at short observation distances (Thomas et al. 2004). Additional details of distance sampling calculations are given elsewhere (Grundel and Pavlovic 2007). Densities were calculated for each season and relationships between bird density and habitat structure and fire frequency were analyzed by season.

STATISTICAL ANALYSES

We used nonparametric multiplicative regression (NPMR) to analyze species-habitat relationships. NPMR readily models nonlinear species abundance-habitat relationships, automatically considers interactions among predictors, and, by combining the effects of predictors multiplicatively, potentially better accounts for the effects of unacceptable habitat conditions on species abundance than do additive modeling techniques (McCune and Mefford 2004, McCune 2006).

To understand computation of the local mean NPMR (lm-NPMR) model used here, consider an environmental space defined by tree density and shrub density. We wish to predict density of a bird species at a target point defined by a given tree density and shrub density in this space. In lm-NPMR, a species' predicted density at the target point equals a weighted mean of the densities observed at survey points placed throughout the environmental space. The contribution of each survey point to estimation of density at the target point is determined by a Gaussian weighting function, centered on the target point, so that survey points closer to the target point in the environmental space are given greater weight in estimating density at the target point. The shape of the Gaussian weighting function is determined by its standard deviation, or tolerance (s). In lm-NPMR, various tolerances for each predictor are tested, and the combination of predictors and tolerances that most accu-

ately estimates density at target points with known density represents the final lm-NPMR model. Fit of the model, or correspondence between observed and estimated density values, is expressed as a cross-validated R^2 .

The statistical tolerance associated with the Gaussian weighting function has a ready ecological interpretation. For instance, if a species' density is most accurately estimated by a narrow tolerance for tree density, this suggests that the species' density is likely to change greatly between habitats with relatively small differences in tree density. Closely related to the predictor's tolerance is the sensitivity of species density to changes in the predictor. Sensitivity (Q) is defined as the average estimated absolute standardized change in density of a species per standardized change in the predictor. A sensitivity of 0.5, for example, means that if we change observed values of a predictor by 2% of the predictor's range, estimated bird density at target points will, on average, change by 1% of the observed range of the bird's density. Sensitivities are calculated within the context of all predictors in a model because response to a predictor is affected by tolerances, and tolerances for a given predictor are determined along with tolerances for all other predictors in a model. Sensitivities are one way to assess a predictor's importance relative to other predictors in that model and even the predictor's importance among models, as long as it is noted that the sensitivity calculated for a given predictor will be affected by the presence of other predictors in a model.

For lm-NPMR calculations, tolerances for each potential predictor were varied, in 1% increments, between 1% and 75% of the predictor's range. Combinations of different predictors and tolerances were tested in a step-wise procedure to find the combination of predictors and tolerances that maximized R^2 . To balance the trade-off between model fit and model complexity, a predictor was added to the model only if it improved model R^2 by at least 0.05. Significance of the final selected model was determined as the percentage of 100 Monte Carlo trials with R^2 greater than or equal to the R^2 of the final selected model, when observed predictor values were randomly reassigned among survey points during each trial. Given the 102 survey points, the estimated density of a bird species at one of those points is

a weighted average of the densities at the other 101 points. The weight given to any one point is between 0 and 1, and the sum of these weights is termed the neighborhood size. Models were rejected if the mean neighborhood size across the 102 points was <5 . This helps to guard against estimates based on too few data points and against potential effects of outlier species densities. We also set the minimum allowable neighborhood size equal to 1 for prediction of species density at any given survey point. If more than 5% of survey points had a neighborhood size <1 , we also rejected this model to avoid producing a model fit based on a limited subset of the available data. As a final guard against models produced from limited data, we analyzed only the 72 species, excluding raptors and swallows, that were present at $>10\%$ of survey points within a season. To mitigate for possible effects of between-season variation in habitat use, we modeled habitat relationships on a seasonal basis for each species. We generally present results from a single season's analysis, selecting either the season with the highest density of the species averaged across all 102 points, the model with the best fit (highest R^2), or models exceeding a minimum R^2 .

Different ways of using regression analysis to assess predictor importance include: (1) obtaining a single best predictive model and designating the predictors in that model as most important, and (2) determining how much variance in the response each possible predictor can independently explain (Mac Nally 2000). One method for achieving goal (2) among non-NPMR regression methods is hierarchical partitioning, which determines the percentage of explained variation attributable to the independent effect of each predictor across all possible regression models associated with a set of predictors (Mac Nally 2000). While NPMR as currently implemented is mainly oriented toward the first goal of obtaining a single explanatory model based on a subset of predictors, inference about the relative importance of different predictors may be stronger under the hierarchical partitioning approach. Potential differences in predictor importance as determined by selecting the best predictive model, which contains a single subset of variables that are designated as the most important predictors, versus basing importance on the proportion of variance explained by each

predictor can arise due to collinearity among predictors (Mac Nally 2000). We therefore evaluated possible multicollinearity among predictors, using the criterion that significant multicollinearity existed if a conditioning index >30 for a given dimension was found coupled with a variance proportion >0.50 for at least two predictors (Tabachnick and Fidell 2007). To compare how well predictors selected as important by NPMR and by hierarchical partitioning did in explaining variation in bird density, we performed a hierarchical partitioning of variance explained by the seven habitat predictors within a multiple regression analysis. We used these hierarchical partitioning results to compare the amount of variation in a species' density accounted for by predictors selected as most important by NPMR versus those selected as most important by hierarchical partitioning (Walsh and Mac Nally 2005).

Results of lm-NPMR analyses are displayed as graphs illustrating the relationship between the selected predictors and estimated density response. Two types of graphs may potentially be presented for each species. A contour graph illustrates how the predicted species density varies as a function of the values of the two most sensitive predictors. The second set of graphs illustrates the predicted relationship between single predictors and the density response. In these univariate graphs only the relationship between the single predictor and density is modeled, ignoring possible interactions with other predictors. To understand how within- and between-year sampling variation might affect our species-habitat predictions, we based these single predictor graphs on bootstrapped resamples (Canty and Ripley 2006). For a given season, we surveyed birds at a point 8–14 times across 3–5 years. For the multiple-predictor contour graphs, we averaged density across those 8–14 surveys and used the average density to calculate the NPMR. For univariate graphs associated with the contour graphs, we resampled densities from among those 8–14 densities at each survey point. Resampling was with replacement, so if a point had been surveyed 14 times we selected from that pool of 14 densities 14 times, each time replacing the selected density back into the pool of potential selections. The 14 resamples selected were then averaged to yield a mean density for that point. These averaged data at the 102 points were then

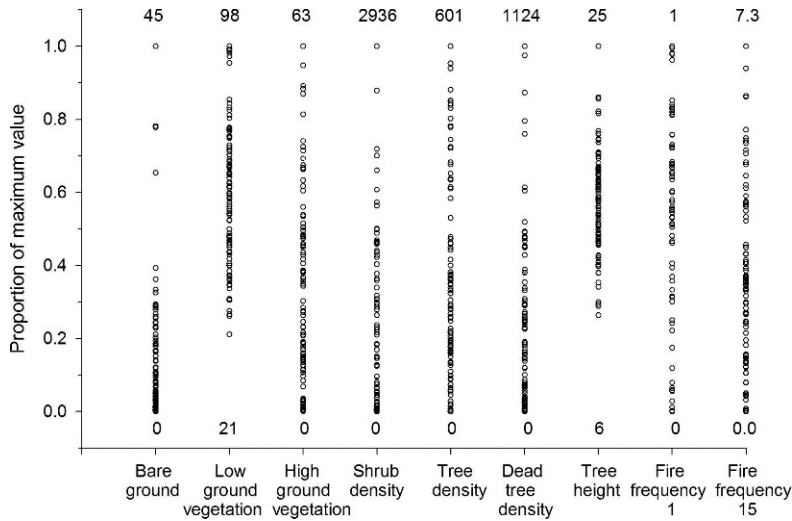


FIGURE 1. Distribution of habitat and fire frequency variables across 102 bird observation points surveyed in northwestern Indiana between 1998 and 2002. One dot is shown per survey point. Values have been relativized by dividing by their respective maxima. Actual maximum and minimum values for each variable are shown above and below the distributions, respectively. Units for predictors are as follows: bare ground, low ground vegetation, and high ground vegetation = %, shrub density = shrubs ha^{-1} , tree density = trees ha^{-1} , dead tree density = dead trees ha^{-1} , tree height = meters, fire frequency 1 = fires yr^{-1} , and fire frequency 15 = fires 15 yr^{-1} .

used to estimate density at target points using NPMR. Resampling and NPMR analysis were repeated 200 times. Bird species densities estimated by NPMR from each of these 200 bootstrap samples were averaged and the standard deviation of these 200 samples was calculated as the standard error of the mean (Quinn and Keough 2002). This bootstrap procedure helps us to understand how variation in density seen among multiple samples taken within a season and across years might affect the reliability of model predictions.

RESULTS

Sampling points were selected along a gradient of tree density (Fig. 1). For 72 species, we used NPMR to regress tree density against species density during the season of highest average density for each species. Three species, Field Sparrow (*Spizella pusilla*; $R^2 = 0.50$), Eastern Wood-Peezee (*Contopus virens*; $R^2 = 0.48$), and Ovenbird (*Seiurus aurocapilla*; $R^2 = 0.46$), had an $R^2 > 0.45$, 16 species had an R^2 of 0.10–0.30, and 52 species had an $R^2 < 0.10$, suggesting that tree density alone did not strongly predict distributional patterns of many species.

We built NPMR models that described the relationship between species density and the seven vegetation variables, but not the measures of fire frequency, during each species' season of highest average density. Of the 72 species, 24 did not yield significant ($P < 0.05$, Monte Carlo test) NPMR models, indicating that the seven habitat variables were not effective in estimating density of one-third of the species. Among the 48 species with significant models, up to three predictors were selected for inclusion, although the greatest number of models (22) had two predictors. Shrub density was the most frequently selected predictor (21 species), followed by tree density (18), tree height (16), low ground vegetation (15), dead tree density (10), high ground vegetation (9), and bare ground (3).

Although some predictor pairs were significantly ($P < 0.05$) correlated (maximum $r = 0.57$), we did not find significant multicollinearity among predictors (Tabachnick and Fidell 2007). For the 48 species with significant NPMR models, we used hierarchical partitioning to evaluate the independent contribution that each predictor made toward explaining the

total amount of variation accounted for by a linear regression model. The predictors selected by the NPMR model independently accounted for a total of $13.2\% \pm 1.3\%$ SE of density variation in the linear model. If we instead used the same number of predictors but selected those predictors based on their importance as determined by the amount of variation they accounted for in the hierarchical partitioning, the amount of variation accounted for by these selected predictors was $16.8\% \pm 1.4\%$ SE. By definition, this amount will always be greater than or equal to the amount accounted for by the NPMR-selected predictors, because in the second case the predictors are selected to be the ones accounting for the most variation in the linear model. However, the difference in variation explained between the predictors selected by NPMR and the predictors selected by hierarchical partitioning was not great, implying that the predictors selected by NPMR as important were similar to the predictors selected by the hierarchical partitioning method due to their ability to predict variation in density in the linear model.

From the 48 significant models, NPMR models for 19 species are illustrated (Fig. 2). These represent the species with the best model fits ($R^2 > 0.45$) or, for models with $R^2 > 0.2$, the species with the highest sensitivities (Q) to the habitat predictors. We also included one species of special interest, the Brown-headed Cowbird (*Molothrus ater*) during the breeding season, when it is the chief brood parasite in this region, even though the breeding season was not this species' season of highest density. Bootstrapped standard errors associated with predicted responses to individual predictors did not generally obscure trends in estimated densities, suggesting that averaging observed densities across years within a season was often appropriate for calculating NPMR analyses. Larger standard errors around estimated densities in parts of predictors' ranges indicate situations where model results were more likely to vary from year to year.

Most of the species illustrated in Figure 2 were at maximum predicted density near the extremes of one or more of the environmental gradients. The American Tree Sparrow (*Spizella aborea*), for example, reached its maximum predicted density near the highest observed values of bare ground. This occurred

despite the fact that local mean models, such as lm-NPMR, tend to bias estimates at predictor extremes toward a species' mean density (McCune 2006). Many species (e.g., Common Yellowthroat [*Geothlypis trichas*]) exhibited a continuous gradient of density change across the environmental spaces shown in the contour graphs of Figure 2. Relatively few species exhibited distinct hump-shaped global responses, with a peak of estimated density near the midpoint of a given habitat gradient. A few examples of such a relationship were evident, however, including the distribution of Blue-gray Gnatcatchers (*Polioptila caerulea*) and Scarlet Tanagers (*Piranga olivacea*) along the tree height gradient, Red-headed Woodpeckers (*Melanerpes erythrocephalus*) along the tree density gradient, and Red-breasted Nuthatches (*Sitta canadensis*; not shown in Fig. 2) along the dead tree gradient. For most species, the highest decile of projected density typically occupied only a small section of the ecological space defined by the habitat gradients. For example, the highest decile of density of the Brown-headed Cowbird occupied a small section of the space defined by density of dead trees and shrubs. Brown-headed Cowbirds were more sensitive (higher Q) to dead tree density than to shrub density and the zone of highest cowbird density was subsequently more restricted along the gradient of dead trees, suggesting a distribution concentrated in areas with occasional dead trees.

Sensitivities (Q) shown in Figure 2 vary from 0.08 for the sensitivity of American Tree Sparrows to bare ground to 2.4 for the sensitivity of Eastern Wood-Peepees to tree density. Some species with relatively high sensitivities to habitat characteristics included the Veery (*Catharus fuscescens*; $Q = 1.42$) to low ground vegetation, Red-winged Blackbird (*Agelaius phoeniceus*; $Q = 2.22$), Northern Bobwhite (*Colinus virginianus*; $Q = 1.55$), and American Robin (*Turdus migratorius*; $Q = 1.32$) to high ground vegetation, Field Sparrow ($Q = 2.15$) to tree density, and Brown-headed Cowbird ($Q = 1.95$) to dead tree density. Northern Bobwhites ($Q = 0.20$) exhibited the highest sensitivity to bare ground, Red-headed Woodpeckers ($Q = 0.90$) to shrub density, and Blue-gray Gnatcatchers ($Q = 0.79$) to tree height.

Savannas are typically characterized by intermediate tree densities, low shrub cover, and

robust groundlayer vegetation (Anderson 1998). A true savanna specialist therefore might exhibit its highest concentration at these levels of vegetation cover and relatively high sensitivity to these habitat characteristics. No species met this description precisely, but the Red-headed Woodpecker exhibited a well-defined, though somewhat broad, peak of density at intermediate tree densities and a sharp decline in estimated abundance with increasing shrub density. Density responses of other species, such as the Eastern Wood-Pee-wee, exhibited compatibility with predicted savanna or woodland conditions, but peak estimated densities were not sharply concentrated at these conditions.

One of the strengths of NPMR is that it explicitly shows the range over which sufficient data are available to make response predictions. Failure to generate estimates is seen in unshaded regions of the contour graphs and arises for at least two reasons. First, sample distributions along predictor ranges were not uniform (Fig. 1). For example, prediction of Northern Bobwhite density along the gradient of bare ground (Fig. 2) was affected by lack of intermediate (15%–30%) percentages of bare ground across sites (Fig. 1). Second, species differ in their tolerances (s) to predictors. Greater tolerance means that densities from a larger neighborhood of points in an environmental space are effectively used when calculating the local mean density at a target point. This essentially brings more data to bear in the calculation of estimated density at any target point, making it more likely that enough data will be available to meet minimum standards (minimum neighborhood size) for successful calculation of a density estimate at a given target point. For example, the American Tree Sparrow was best modeled with greater tolerance to both high ground vegetation and bare ground than was the Northern Bobwhite (Fig. 2). Therefore, there were fewer points in the high ground vegetation–bare ground environmental space at which density for the American Tree Sparrow could not be estimated because of insufficient data than was true for the Northern Bobwhite.

With the exception of the Brown-headed Cowbird, graphs in Figure 2 are depicted for the season of highest density. However, many species were present during several seasons, so

we examined whether model results were consistent across seasons. Among all species, the relative frequency with which individual predictors were included in NPMR models did not differ significantly across seasons ($\chi^2_{18} = 21$, $P = 0.3$, for seasonal models with $R^2 > 0.15$). For example, the percentage of models that incorporated tree density varied between 25% and 27% across the four seasons. The most extreme seasonal difference was that six of seven models that included bare ground were from fall or winter. To assess similarity of models across seasons, we examined how consistently the most sensitive predictor from the season of highest density ($n = 32$ species from multivariate models with $R^2 > 0.2$) predicted density across seasons. For 16 of 32 species with univariate $R^2 > 0.05$ in more than one season for the most sensitive predictor, univariate density-habitat curves for the most sensitive predictor were generally similar across seasons (Fig. 3). For all species having multivariate models with $R^2 > 0.15$ in more than one season, we also examined seasonal differences in responses to all habitat predictors with univariate $R^2 > 0.05$ in a given season, regardless of whether that predictor was included in the multivariate model. Of 74 sets of species-by-predictor univariate curves across seasons, 47 (64%) had curves of similar shape within a set, with densities reaching either their highest or lowest values at about the same habitat value across seasons. For the remaining 36% of sets, the highest or the lowest densities were not predicted by similar values of the predictor across seasons or the shape of the response curves was fundamentally different across seasons. Dead tree density was the most inconsistent predictor across seasons, with univariate curves predicting bird density from dead tree density differing substantially across seasons for 10 of 15 species, compared to six of 18 for tree density, four of 14 species for low ground vegetation, and two of 11 for shrub density. For example, the peak estimated density of Red-headed Woodpeckers shifted to areas with increasing densities of dead trees from the breeding season to winter.

We repeated NPMR analyses to include both habitat and fire frequency variables as predictors. For species with significant models, fire frequency 15 was the most commonly included predictor (16 species) and fire frequency 1 was

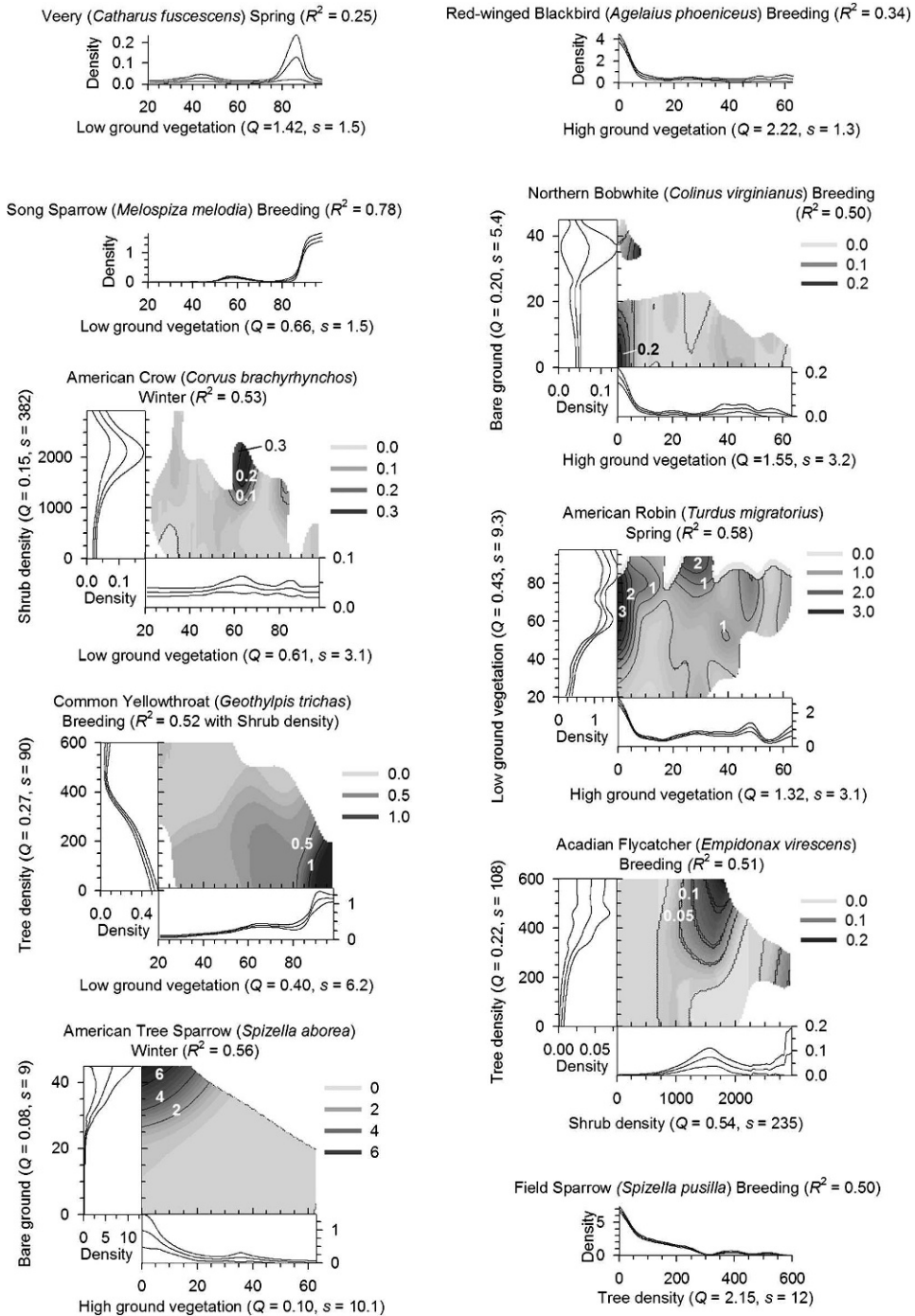
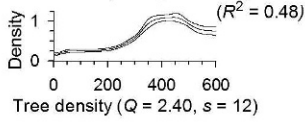
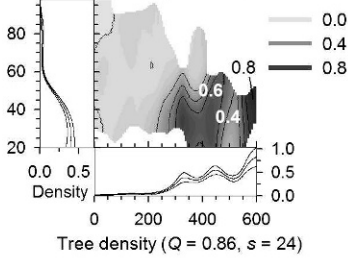
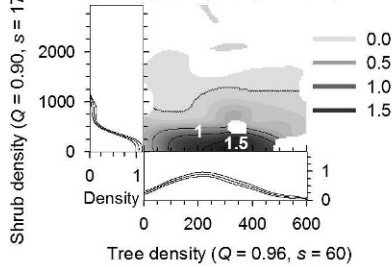
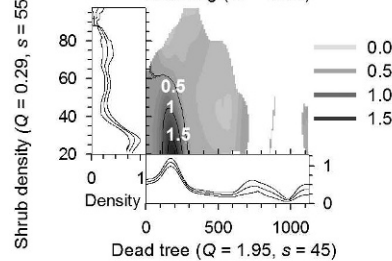
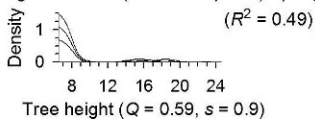
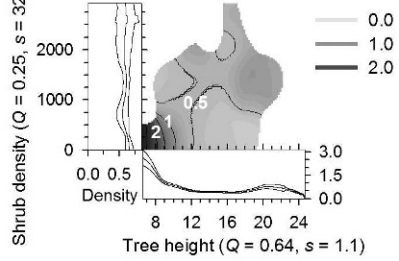
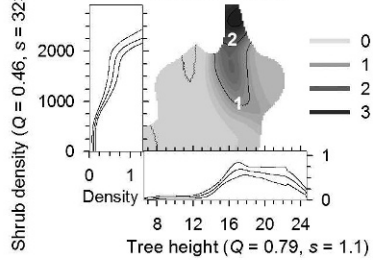
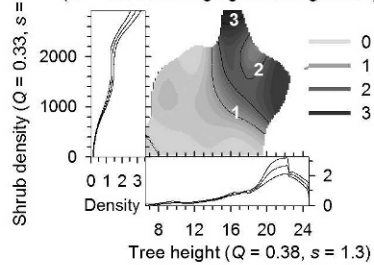
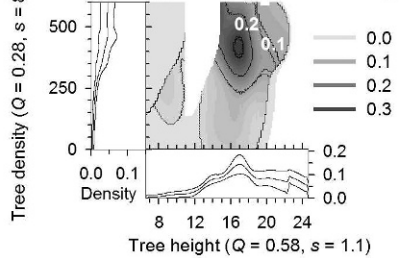


FIGURE 2. Estimated bird density (birds ha^{-1}) as a function of seven habitat predictors, determined by nonparametric multiplicative regression (NPMR) for birds surveyed at 102 observation points in northwestern Indiana between 1998 and 2002. For each species with >1 significant predictor, a single multivariate contour graph and two univariate graphs are shown. The contour graph illustrates predicted density as a function of the predictor that the species density is most sensitive to (x axis) and second most sensitive to (y axis). Darker shading corresponds to higher predicted density. White areas represent locations in the environmental space

Eastern Wood-Peezee (*Contopus virens*) BreedingLow ground vegetation ($Q = 0.21, s = 10$)Ovenbird (*Seiurus aurocapilla*)Spring ($R^2 = 0.61$)Red-headed Woodpecker (*Melanerpes erythrocephalus*) Fall ($R^2 = 0.34$)Brown-headed Cowbird (*Molothrus ater*) Breeding ($R^2 = 0.36$)Blue-winged Warbler (*Vermivora pinus*) SpringAmerican Goldfinch (*Carduelis tristis*)Spring ($R^2 = 0.56$)Blue-gray Gnatcatcher (*Poliophtila caerulea*)Spring ($R^2 = 0.51$)Red-eyed Vireo (*Vireo olivaceus*) Breeding ($R^2 = 0.76$ with High ground vegetation)Scarlet Tanager (*Piranga olivacea*)Breeding ($R^2 = 0.46$ with Shrub density)

where no prediction was made. If a third significant predictor was included in the NPMR model this is indicated next to model R^2 . Univariate graphs along the x and y axis illustrate predicted density as a function of each predictor, ignoring possible interactions with the other predictor. The lines in these univariate graphs represent bootstrapped mean \pm SE from 200 bootstrap resamples. Shown next to each predictor's name is the sensitivity (Q) and tolerance (s) associated with the predictor, calculated from the multivariate model. Tolerances are in the same units as the predictor. Graphs are arranged by the vegetation stratum represented by the x axis.

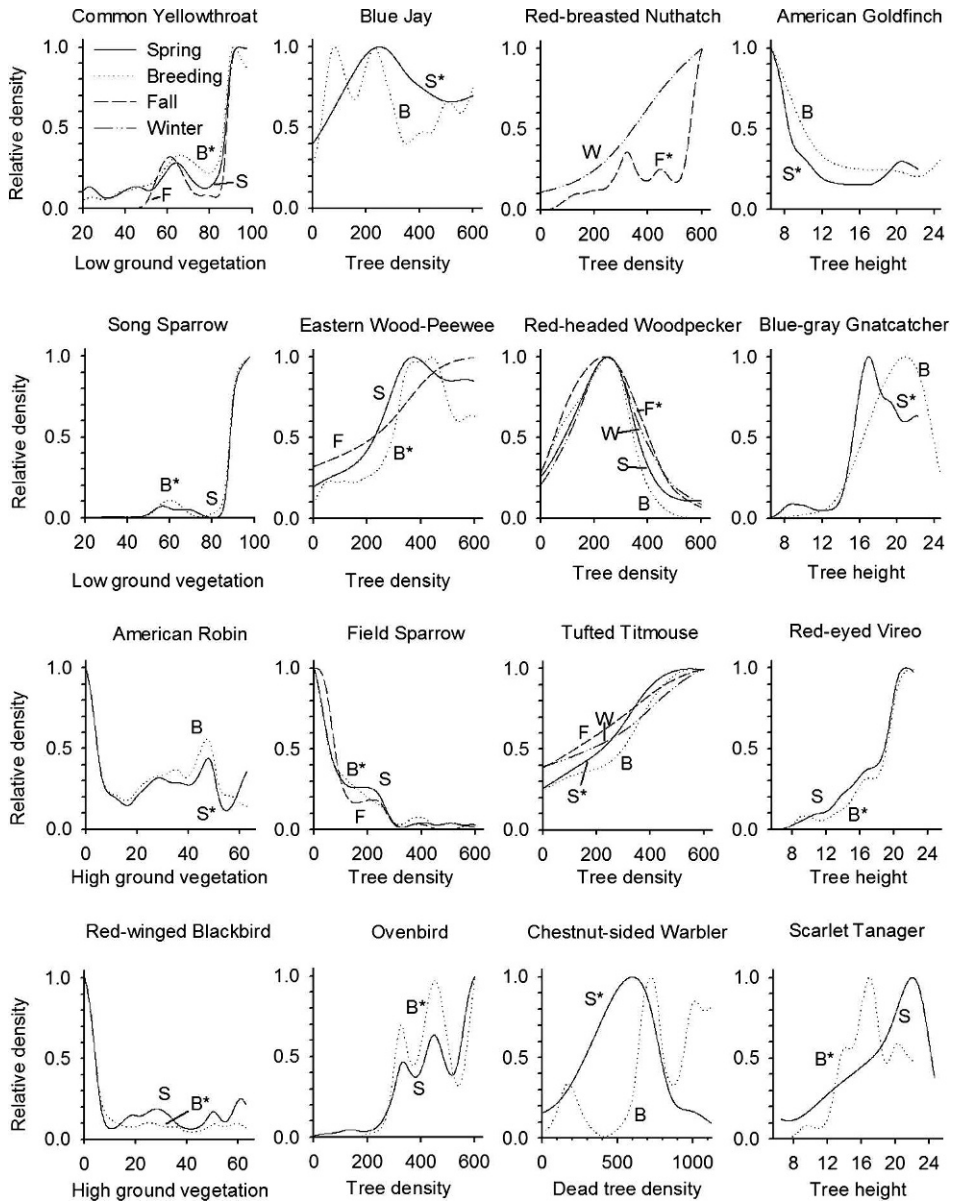


FIGURE 3. Predicted densities in different seasons as a function of the most sensitive predictor shown in Figure 2, as determined by nonparametric multiplicative regression (NPMR). Based on birds surveyed at 102 observation points in northwestern Indiana between 1998 and 2002. Each line represents predicted densities from a different season: (S)pring, (B)reeding, (F)all, (W)inter. The season of highest average density is indicated by an asterisk. Predicted bird densities were relativized in each season by dividing by the seasonal maximum predicted density. $R^2 > 0.05$ for all univariate seasonal regressions shown. Latin names for species not referenced in the text: Chestnut-sided Warbler (*Dendroica pensylvanica*), Blue Jay (*Cyanocitta cristata*).

included in models for six more species. This suggests that fire frequency may be an important determinant of habitat use in ways not totally accounted for by the measured habitat variables. We examined this further by regres-

sing fire frequency 15 on seasonal density in univariate NPMR models and selecting the season with the best fit for each species (Fig. 4). Fire frequency 15 accounted for $>20\%$ of the variation in density of 18 species. A continuum

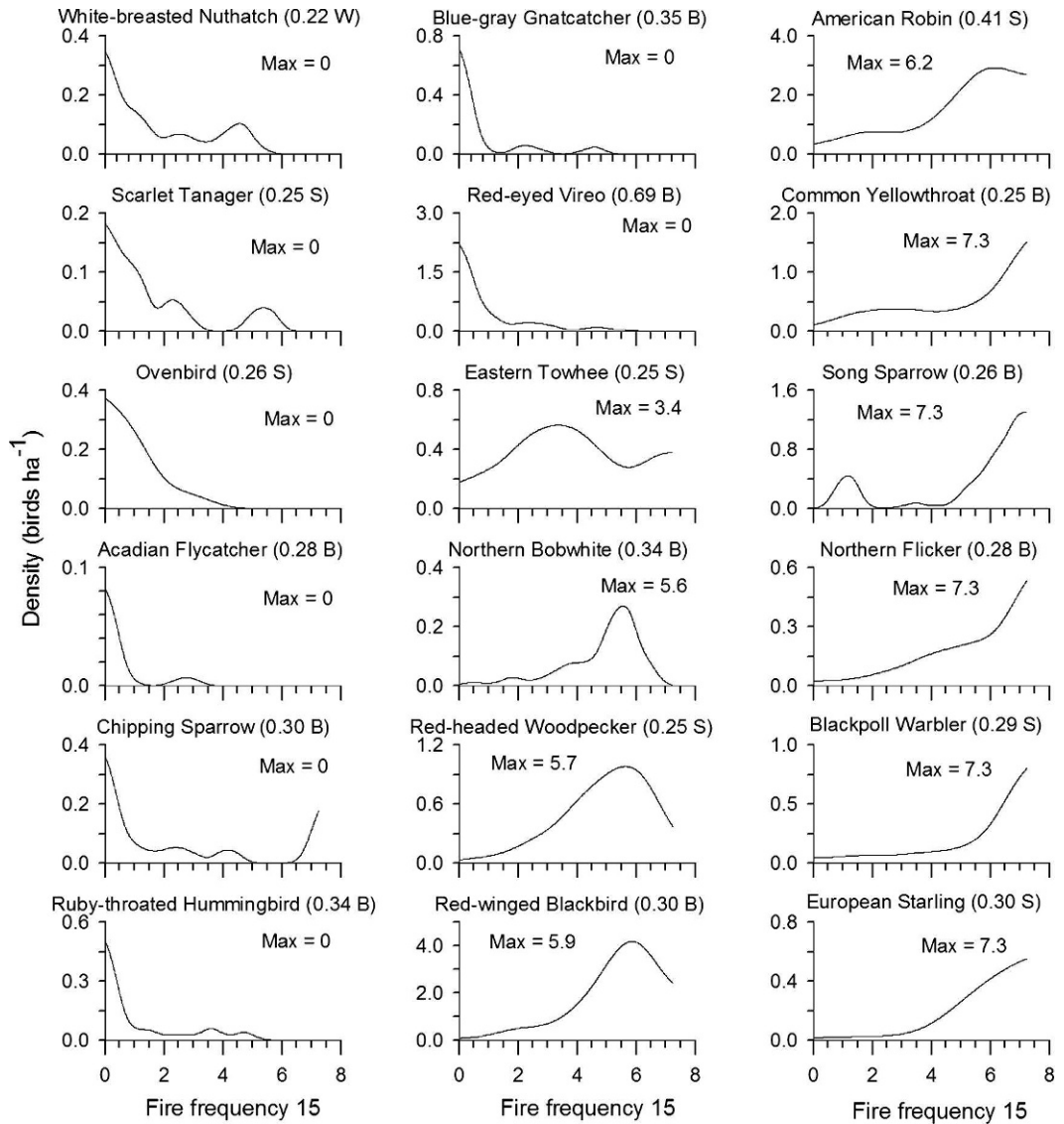


FIGURE 4. Univariate nonparametric multiplicative regression (NPMR) model results for regression of fire frequency 15 (fires 15 yr⁻¹) on bird density. Based on birds surveyed at 102 observation points in northwestern Indiana between 1998 and 2002. Models with $R^2 > 0.20$ are shown for season with highest R^2 . R^2 values are shown along with season: (S) spring, (B) breeding, (W) winter. Max indicates the fire frequency 15 at which estimated bird density reached a maximum. Highest possible value for Max is 7.3 fires per 15 years, representing the observed maximum fire frequency in this study. Latin names for species not referenced in the text or in Figure 3: White-breasted Nuthatch (*Sitta carolinensis*), Chipping Sparrow (*Spizella passerina*), Blackpoll Warbler (*Dendroica striata*), European Starling (*Sturnus vulgaris*).

of response to fire was apparent, ranging from species predicted to rarely occur in burned areas (e.g., Acadian Flycatcher [*Empidonax virens*]), to species with density peaks at intermediate fire frequencies (Eastern Towhee [*Pipilo erythrophthalmus*], Northern Bobwhite,

and Red-headed Woodpecker), to species with little representation in unburned areas and fairly linear positive responses to moderate-to-high fire frequencies (e.g., Northern Flicker [*Colaptes auratus*]). In the models incorporating habitat and fire predictors, three species (Ruby-

throated Hummingbird [*Archilochus colubris*], Red-eyed Vireo [*Vireo olivaceus*], and Red-headed Woodpecker) exhibited especially strong sensitivity ($Q > 2$) to fire frequency 15, indicating that divergence from the fire frequency associated with maximum densities might cause great changes in abundance of these species. This was also observed anecdotally at one forested sampling point that had not burned in the 15 years prior to this study and at which we recorded no Red-headed Woodpeckers in 48 visits. After the conclusion of our study this area was burned, probably for the first time in >50 years. On our first subsequent visit to the area, several weeks after the fire, three Red-headed Woodpeckers were observed.

DISCUSSION

The historical grasslands, savannas, woodlands, scrublands, and forests of the Midwestern United States have largely been converted to agricultural, industrial, and residential use (Auclair 1976, Nuzzo 1986). In remaining conservation areas, managers involved in restoration consider landscape alternatives that are often chiefly defined by tree density (Anderson 1998). Variation in vegetation cover, measured in strata from the ground to the canopy, did not significantly predict density responses of about one-third of species studied. Tree density was an effective predictor of the density response in about 40% of the remaining species but, even then, usually only in conjunction with other vegetation characteristics. Therefore, we can consider tree density to be a useful, incomplete, but not ubiquitous predictor of avian density in the study area. For those interested in restoration and management of oak savannas, this is important, not only because restoration goals are often set by tree densities, but because the primary tools used to manipulate tree density in savanna restoration are prescribed burning and cutting. Prescribed burning of sufficient frequency to restore savannas from more forested areas often suppresses subcanopy woody vegetation (Peterson and Reich 2001), and shrub density, a measure of subcanopy woody vegetation, was a habitat characteristic that was often significant in predicting bird density.

While savannas are usually defined by low to moderate canopy cover and presence of a grassy understory (Scholes and Archer 1997), avian

diversity in Midwestern oak savannas may be enhanced by an intervening shrub layer. Only a handful of studies have compared birds in Midwestern oak savannas to birds in more forested or more open habitats (Davis et al. 2000, Hartung and Brawn 2005, Brawn 2006, Grundel and Pavlovic 2007), but each has concluded that some bird species potentially present in restored savannas will be negatively affected by lack of shrubs and saplings, as might occur with restoration based on very frequent burning or in some programs of physical removal of woody vegetation. The results presented here suggest that of the species responding to understory woody vegetation, many species reach highest densities at shrub and sapling densities that are higher (2000–3000 stems ha^{-1}) than usually associated with savannas or are species that appear to be averse to shrub cover (e.g., Red-headed Woodpecker). Therefore, the balance in favor of enhancing shrub density in savanna restorations may depend on the relative value placed on species with affinities to high or low shrub density and on the suitability of high subcanopy woody vegetation in savanna restoration that often strives to minimize this vegetation layer.

In addition to pointing out the interacting effects of vegetation layers in the prediction of bird density, the models suggested two other characteristics of density response with important implications for management. First, species density was often highest near the extremes of the habitat variables examined or exhibited plateaus across much of the predictor range. The relative lack of species with strong peaks in abundance in the midrange of predictors is another indication that savannas and woodlands, which are defined as being at the low- to midrange of tree density (Scholes and Archer 1997), have few avian specialists (Brawn 2006, Grundel and Pavlovic 2007). Thus, while midrange values of the predictors may represent acceptable conditions for many species, setting restoration goals to match these intermediate states will bring in few restricted species. The second aspect of density response important to management is the emphasis placed by NPMR on the evaluation of species' sensitivities and tolerances to habitat variables. Sensitivity to a habitat characteristic can inform managers of the ability to retain species over a range of values of that characteristic. For example, the

Field Sparrow and Eastern Wood-Pee-wee were especially sensitive to tree density, so managers undertaking habitat restoration would have to pay special attention to target tree densities if either of these were priority species in the evaluation of restoration success. Deviating from the tree density associated with peak estimated density of these species will produce a greater decline in density than for species with a lower sensitivity to tree density. This illustrates that the value of habitat models can be increased if we not only understand what characteristics a species responds to but also the breadth of that response across long habitat gradients. Nonlinear modeling techniques might be especially important in improving this understanding, because they readily show where the density response peaks in reference to predictors (McCune 2006). Models also increase in value if they explicitly show the range of habitat values over which the model was effectively calculated, as NPMR does.

When multiple species are considered in an ecosystem, habitat use across seasons is often a mixture of consistency and variability (Bowen et al. 2007), as was true along the open-forest gradients in northwestern Indiana. For the most sensitive predictors, a species' density response across a predictor's range was usually similar across seasons. However, among seasons there were some shifts in the best predictors of bird distribution and in how species responded to habitat characteristics. For example, bare ground, which was often associated with sparse but seed-rich vegetation in the sandy soils of our study sites, was most frequently selected as a predictor of bird density in fall and winter when this vegetation may be an especially important seed source. In more than one-third of cases, curves describing estimated density as a function of habitat characteristics were substantially different across seasons for a species. Habitat management often deals with this variability by managing for the breeding season. Alternatives might include managing a species' habitat for the season of greatest abundance or the season with the greatest effect on fitness. Of course, these alternatives for different species must be reconciled in a single landscape that will serve all species.

Because prescribed burning is the primary method for manipulation of tree density and

ground cover in this region, studies of avian ecology in Midwestern oak savannas often emphasize differences in bird responses to burned and unburned habitats (Callahan 1996, Davis et al. 2000, Brawn 2006). Responses of species to changes in fire frequency can be marked, including the return of species previously missing from an area with the reintroduction of fire (Davis et al. 2000), as we too observed. We often do not understand how density of individual species might change along a gradient of fire frequency, an important need in improving our ability to assess trade-offs inherent in different fire regimes (Artman et al. 2005). Above and beyond the current vegetation structure, fire frequency over a 15-year period was an important predictor of density for about one-quarter of the species we examined, suggesting that the measured vegetation parameters captured only part of the important effects relating fire to bird abundance. As was true for the habitat characteristics, density of many of these species was highest at the extremes of fire frequency—no fires over 15 years to approximately one fire every two years. However, a similar number of species exhibited a density peak at intermediate fire frequencies. Thus, for the fraction of species whose densities were most likely related to fire frequency, the fire frequency associated with peak density may be an especially important consideration during restoration and maintenance of habitats along the open-forest gradient. The list of species with the strongest density relationship to fire included several that are thought to have an affinity for savannas and woodlands, including American Robins, Northern Bobwhites, Eastern Towhees, and Red-headed Woodpeckers (Davis et al. 2000, Brawn 2006, Grundel and Pavlovic 2007). The mean fire return interval associated with maximum density for these species was approximately one fire every three years. Given the central role of fire in maintaining and restoring Midwestern oak savannas, this interval may represent a standard for use in future studies on the possible benefits of savanna restoration for avian species.

ACKNOWLEDGMENTS

We thank Gary Dulin, David Beamer, Ryan Deering, LuAnn Forste, Matt Buffington, Ross Phillips, John Taylor, Marty Prydzia, Anthony Zammit, Krystal

Frohenapple, and Gary Glowacki for assistance with vegetation analysis and data entry. Bruce McCune provided valuable comments that improved presentation of the NPMR results. Jean Adams assisted in programming the bootstrap resampling procedure. Research was conducted with permission and assistance of the National Park Service (NPS) and the Indiana Department of Natural Resources, Division of Nature Preserves. Funding was provided by a U.S. Geological Survey–NPS technician support grant and by the USGS Grasslands Research Funding Initiative. This article is Contribution 1435 of the USGS Great Lakes Science Center.

LITERATURE CITED

- ANDERSON, R. C. 1998. Overview of Midwestern oak savannas. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* 86:1–18.
- ARTMAN, V. L., T. F. HUTCHINSON, AND J. D. BRAUN. 2005. Fire ecology and bird populations in eastern deciduous forests. *Studies in Avian Biology* 30:127–138.
- AUCLAIR, A. N. 1976. Ecological factors in the development of intensive-management systems in the Midwestern United States. *Ecology* 57: 431–444.
- BACONE, J. A., R. K. CAMPBELL, AND G. S. WILHELM. 1980. Presettlement vegetation of the Indiana Dunes National Lakeshore. *Proceedings of the Second Conference on Scientific Research in the National Parks* 4:156–191.
- BOWEN, L. T., C. E. MOORMAN, AND J. C. KILGO. 2007. Seasonal bird use of canopy gaps in a bottomland forest. *Wilson Journal of Ornithology* 119:77–88.
- BRAUN, J. D. 2006. Effects of restoring oak savannas on bird communities and populations. *Conservation Biology* 20:460–469.
- BRAUN, J. D., S. K. ROBINSON, AND F. R. THOMPSON III. 2001. The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics* 32:251–276.
- BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, AND L. THOMAS. 2001. *Introduction to distance sampling*. Oxford University Press, Oxford, UK.
- CALLAHAN, T. R. 1996. Avian community structure within restored oak-savanna and unburned oak-woodland in Missouri. M.Sc. thesis. University of Missouri, Columbia, MO.
- CANTY, A., AND B. D. RIPLEY [ONLINE]. 2006. boot: Bootstrap R (S-Plus) Functions (Canty). R package version 1.2-27. S original by Angelo Canty. R port by Brian Ripley. R Foundation for Statistical Computing, Vienna, Austria. <<http://cran.r-project.org/>> (30 November 2006).
- COWLES, H. C. 1899. Ecological relations of the vegetation on sand dunes of Lake Michigan. *Botanical Gazette* 27:95–117, 167–202, 281–308, 361–391.
- DANCEY, H. E. 1991. A bird population survey of the Tefft Savanna Nature Preserve, Jasper County, Indiana, 1988. *Indiana Audubon Quarterly* 69:18–33.
- DAVIS, M. A., D. W. PETERSON, P. B. REICH, M. CROZIER, T. QUERY, E. MITCHELL, J. HUNTINGTON, AND P. BAZAKAS. 2000. Restoring savanna using fire: impact on the breeding bird community. *Restoration Ecology* 8:30–40.
- ELZINGA, C. L., D. W. SALZER, AND J. W. WILLOUGHBY. 1998. *Measuring and monitoring plant populations*. Bureau of Land Management, Denver, CO.
- GRUNDEL, R., AND N. B. PAVLOVIC. 2007. Distinctiveness, use, and value of Midwestern oak savannas and woodlands as avian habitats. *Auk* 124:969–985.
- HARTUNG, S. C., AND J. D. BRAUN. 2005. Effects of savanna restoration on the foraging ecology of insectivorous songbirds. *Condor* 107:879–888.
- HOEKSTRA, J. M., T. M. BOUCHER, T. H. RICKETTS, AND C. ROBERTS. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters* 8:23–29.
- LEACH, M. K. AND L. ROSS [EDS.]. 1995. *Midwest oak ecosystems recovery plan: a call to action*. U.S. Environmental Protection Agency Great Lakes National Program Office, Chicago.
- MAC NALLY, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between—and reconciliation of—‘predictive’ and ‘explanatory’ models. *Biodiversity and Conservation* 9:655–671.
- MCCUNE, B. 2006. Non-parametric habitat models with automatic interactions. *Journal of Vegetation Science* 17:819–830.
- MCCUNE, B., AND M. J. MEFFORD. 2004. *HyperNiche. Nonparametric multiplicative habitat modeling*. MjM Software, Gleneden Beach, OR.
- NUZZO, V. A. 1986. Extent and status of Midwest oak savanna: presettlement and 1985. *Natural Areas Journal* 6:6–36.
- PETERSON, D. W., AND P. B. REICH. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecological Applications* 11:914–927.
- QUINN, G. P., AND M. J. KEOUGH. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, UK.
- SAUER, J. R., J. E. HINES, AND J. FALLON [ONLINE]. 2005. The North American Breeding Bird Survey, results and analysis 1966–2005. <<http://www.mbr-pwrc.usgs.gov/bbs/bbs.html>> (24 August 2006).
- SCHOLES, R. J., AND S. R. ARCHER. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28:517–544.
- TABACHNICK, B. G., AND L. S. FIDELL. 2007. *Using multivariate statistics*. Allyn and Bacon, Boston.
- THOGMARTIN, W. E., J. R. SAUER, AND M. G. KNUTSON. 2004. A hierarchical spatial model of avian abundance with application to Cerulean Warblers. *Ecological Applications* 14:1766–1779.
- THOMAS, L., J. L. LAAKE, S. STRINDBERG, F. F. C. MARQUES, S. T. BUCKLAND, D. L. BORCHERS, D. R. ANDERSON, K. P. BURNHAM, S. L.

- HEDLEY, J. H. POLLARD, AND J. R. B. BISHOP [ONLINE]. 2004. Distance 4.1. Release 2. <<http://www.ruwpa.st-and.ac.uk/distance/>> (17 July 2005).
- WALSH, C., AND R. MAC NALLY [ONLINE]. 2005. hier.part: hierarchical partitioning. R package version 1.0-1. R Foundation for Statistical Computing, Vienna, Austria. <<http://cran.r-project.org/>> (14 June 2006).
- WILCOX, C. A., Y.-M. CHUN, AND Y. D. CHOI. 2005. Redevelopment of black oak (*Quercus velutina* Lam.) savanna in an abandoned sand mine in Indiana Dunes National Lakeshore, USA. *American Midland Naturalist* 154:11–27.