

Scaling local species-habitat relations to the larger landscape with a hierarchical spatial count model

Wayne E. Thogmartin · Melinda G. Knutson

Received: 20 September 2005 / Accepted: 9 April 2006 / Published online: 14 June 2006
© Springer Science+Business Media B.V. 2006

Abstract Much of what is known about avian species-habitat relations has been derived from studies of birds at local scales. It is entirely unclear whether the relations observed at these scales translate to the larger landscape in a predictable linear fashion. We derived habitat models and mapped predicted abundances for three forest bird species of eastern North America using bird counts, environmental variables, and hierarchical models applied at three spatial scales. Our purpose was to understand habitat associations at multiple spatial scales and create predictive abundance maps for purposes of conservation planning at a landscape scale given the constraint that the variables used in this exercise were derived from local-level studies. Our models indicated a substantial influence of landscape context for all species, many of which were counter to reported associations at finer spatial extents. We found land cover composition provided the greatest contribution to the relative explained variance in counts for all three species; spatial structure was second in importance. No single spatial scale dominated any model, indicating that these species are responding to factors at multiple

spatial scales. For purposes of conservation planning, areas of predicted high abundance should be investigated to evaluate the conservation potential of the landscape in their general vicinity. In addition, the models and spatial patterns of abundance among species suggest locations where conservation actions may benefit more than one species.

Keywords Abundance map · Black-billed cuckoo · Hierarchical model · Information-theoretic model selection · Multi-level model · Red-headed woodpecker · Spatial count model · Wood thrush

Introduction

Land managers want to focus their efforts to conserve bird populations by geographically targeting conservation areas (Sample and Mossman 1997) for those species in greatest need (Rich et al. 2004; U.S. Fish and Wildlife Service 2002). Models of bird habitat associations are used to better understand observed patterns of occupancy and abundance and identify environmental factors subject to management (Seoane et al. 2004; Thogmartin et al. 2004). Most habitat models are represented as linear combinations of environmental factors representing local-scale features of the habitat (Burnham and Anderson 2002; Scott

W. E. Thogmartin (✉) · M. G. Knutson
U.S. Geological Survey, Upper Midwest
Environmental Sciences Center, 2630 Fanta Reed
Road, La Crosse, WI 54603-1223, USA
e-mail: wthogmartin@usgs.gov

et al. 2002). Regional scale maps are often habitat suitability maps relying on assumptions about how different species use the larger-scale landscape (e.g., Roseberry and Sudkamp 1998); this approach to mapping species occurrence and abundance is often referred to as a ‘coarse filter’ approach (Scott et al. 1993; Pearlstine et al. 2002; Diamond et al. 2003; Noon et al. 2003). However, these assumptions about how species use the landscape are primarily derived from studies conducted at a local level, but are assumed to represent the habitat relations of a species at the larger landscape scale.

Variability in bird habitat associations across spatial scales complicates our understanding of how birds use habitats. Species habitat associations may change in strength and direction across spatial scales (Wiens 1981; Wiens et al. 1987). It is necessary to address these multiple spatial scales in habitat analyses (Brennan et al. 2002; Holland et al. 2004) to test the importance of our local level understanding about bird-habitat associations at these coarser landscape scales.

Such coarse-filter models are rarely tested against data collected systematically across a region and rarely are they represented as maps of predictions across an entire region. Because of these deficiencies, these coarse-filter models are limited in their usefulness. Data-based models are preferable over these coarse-filter approaches because they are developed in the face of data and allow for mapped predictions useful for regional conservation planning (Venier et al. 1999; Gustafson et al. 2002; McKenney et al. 2002; Thogmartin et al. 2004, 2006)

Maps of predicted bird abundances are visual and quantitative tools readily useable by conservation planners (Scott et al. 2002; Rempel and Kushneriuk 2003; Thogmartin et al. 2004). We employ a hierarchical mixed-effects modeling approach that accommodates nuisances associated with the response data; hierarchical models may address the temporal and spatial correlation common in many ecological data sets (Gelman et al. 1995; Link et al. 2002; Thogmartin et al. 2004). In this paper we derived habitat models and mapped predicted abundances for three bird species using bird counts, environmental variables, and hierarchical models applied at multiple

spatial scales. We focused on three forest bird species of eastern North America, the Black-billed Cuckoo (BBCU; *Coccyzus erythrophthalmus*), Red-headed Woodpecker (RHWO; *Melanerpes erythrocephalus*), and Wood Thrush (WOTH; *Hylocichla mustelina*). Each of these bird species are identified by the U.S. Fish and Wildlife Service as regional and national resource conservation priorities (U.S. Fish and Wildlife Service 2002; Rich et al. 2004).

We specifically address the following questions: (1) Can local species-habitat relations be extrapolated to landscape-scale habitat associations? (2) Can environmental factors explain spatial structure in forest bird abundance? (3) What are the most important species habitat associations explaining forest bird abundance? (4) What patterns of abundance do we expect from a hierarchical spatial count model for the three bird species?

Methods

Study area

In North America, bird conservation planning occurs within physiographically defined bird conservation regions that are comprised of similar bird communities, habitats, and management issues (<http://www.nabci-us.org/bcrs.html>). We modeled avian abundance for populations occurring in Bird Conservation Region 23, the Prairie Hardwood Transition of the United States, a region historically dominated by prairies in the south and west and beech-maple forest in the north and east, separated by an oak savanna (McNab and Avers 1994; U.S. NABCI Committee 2000). The Prairie Hardwood Transition occupies 230,111 km², stretching from central Minnesota through central and southern Wisconsin and Michigan, including small sections of northeastern Iowa, and northern Illinois and Indiana; Lake Michigan bisects the region. The predominant land uses/land covers in this region are row crop agriculture (36%), agricultural grassland (27%), and deciduous forest (21%). Much of the region is a rolling plain of loess-mantled ridges over sandstone and carbonate

bedrock and pre-Illinoian ground moraine, contributing to a diversity of topographic relief and vegetation (McNab and Avers 1994). The Prairie Hardwood Transition, as its name implies, gradually changes from beech-maple forest in the north to agriculture (historically tallgrass prairie) in the south. There is also a gradient in climate (primarily increasing precipitation) from northwest to southeast, with climatic differences most pronounced east of Lake Michigan.

The data

We used 1840 bird counts collected by the North American Breeding Bird Survey (BBS) as the response in our models. Each BBS route contains 50 evenly spaced survey locations (stops) at which an observer counts all birds seen or heard in a 3-min period. Stops on survey routes are separated by ~800 m, and routes are ~40 km in length. We used the sum of counts from the 50 stops in a year's route survey as an index of abundance along the route for that year. The 1840 counts we used for model building were produced by 310 observers over 140 routes between 1981 and 2001; an additional 396 counts were held back for model evaluation. Over a 20-year period observers changed; not all routes were run each year and no route was run more than once per year.

Modeling approach

We employed a hierarchical modeling approach to map predicted abundances for bird species at a regional scale. Our modeling approach was hierarchical in two ways. First, we used a multilevel Bayesian model (Gelman et al. 1995; Link et al. 2002) to derive unbiased estimates of associations between environmental covariates and bird abundance. The approach was statistically hierarchical because multiple parameters in the model (i.e., the observer, year, and spatial dependence effects described below) were related by a joint probability model that reflected the dependence among them (Gelman et al. 1995). In our case, bird counts were similar to each other to varying degrees because of temporal and spatial correlation and correlated observational error (Link and Sauer 2002), each of which created a level of

correlated structure between survey counts. The nesting of observers within routes over time constituted the hierarchy organizing the data.

The second means by which our approach was hierarchical was that we evaluated the association of environmental parameters to bird counts at multiple spatial extents. This is a common consideration in studies of avian occurrence, distribution, and abundance (Scott et al. 2002). The approach was ecologically hierarchical because bird-habitat associations were evaluated and mapped at three logarithmically related, nested spatial extents representing spatial scales of ecological processes influencing avian population dynamics on the breeding grounds.

Thogmartin et al. (2004) introduced the methodology we employed to assess associations between bird abundance and environmental variables. Avian counts were modeled as a Poisson process resulting from a loglinear function of explanatory variables describing habitat, spatial relatedness, and individual effects of observer and year (Long 1997). The model is written as:

$$Z(s_i) = \mu(s_i) + \sum_{k=1}^n c_{ik}(Z(s) - \mu(s_k)) + \omega(s_i) + \eta\mathbf{I}(s_i) + \gamma(s_i) + \varepsilon(s_i)$$

where Z is the response at location i at spatial coordinates s_i , $\mu(s_i)$ is the large-scale, non-spatial trend surface that may depend on covariates (independent environmental variables), ε are the error terms that are independent with zero mean and constant variance τ^2 , c_{ik} are the spatial dependence parameters, $i, k=1, \dots, n$ where the dependence is symmetric and pair-wise dependence occurs only between neighboring survey locations. Spatial dependence between survey counts was incorporated as a first-order conditional autoregression based upon an irregular lattice describing the spatial neighborhood of routes. Observer effects $\eta\mathbf{I}$ (novice) and ω (observer) were accommodated in the model so as to minimize bias in the parameter estimates (Link and Sauer 2002). Because novice observers are often overwhelmed by their responsibilities the novice effect led to the exclusion of their counts; experienced observers still exhibit differences in

how frequently they count some species, so we included a random effect to control for these observer-specific differences. Route-regression methods (Geissler and Sauer 1990), a standard method for estimating trend in BBS data, suggested each of the species we modeled exhibited substantial declines or increases in relative abundance in the Prairie Hardwood Transition between 1981 and 2001 (J. Sauer, USGS Patuxent Wildlife Research Center, unpublished data). Thus, a linear year effect γ was included to remove this temporal trend in the counts to reveal a temporally unbiased estimate of counts relative to environmental characteristics. In effect, the general model was an over-dispersed Poisson regression with fixed and random effects, with diffuse or non-informative priors and hyper-priors assigned to each parameter (Table 1).

The initial environmental variables ($\mu(s_i) = \beta_1 \cdot x_{i1} + \dots + \beta_p \cdot x_{ip}$) considered in the models were identified *a priori* from published habitat associations of the three bird species (Table 2) (Roth et al. 1996; Smith et al. 2000; Hughes 2001). Species experts reviewed each *a priori* global model. Interactions were included if suggested by the biology of the species. Each variable was evaluated at three scales, derived from logarithmically related buffers around BBS routes. These buffers were 0.1, 1, and 10 km, and corresponded to 800, 8,000, and ~80,000 ha spatial extents, respectively.

We conducted model fitting in WinBUGS 4.1 (Spiegelhalter et al. 2003), a statistical package

conducting Bayesian inference with Markov chain Monte Carlo (MCMC) methods (Gibbs Sampling) (Link and Sauer 2002). MCMC is a generic term describing a collection of methods simulating draws from complex distributions. In an MCMC approach, the previous sample values are used to randomly generate the next sample value, generating a Markov chain (the transition probabilities between sample values are only a function of the most recent sample value). Explanatory continuous variables in the model were standardized; this aided model convergence and placed the slope coefficients on a comparable scale. For each model we ran the Markov chain until convergence occurred (15,000 iterations) and an additional 3000 iterations past convergence. This chain creation was conducted five times to create replicate chains for the Gelman-Rubin diagnostic (Brooks and Gelman 1998; Spiegelhalter et al. 2003), comparing within-chain and between-chain variability. Code for the model we implemented is available in Thogmartin et al. (2004: <http://www.esapubs.org/archive/appl/A014/035/suppl-1.htm>).

Models were developed within each of the three scales (800, 8000, and ~80,000 ha); that is, the variables within any single model were derived from the same spatial scale. We followed an information-theoretic approach to ranking these models (Burnham and Anderson 2002) using the Deviance Information Criterion (DIC), where $DIC = \bar{D} + p_D$, which is the posterior mean of

Table 1 Priors and effect type for the main model effects for the model. $Z(s_i) = \mu(s_i) + \sum_{k=1}^n c_{ik} (Z(s_k) - \mu(s_k)) + \omega_k(s) + \eta I(s) + \gamma_k(s) + \varepsilon(s_k)$

Variable	Definition	Effect type	Prior distribution (expected value, precision ^a)
μ	Environmental factors	Fixed	Normal (0.0, 0.000001) ^b
Z	Spatial relatedness	Random	Flat (for the CAR-related intercept) ^c $\tau_{\text{Space}} \sim \text{Gamma}(0.5, 0.0005)$
ω	Observer-experience effect	Random	Normal (0.0, τ_{Observer}) $\tau_{\text{Observer}} \sim \text{Gamma}(0.001, 0.001)$
η	Novice-observer effect	Fixed	Normal (0.0, 0.000001)
γ	Year effect	Random	Normal (0.0, τ_{Year}) $\tau_{\text{Year}} \sim \text{Gamma}(0.001, 0.001)$
ε	Error	Random	Normal (0.0, τ_{Noise}) $\tau_{\text{Noise}} \sim \text{Gamma}(0.001, 0.001)$

^aPrecision rather than variance is described, with precision simply 1/variance

^bEssentially a flat or non-informative prior distribution

^cSee Thomas et al. (2002) for details regarding flat prior relating to the conditional autoregression implemented in WinBUGS

Table 2 Environmental covariates included in initial (global) models of habitat associations for three forest birds in Bird Conservation Region 23, the Prairie-Hardwood Transition

Environmental suite	Variable	Species
Land cover composition	Beech-oak forest (%)	BBCU
	Pine forest (%)	WOTH
	Deciduous forest (%)	RHWO, WOTH
	Wooded wetland (%)	BBCU, WOTH
	Grassland (%)	RHWO
	Urban grass (%)	BBCU, RHWO
	Row crop (%)	RHWO
Land cover configuration	Area-weighted forest patch size (ha)	BBCU
	Patchy forest (%) ^a	RHWO
	Perforated forest (%) ^a	RHWO
Terrain heterogeneity and physiognomy	Mean static wetness index (scales between 1 [dry] to 19 [moist]) ^b	BBCU, RHWO, WOTH
	River density (km/km ²)	RHWO
Spatial correlation	Normal conditional autoregression ^c	BBCU, RHWO, WOTH

^aMean composition of constituent forest fragmentation types for 81 km² areas. Patchy forests were areas where forest composition was <40%; and perforated forests were >60% forest with high connectivity of forest patches (Riitters et al. 2000)

^bAlso known as the topographic convergence index, static wetness is measured as $\ln(\text{Catchment Area}/\text{tangent of the slope angle})$

^cSecond-order (small area) correlation

the deviance (\bar{D}) plus the effective number of parameters (p_D) (Spiegelhalter et al. 2002). As a means of assessing the weight of models relative to each other in the best subset of models, DIC model weights were calculated as:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{i=1}^R \exp(-\frac{1}{2}\Delta_i)},$$

where Δ_i is the difference between model i and the best model.

Because a single ‘best’ model may vary from data set to data set despite being collected from the same underlying process (Burnham and Anderson 2002, p. 151), we conducted multi-model inference by averaging across model parameters to create an average model. We averaged the model parameters using the model weights *sensu* Burnham and Anderson (2002). Models averaged across the different scales allowed us to determine the relative weight or merit of the individual spatial scales. Inference and model averaging were constrained to only those models within 5 DIC units of the best model. As a reference, we also calculated a null model for each species that contained observer, year, and

autocorrelation effects, but which did not contain environmental covariates. As a means of inferring relative contributions of environmental and spatial variables, we calculated the relative portion of the explained variance explained by the various suites of variables.

Because most of what is known about forest birds is derived from local-level studies, habitat associations appearing at only coarse spatial scales are largely unknown. Following an approach outlined in Thogmartin et al. (2004), we supplemented our *a priori* models with variables identified through *post hoc* exploration of various environmental variables. The aim of the *post hoc* exploration was to remove residual spatial autocorrelation in bird counts and increase explained variance. The *post hoc* exploration included five suites of variables: landscape composition, landscape configuration, terrain heterogeneity and physiognomy, potential human disturbance, and interspecies competition (Thogmartin et al. 2004). There was little or no information in the literature on the influence of climate on these forest species, unlike grassland species from the same region (Thogmartin et al. 2006). In addition, climate and land cover are often highly correlated and, therefore, climate may not improve models

that include land cover (Venier et al. 2004). Therefore, climate variables were not included *a priori* but were examined post hoc. A regression tree approach was implemented to identify the best candidates for inclusion (De'ath and Fabricius 2000; O'Connor and Wagner 2004). The inclusion of these post-hoc variables in the hierarchical models was evaluated with DIC, but if the 95% Bayesian credibility intervals overlapped zero the variable was not included in the final model and map.

We mapped predicted abundance by summing geographic information system grid layers of standardized environmental predictors with weights according to their model-averaged slope coefficients, using the ArcGIS Spatial Analyst grid calculator (ArcGIS 8.0 and 9.x, Environmental Systems Research, Inc., Redlands, CA) (Thogmartin et al. 2004, 2006). Final map resolution was 1 ha. The route-level posterior estimates of the standard deviation of the predictions were included in the maps of predicted relative abundance.

Gelman et al. (1995: chapter 6) described a procedure for assessing goodness of fit using a posterior predictive check whereby parameter sets derived from the original data (15,000 sets of parameters [5× 3000 iterations]) are compared to parameter sets derived for a replicate data set generated following model specifications. A poorly fitted model will exhibit a diagnostic near 0 or 1, whereas values close to 0.5 are desired as indicating neither over- nor under-fitting.

We used Breeding Bird Survey data held back from model calibration and independent point counts conducted on public lands to assess the accuracy of the models and maps we developed. The point counts were from 17 locations within the Prairie Hardwood Transition (Thogmartin et al. 2004) and were available from the National Point Count Database (<http://www.mp2-pwrc.usgs.gov/point/index.htm>). The root mean square prediction error (RMSPE) was calculated as a measure of model fit against independent data. The RMSPE is the square root of the squared differences between the observed (i.e., withheld BBS or independent point counts) and the expected (model predictions) divided by the sample size, with a smaller number indicating

better model performance relative to the independent data. Methodology used to gather counts differed between the point counts and the BBS and, therefore, when the point and BBS counts were compared they were first natural log-transformed ($\ln(x+1)$) to place the data on a similar scale. We also did not accommodate the very factors that we posited as being potential nuisances biasing our results, that of year, observer, and spatial correlation; failure to accommodate these factors immediately places the model evaluation at a disadvantage. A proper assessment would entail stripping from the evaluation data year, observer, and spatial correlation effects, something that we could not do because we lacked certain necessary information (particularly for the point count data). Regardless of this potential for bias in the model assessment, a comparison between the model predictions and independent, uncorrected field data provides information on the magnitude of discrepancies that one might expect when using the model for conservation purposes such as site acquisition.

Results

Wood Thrushes occurred at more sites than either Red-headed Woodpeckers or Black-billed Cuckoos, but Red-headed Woodpeckers, when they did occur, were more abundant (Table 3). Black-billed Cuckoos were least frequent in their occurrence and abundance. Distributions of all species counts were highly kurtotic, resulting in high pre-modeling overdispersion for each species.

Models of bird abundance indicated a substantial association with environmental variables for all species; the null model tended to perform poorly in comparison to models with explanatory variables (Table 4). The final averaged models were composed almost entirely of variables selected *a priori*; only one additional explanatory variable was identified during the *post hoc* exploration (Table 5). However, some *a priori* variables chosen because of previously reported positive associations with species abundance turned out to have negative associations at the spatial extents we examined. For instance, we had

Table 3 Summary statistics for breeding bird survey counts collected 1981–2001 for three forest bird species in the Prairie-hardwood Transition of the upper midwestern US

Species	Mean	Variance	Count sum	Total zero counts (%)	Non-zero mean	Non-zero variance
Black-billed Cuckoo	0.90	2.62	1654	59.3	2.21	3.55
Red-headed Woodpecker	2.25	17.13	4133	41.6	3.85	23.19
Wood Thrush	1.28	3.84	2351	47.7	2.44	4.49

expected Black-billed Cuckoos to be more abundant in landscapes abundant in urban grass as these birds are often sighted in the context of golf courses; our model suggested urban grass negatively influenced Black-billed Cuckoo abundance. Similarly, we had expected Red-headed Woodpeckers to be positively associated with patchy forest, which we believed would have provided the field-forest conditions most similar to the savannah conditions emblematic of this species; we found this species to be negatively associated with patchy forest at the coarsest scale. Models for the three species also retained the spatial correlation term, contrary to our expectation that an appropriate set of environmental covariates would obviate the need for its inclusion.

All of the models were well fitted. Bayes' p -values of the Gelman et al. diagnostic for the best model equaled 0.53, 0.62, and 0.38 for Black-billed Cuckoo, Red-headed Woodpecker, and Wood Thrush, respectively (Tables 4 and 5).

Eight models competed for the best subset of variables for Black-billed Cuckoo, indicating some model uncertainty (Table 4). The best-performing models suggested Black-billed Cuckoo abundance was associated with beech-oak forest and sensitive to forest patch size. In addition, the Black-billed Cuckoo was more abundant in wooded wetlands embedded within drier landscapes (riparian systems); they were negatively associated with urban grass. The habitat associations were consistent across all three scales we assessed (Table 5). We predicted the Black-billed Cuckoo to be most abundant in northern portions of the Prairie Hardwood Transition, in north central Wisconsin and northwestern Michigan (Fig. 1).

The two best models for the Red-headed Woodpecker had a combined weight of 91%, indicating low model uncertainty (Table 4). Red-headed Woodpecker abundance was higher in dry landscapes with a high proportion of grassland,

deciduous forest, and row crops as found at coarse spatial scales (Table 5). Associations with grassland, urban grass, and row crops were also measured at fine spatial scales. Red-headed Woodpeckers were predicted to be most abundant in the Driftless Area Ecoregion (McNab and Avers 1994) of southwestern Wisconsin, north-eastern Iowa, and southeastern Minnesota (Fig. 1).

The Wood Thrush had the highest model uncertainty. Ten models were contenders for the best model and the null model had a weight of 4% (Table 4). However, interpretation was simplified because the same variables appeared at multiple spatial scales, indicating the uncertainty was with the scale of analysis rather than the variables included in the models. Wood Thrush abundance had a strong positive association with the proportion of the landscape in deciduous forest at all spatial scales and a weak positive association with wooded wetlands at intermediate and coarse spatial scales (Table 5). We predicted Wood Thrush abundance to be lower in landscapes with more pine forests. Associations with wetness were more complex; Wood Thrush abundance tended to be higher in drier landscapes, as measured at fine and coarse scales, but weakly higher in wetter landscapes, as measured at intermediate spatial scales. The map indicated that the Driftless Area Ecoregion and parts of northern Wisconsin and Michigan were predicted to have the highest abundances for this species (Fig. 1). The Wood Thrush was the only species to include a credible environmental covariate identified post-hoc in the model set describing its abundance; this variable, forest proximity, measures both the degree of patch isolation and the degree of fragmentation of forest within 1 km of each focal patch (Gustafson and Parker 1992). In this case, Wood Thrushes were more abundant in landscapes in which forests were comprised of large patches in close proximity to one another.

Table 4 Parameter estimates for the best subset of models fitted to 1981–2001 Breeding Bird Survey route counts for three forest bird species in the Prairie-hardwood Transition of the upper midwestern US

Best subset model	Explanatory variable	Scale (ha)	Parameters ^a	DIC ^b	Δ DIC ^c	w_i^d	Evidence ratio ^e
<i>Black-billed Cuckoo</i>							
1	Beech-oak forest, forest patch area, wooded wetlands, urban grass	8,000	513.4	3977.9	0	0.23	1.00
2	Beech-oak forest, wooded wetlands, urban grass	8,000	514.0	3978.1	0.2	0.21	1.11
3	Beech-oak forest, wooded wetlands, urban grass	80,000	516.4	3979.3	1.45	0.11	2.06
4	Beech-oak forest, forest patch area, wetness, wooded wetlands, urban grass	800	512.8	3979.3	1.48	0.11	2.10
5	Beech-oak forest, forest patch area, wetness, wooded wetlands, urban grass	8,000	511.2	3979.3	1.49	0.11	2.11
6	Beech-oak forest, forest patch area, wetness, wooded wetlands, urban grass	80,000	517.0	3979.7	1.84	0.09	2.51
7	Beech-oak forest, wetness, wooded wetlands, urban grass	800	512.4	3979.8	1.94	0.09	2.64
8	Beech-oak forest, wetness, wooded wetlands, urban grass	80,000	517.0	3980.6	2.7	0.06	3.86
Null			519.9	3985.5	7.65	0.01	45.83
<i>Red-headed Woodpecker</i>							
1	Grassland, deciduous forest, row crop, river density, patchy forest	80,000	416.3	5256.3	0	0.67	1.00
2	Grassland ₈₀₀ , urban grass, row crop, perforated forest, wetness	800	412.5	5258.3	2.06	0.24	2.80
Null			420.0	5265.7	9.44	0.01	112.17
<i>Wood Thrush</i>							
1	Deciduous forest	8,000	388.3	4621.5	0	0.13	1.00
2	Wetness, deciduous forest, evergreen forest	80,000	394.6	4621.7	0.22	0.12	1.12
3	Wetness, deciduous forest, evergreen forest, wooded wetland	8,000	390.0	4621.8	0.27	0.12	1.14
4	Wetness, deciduous forest	800	390.2	4621.9	0.35	0.11	1.19
5	Wetness, deciduous forest, evergreen forest, wooded wetland	80,000	394.9	4622.2	0.66	0.10	1.39
6	Wetness, deciduous forest, forest proximity ^f	8,000	395.6	4622.5	0.97	0.08	1.62
7	Wetness, deciduous forest, evergreen forest	8,000	396.9	4622.5	0.98	0.08	1.63
8	Deciduous forest, evergreen forest	80,000	397.1	4622.5	1.04	0.08	1.68
9	Deciduous forest	80,000	396.3	4622.8	1.25	0.07	1.87
10	Wetness, deciduous forest, forest proximity ^f	80,000	392.8	4623.1	1.61	0.06	2.24
Null			399.7	4623.7	2.21	0.04	3.02

The Null model, included for comparison, in each case is a model with observer, year, and spatial correlation, but without environmental covariates. Model weights, w_i , do not sum to 1 because of rounding error and inclusion of only those models within 5 DIC of the best model

^aParameters is the effective number of parameters (pD), and is given by the posterior mean of the deviance minus the deviance of the posterior means

^bDIC is Deviance Information Criterion. See text for details

^c Δ DIC is the difference between the best model and the model of interest

^d w_i is the model weight, as described in the text

^eEvidence ratio is the model weight for the best model divided by the weight for the model of interest

^fThe post hoc contributed variable, forest proximity, was included at the 800 ha scale

Observations from the withheld BBS data indicated slightly higher counts for the Black-billed Cuckoo than we predicted (RMSPE = 0.51;

Fig. 2) and counts for the Wood Thrush were considerably higher than predicted (RMPSE = 2.67). Of withheld BBS counts for Black-billed

Table 5 Median and lower (LCL) and upper (UCL) confidence limits of the posterior distribution of explanatory variable slopes for an average model derived from the Kullback–Leibler best subset of models for three forest bird species in the Prairie-hardwood Transition of the upper midwestern US

Species	Explanatory Variable	Scale (ha)	Median	95% LCL	95% UCL	Variable Importance	
<i>Black-billed Cuckoo</i>	Beech-Oak Forest (%)	800	0.232	0.228	0.236	0.20	
		8000	0.179	0.175	0.184	0.54	
		80,000	0.251	0.246	0.256	0.26	
	Area-weighted Forest Patch Size (ha)	800	0.066	0.062	0.069	0.11	
		8000	0.104	0.101	0.108	0.34	
		80,000	0.016	0.012	0.020	0.09	
	Mean Static Wetness Index (scales between 1 [dry] to 19 [moist])	800	−0.161	−0.165	−0.156	0.20	
		8000	−0.052	−0.056	−0.048	0.11	
		80,000	−0.083	−0.087	−0.078	0.15	
	Wooded Wetland (%)	800	0.187	0.183	0.191	0.20	
		8000	0.205	0.202	0.209	.54	
		80,000	0.192	0.188	0.197	0.26	
	Urban Grass (%)	800	−0.297	−0.301	−0.292	0.20	
		8000	−0.372	−0.377	−0.367	0.54	
		80,000	−0.237	−0.241	−0.232	0.26	
Normal Conditional Autoregression			−1.092	−1.098	−1.085	1.00	
<i>Red-headed Woodpecker</i>	Grassland (%)	8000	0.285	0.280	0.289	0.26	
		80,000	0.329	0.324	0.333	0.74	
	Urban Grass (%)	800	0.130	0.127	0.133	0.26	
	Deciduous Forest (%)	80,000	0.298	0.291	0.304	0.74	
		800	0.484	0.479	0.489	0.26	
	Row Crop (%)	80,000	0.375	0.369	0.381	0.74	
		80,000	−0.164	−0.167	−0.160	0.74	
	Patchy Forest (%)	80,000	−0.264	−0.268	−0.259	0.74	
	Perforated Forest (%)	800	0.134	0.130	0.138	0.26	
		800	−0.331	−0.337	−0.326	0.26	
	Mean Static Wetness Index (scales between 1 [dry] to 19 [moist])			−0.331	−0.337	−0.326	0.26
	Normal Conditional Autoregression			−0.221	−0.224	−0.217	1.00
<i>Wood Thrush</i>	Mean Static Wetness Index (scales between 1 [dry] to 19 [moist])	800	−0.246	−0.251	−0.241	0.11	
		8000	0.096	0.091	0.100	0.28	
		80,000	−0.025	−0.028	−0.022	0.28	
	Deciduous Forest (%)	800	0.532	0.528	0.536	0.11	
		8000	0.548	0.542	0.553	0.42	
	Wooded Wetland (%)	80,000	0.567	0.561	0.573	0.43	
		8000	0.031	0.026	0.035	0.12	
	Pine Forest (%)	80,000	0.003	−0.002	0.009	0.10	
		8000	−0.095	−0.101	−0.089	0.20	
	Area-weighted Forest Proximity ^a	8000	−0.086	−0.092	−0.080	0.30	
		800	0.233	0.229	0.237	0.14	
Normal Conditional Autoregression			−0.426	−0.431	−0.422	1.00	

Variable importance is the sum of the model weights for those models in the Kullback–Liebler best subset of models in which the variable occurs

^aPost-hoc identified variable

Cuckoo, 95% were within 1 bird of the prediction, whereas 95% of Wood Thrush counts were within 5.3 birds of the prediction. Red-headed Woodpecker counts were higher than predicted (RMPSE = 2.40); 95% of Red-headed

Woodpecker counts were within 4.8 birds of the prediction. The model and map for the Red-headed Woodpecker seem to have predicted unreasonably high counts in the Driftless Area of Wisconsin, southeastern Minnesota, and

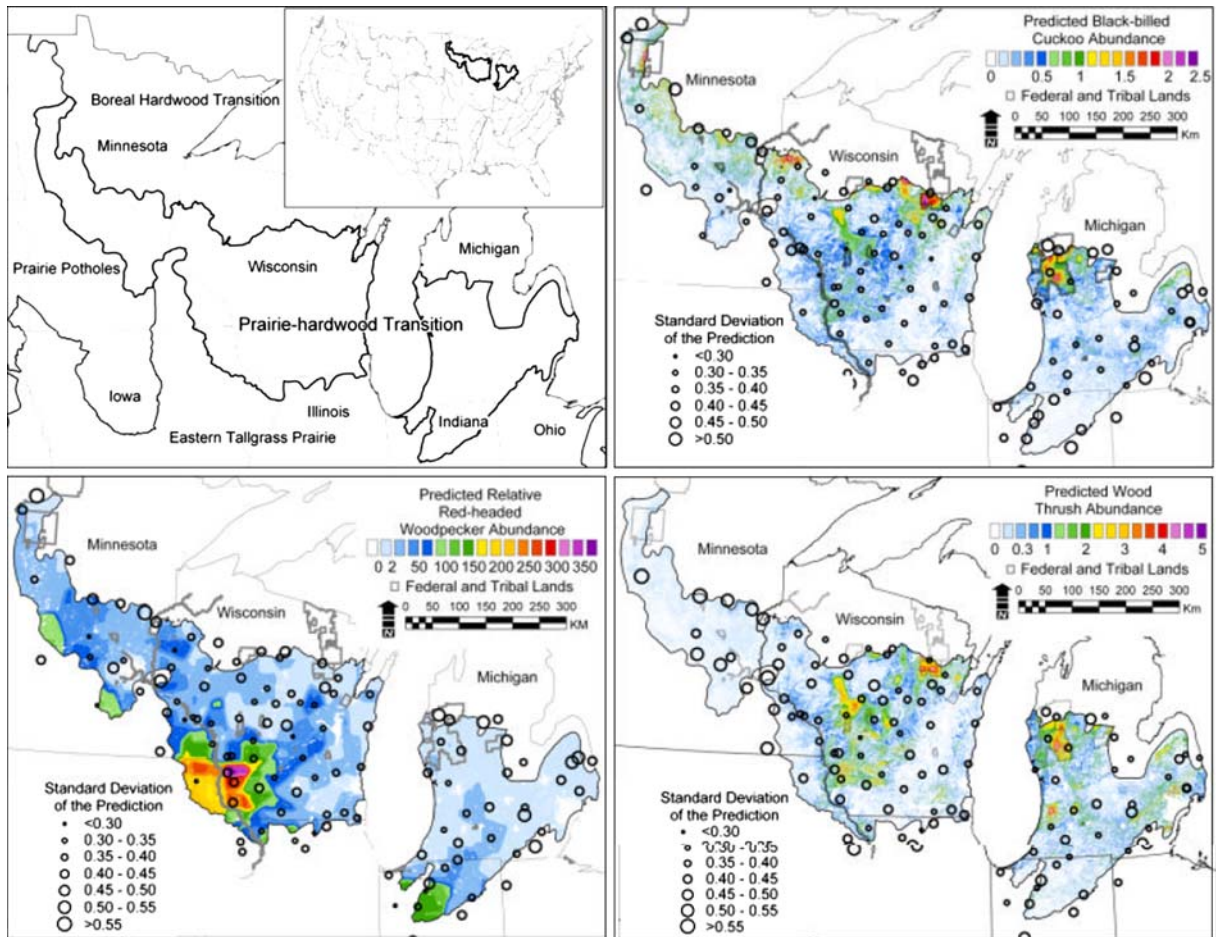


Fig. 1 Maps of predicted relative abundance for three forest bird species in the Prairie-hardwood transition of the upper midwestern U.S. Dots represent the standard deviation of the prediction

northeastern Iowa where Red-headed Woodpecker are common (Fig. 1).

Point counts from 17 study locations in the Prairie Hardwood Transition suggested that Black-billed Cuckoo and Wood Thrush observations were roughly in line with predictions (RMPSE = 1.38 and 1.13, respectively), and Red-headed Woodpecker counts were considerably below predictions (RMPSE = 1.36; Fig. 3). As expected, the point count observations exhibited considerably more variability relative to the predictions as a consequence of not controlling for annual and observer effects in the point counts. Individual point counts were frequently zero despite an expectation of a positive count, possibly as a result of issues relating to species detectability.

Discussion

Local species-habitat applied to landscape scales

For forest birds in the Prairie Hardwood Transition, the final models we generated generally consisted of environmental variables selected *a priori*, variables that had been measured in fine-scale studies of these species. Only one species, the Wood Thrush, had a model substantially improved by the addition of a post hoc-identified variable. Therefore, we believe that our results captured relevant ecological processes structuring regional abundances of these birds and that, for these birds in this region, findings identified at the local scale generally scale linearly to the larger landscape.

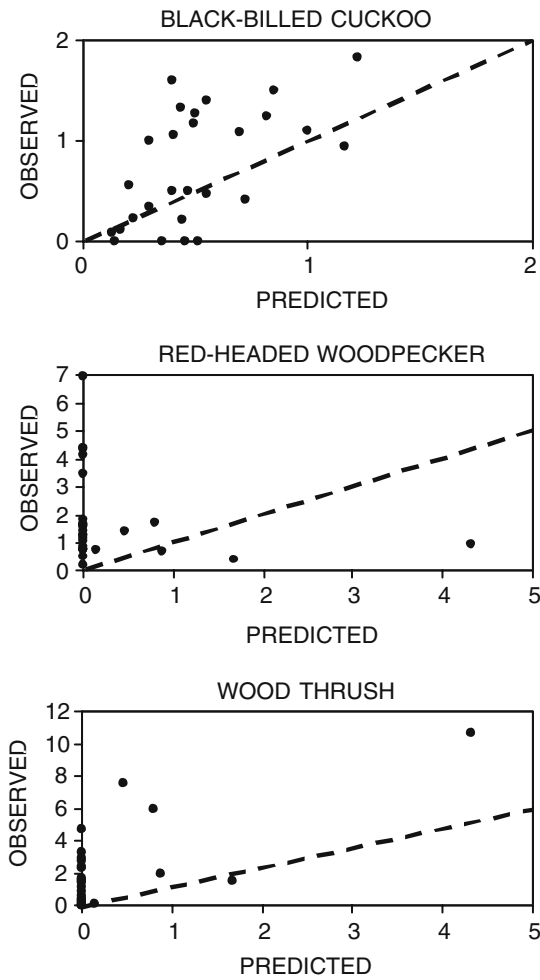


Fig. 2 Observed Breeding Bird Survey counts for three forest birds in the Prairiehardwood Transition of the upper midwestern U.S., withheld from model construction and fitted to expected counts. The solid line is a least-squares regression whereas the dotted line is the one-to-one line of correspondence. Sample size was $n=396$ for each species

The strength of the relations between the environmental variables and the species counts differed by scale, but the posited direction of the relationships generally held true for each species.

Exceptions included the negative relationship of Black-billed Cuckoo with urban grass composition. Black-billed Cuckoos are sometimes found in parks, golf courses, and residential gardens associated with human habitation (Hughes 2001). Our finding that Black-billed Cuckoos are negatively associated with urban grass suggests the local level result may be misleading. It is conceivable that Black-billed Cuckoos are simply

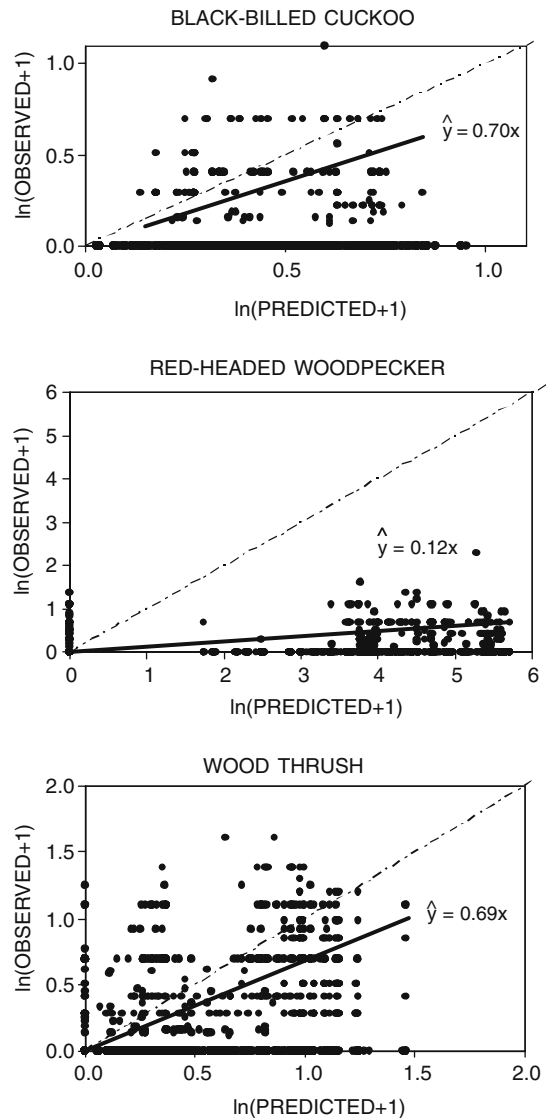


Fig. 3 Observed point counts of forest birds collected on 17 Federal lands in the Prairie-hardwood Transition of the upper midwestern U.S. plotted against hierarchical spatial count model predictions (predicted)

more observable in parks, golf courses, and residential gardens when they occur there. We also found seemingly contradictory results for Wood Thrush relations with mesic conditions. Wood Thrushes were strongly negatively related to mesic conditions at the finest resolution of study and somewhat positively related at the intermediate scale of study. We interpret these findings in the following manner: that Wood Thrushes are most abundant in xeric patches embedded within relatively moist landscapes.

No single spatial scale dominated any model, indicating that these species are responding to factors at multiple spatial scales. Lee et al. (2002), working in eastern Canada, similarly observed that the relative importance of habitat variables varied by bird species and with the scale of measurement; no single scale of inquiry was of primary importance. This concurs with the observations of Wiens et al. (1987) who found that habitat associations of shrubsteppe birds varied with the spatial scale of analysis. A single species could have a positive association with a habitat variable measured at a local scale and negative or no associations with the same variable measured at regional or biogeographic scales. We observed the same phenomenon for the Wood Thrush, which was positively associated with an index of wetness at the intermediate spatial scale and negatively associated at the smallest and largest spatial scales. It was perhaps more surprising that we found generally consistent habitat associations across scales for each species.

Importance of spatial structure

As with the grassland birds we studied earlier (Thogmartin et al. 2006), extensive spatial structuring related to the spatial autocorrelation term remained unaccounted for by relevant ecological factors. While land cover configuration and composition have received much emphasis in the wildlife and ornithological literature, much less attention has been devoted to spatial structure (Koenig 2001; Lichstein et al. 2002). Yet, it is reasonable to presume routes close together tend to be more similar in bird species composition and abundance than those farther apart. We know that bird abundances are often expressed along a spatial gradient of increasing or decreasing abundance, even if we do not know exactly what is driving this gradient. Using a model that includes a term for spatial autocorrelation will reduce error and help clarify explanatory environmental factors.

Species habitat associations

Very little research has focused on the Black-billed Cuckoo; much of our information heretofore

was derived from state and provincial atlases and a few focused behavioral nesting studies (Hughes 2001). Black-billed Cuckoo populations are believed to strongly depend upon insect outbreaks, primarily caterpillars (Lepidoptera larvae) and cicadas (Cicadidae) (Hughes 2001). Given this major ecological driver, we might expect habitat associations to be relatively weak. However, recent work by Gale et al. (2001) examining Breeding Bird Census data in association with gypsy moth (*Lymantria dispar*) outbreaks in Pennsylvania showed patterns inconsistent with the notion that gypsy moths stimulate general and predictable increases in bird populations.

Our findings for Black-billed Cuckoo support previous observations of an association with wooded wetlands, riparian areas, and deciduous forests (Hughes 2001). However, we also identified specific forest type associations as well as area sensitivity, unusual for a shrub-nesting species (Galli et al. 1976; Martin 1981). What emerges is a shrub-nesting species associated with riparian and wetland habitats within more heavily forested landscapes, and a species that is less abundant in urban/suburban areas.

We derived new information about habitat associations of the Red-headed Woodpecker at regional spatial scales. Our finding that landscapes with roughly equal proportions of grassland, row crops, and deciduous forest were associated with high abundances of Red-headed Woodpeckers has not, to our knowledge, previously been reported. This combination of major land cover types may be most likely to have the tall, dead trees suitable for nesting (Giese and Cuthbert 2003) and mast trees needed for food (Smith and Scarlett 1987). Our model also supports previous descriptions of the Red-headed Woodpeckers as associated with dry sites, forests perforated by canopy gaps, and to some extent with parks or golf courses (urban grass) (Smith et al. 2000).

Our model for the Wood Thrush supports its described association with deciduous forests at all spatial scales and sensitivity to forest fragmentation (Roth et al. 1996; Donovan and Flather 2002; Lee et al. 2002). Our observed Wood Thrush associations with wooded wetlands fit reported

associations with mesic forests and with moist soils (Sargent et al. 2003). However, Wood Thrush is not considered a riparian species, and this is reflected in a mixed response to our wetness index across spatial scales.

Expected patterns of abundance

The factors represented by our predictive models have expanded our knowledge of species habitat associations across a range of spatial scales from relatively fine (800 ha) to coarse (80,000 ha) within a single Bird Conservation Region. For the Black-billed Cuckoo and Red-headed Woodpecker, species that have been the subjects of less research than other songbirds, the information contained in these models should strengthen conservation plans for these species. The models we developed could be used as the *a priori* expectation for modeling attempts of a similar nature in other areas of the species range. We might expect, however, that in extrapolating these models to other parts of the species range that the parameter values associated with the variables to change. What is not clear from these results is whether the scale relationships are robust to changes in where the species is modeled.

The maps of predicted abundance across the Prairie Hardwood Transition can be used to suggest locations where conservation efforts should be focused for each species. However, we acknowledge that our models contain some uncertainty; additional field data are needed to verify our predictions.

We suggest that the appropriate spatial scale to address this issue of uncertainty is roughly approximated by political units the size of townships (93 km²) and counties (mean size of counties in the Prairie Hardwood Transition was 790 km²). Because of technical limitations in how the models are translated into maps, inferring conservation value for land units much smaller than a township may not be justified. This necessarily coarse application of the models allows land managers many possible options for how and where to improve habitat for these species.

In addition, the models and spatial patterns of abundance among species can suggest locations where conservation actions may benefit more than one species. The concurrence of models and maps for the Cerulean Warbler (*Dendroica cerulea*; Thogmartin et al. 2004) and Wood Thrush indicates that similar habitat management will benefit both species. Conservation of forests in the northern portions of the Prairie Hardwood Transition, especially in Wisconsin and Michigan, will most benefit Black-billed Cuckoo. Among the species we studied, the Red-headed Woodpecker will require strategies and geographically targeted conservation actions unique to this species. Although the Driftless Area is modeled as a center of abundance for the species, the map indicates that this species has potential for manageable populations across the Prairie Hardwood Transition wherever suitable habitat can be found.

Conclusions

We modeled and mapped the relative abundance of three forest birds of high conservation concern using a hierarchical spatial count model. Our analysis was designed to integrate 20 years of BBS data across a region, looking for associations with relatively stable landscape factors that might be amenable to management. We found that local-scale studies are useful for informing landscape-scale models predicting patterns in regional abundance, at least for the three forest species we studied. These models and maps should be useful in directing regional conservation efforts and can inform modeling activities for these species in other regions.

Acknowledgments We thank the numerous individuals involved in the collection of Breeding Bird Survey data, which made this analysis possible. We thank L. Powell and K. Smith for providing important feedback regarding development of the *a priori* models, J. Sauer, J. Royle, and W. Link for valuable discussion of spatial and hierarchical models in a Bayesian framework, S. Weick and C. Beckman for their attention to the point count model evaluation data, T. Fox and J. Nelson for geographic information systems support, and E. Linder, L. Venier, and anonymous reviewers for their comments on an earlier version of this manuscript.

References

- Brennan JM, Bender DJ, Contreras TA, Fahrig L (2002) Focal patch landscape studies for wildlife management: optimizing sampling effort across scales. In: Liu J, Taylor WW (eds) Integrating landscape ecology into natural resource management. Cambridge University Press, Cambridge, Massachusetts, USA, pp 68–91
- Brooks S, Gelman A (1998) General methods for monitoring convergence of iterative simulations. *J Comput Graphical Stat* 7:434–455
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information theoretic approach, 2nd edn. Springer-Verlag, New York, USA, p 353
- De'ath G, Fabricius KE (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81:3178–3192
- Diamond DD, Gordon TM, True CD, Lea RD, Foster WE (2003) An ecoregion-based conservation assessment and conservation opportunity area inventory for the Lower Midwestern USA. *Nat Areas J* 23:129–140
- Donovan TM, Flather CH (2002) Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecol Appl* 12:364–374
- Gale GA, DeCecco JA, Marshall MR, McClain WR, Cooper RJ (2001) Effects of gypsy moth defoliation on forest birds: an assessment using breeding bird census data. *J Field Ornithol* 72:291–304
- Galli A, Leck CF, Forman RTT (1976) Avian distribution patterns in forest islands of different sizes in central New Jersey. *Auk* 93:356–364
- Geissler PH, Sauer JR (1990) Topics in route-regression analysis. In: Sauer JR, Droege S (eds) Survey designs and statistical methods for the estimation of avian population trends. U.S. Fish and Wildlife Service, Biological Report 90(1), Arlington, Virginia, USA, pp 54–57
- Gelman A, Carlin JB, Stern HS, Rubin DR (1995) Bayesian data analysis. Chapman and Hall, New York, USA, p 526
- Giese CLA, Cuthbert FJ (2003) Influence of surrounding vegetation on woodpecker nest tree selection in oak forests of the Upper Midwest, USA. *For Ecol Manage* 179:523–534
- Gustafson EJ, Knutson MG, Niemi GJ, Friberg MA (2002) Evaluation of spatial models to predict vulnerability of forest birds to brood parasitism by cowbirds. *Ecol Appl* 12:412–426
- Gustafson EJ, Parker GR (1992) Relationships between landcover proportion and indices of landscape spatial pattern. *Landscape Ecol* 7:101–110
- Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. *Bio Science* 54:227–233
- Hughes JM (2001) Black-billed Cuckoo (*Coccyzus erythrophthalmus*). In: Poole A, Gill F (eds) The birds of North America, No. 587. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA, p 24
- Koenig WD (2001) Spatial autocorrelation and local disappearances in wintering North American birds. *Ecology* 82:2636–2644
- Lee M, Fahrig L, Freemark K, Currie DJ (2002) Importance of patch scale vs landscape scale on selected forest birds. *Oikos* 96:110–118
- Lichstein JW, Simons TR, Franzreb KE (2002) Landscape effects on breeding songbird abundance in managed forests. *Ecol Appl* 12:836–857
- Link WA, Cam E, Nichols JD, Cooch E (2002) Of BUGS and birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. *J Wildl Manage* 66:277–291
- Link WA, Sauer JR (2002) A hierarchical analysis of population change with application to Cerulean Warblers. *Ecology* 83:2832–2840
- Long JS (1997) Regression models for categorical and limited dependent variables. Sage Publications, Thousand Oaks, California, USA, p 297
- Martin TE (1981) Limitation in small habitat islands: chance or competition? *Auk* 98:715–734
- McKenney DW, Venier LA, Heerdegen A, McCarthy MA (2002) A Monte Carlo experiment for species mapping problems. In: Scott JM, Heglund PJ, Morrison ML (eds) Predicting species occurrences: issues of accuracy and scale. Island Press, San Diego California USA, pp 377–381
- McNab WH, Avers PE (1994) Ecological subregions of the United States. WO-WSA-5, U.S. Forest Service, Washington, DC, USA
- Noon BR, Murphy DD, Beissinger SR, Shaffer ML, Dellasala D (2003) Conservation planning for US National Forests: conducting comprehensive biodiversity assessments. *Bio Science* 53:1217–1220
- O'Connor RJ, Wagner TL (2004) A test of a regression-tree model of species distribution. *Auk* 121:604–609
- Pearlstine LG, Smith SE, Brandt LA, Allen CR, Kitchens WM, Stenberg J (2002) Assessing state-wide biodiversity in the Florida Gap analysis project. *J Environ Manage* 66:127–144
- Rempel RS, Kushneriuk RS (2003) The influence of sampling scheme and interpolation method on the power to detect spatial effects of forest birds in Ontario (Canada). *Landscape Ecol* 18:741–757
- Rich TD, Beardmore CJ, Berlanga H, Blancher PJ, Bradstreet MS, Butcher GS, Demarest D, Dunn EH, Hunter WC, Inigo-Elias D, Kennedy JA, Martell A, Panjabi A, Pashley DN, Rosenberg KV, Rustay C, Wendt S, Will T (2004) Partners in flight North American landbird conservation plan. Cornell Lab of Ornithology, Cornell, New York, USA, p 84
- Riitters K, Wickham J, O'Neill R, Jones B, Smith E (2000) Global-scale patterns of forest fragmentation. *Conserv Ecol* 4:2756
- Roseberry JL, Sudkamp SD (1998) Assessing the suitability of landscapes for Northern Bobwhite. *J Wildl Manage* 62:895–902
- Roth RR, Johnson MS, Underwood TJ (1996) Wood Thrush (*Hylocichla mustelina*). In: Poole A, Gill F (eds) The birds of North America, No. 246. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, p 28

- Sample DW, Mossman MJ (1997) Managing habitat for grassland birds: a guide for Wisconsin. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA
- Sargent RA, Kilgo JC, Chapman BR, Miller KV (2003) Nesting ecology of Wood Thrush (*Turdidae*: Passeriformes) in hardwood forests of South Carolina. *Southeast Nat* 2:217–222
- Scott JM, Davis F, Csuti B, Noss R, Butterfield B, Groves C, Anderson H, Caicco S, D'Erchia F, Edwards TC Jr, Ulliman J, Wright RG (1993) Gap analysis: a geographic approach to protection of biological diversity. *Wildl Monogr* 123:1–41
- Scott JM, Heglund PJ, Morrison ML, Haufle JB, Raphael MG, Wall WA, Samson FB (2002) Predicting species occurrences: issues of accuracy and scale. Island Press, San Diego, California, USA, p 868
- Seoane J, Bustamante J, DiazDelgado R (2004) Competing roles for landscape, vegetation, topography and climate in predictive models of bird distribution. *Ecol Model* 171:209–222
- Smith KG, Scarlett T (1987) Mast production and winter populations of Red-headed Woodpeckers and Blue Jays. *J Wildl Manage* 51:459–467
- Smith KG, Withgott JH, Rodewald PG (2000) Red-headed woodpecker (*Melanerpes erythrocephalus*). In: Poole A, Gill F (eds) *The birds of North America*, No. 518. The Birds of North America, Inc., Philadelphia Pennsylvania USA, p 28
- Spiegelhalter DJ, Best NG, Carlin BP, van der Linde A (2002) Bayesian measures of model complexity and fit. *J Roy Stat Soc B* 64:583–639
- Spiegelhalter DJ, Thomas A, Best NG (2003) WinBUGS Version 1.4 user manual. Medical Research Council Biostatistics Unit, Cambridge, UK. <http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/manual14.pdf>
- Thogmartin WE, Sauer JR, Knutson MG (2004) A hierarchical spatial model of avian abundance with application to Cerulean Warblers. *Ecol Appl* 14:1766–1779
- Thogmartin WE, Knutson MG, Sauer JR (2006) Predicting regional patterns in rare grassland bird abundance with a hierarchical spatial count model. *Condor* 108:25–46
- Thomas A, Best N, Arnold R, Spiegelhalter D (2002) GeoBugs User Manual, Version 1.1 Beta. Medical Research Council Biostatistics Unit. <http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/geobugs12manual.pdf>
- U.S. Fish and Wildlife Service (2002) Birds of conservation concern. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Washington, DC, USA
- U.S. NABCI Committee (2000) North American bird conservation initiative: bird conservation region descriptions. U.S. Fish and Wildlife Service, Division of Bird Habitat Conservation, Washington, DC, USA
- Venier LA, McKenney DW, Wang Y, McKee J (1999) Models of large-scale breeding-bird distribution as a function of macro-climate in Ontario, Canada. *J Biogeogr* 26:315–328
- Venier LA, Pearce J, McKee JE, McKenney DW, Niemi GJ (2004) Climate and satellite-derived land cover for predicting breeding bird distribution in the Great Lakes Basin. *J Biogeogr* 31:315–331
- Wiens JA (1981) Scale problems in avian censusing. In: Ralph CJ, Scott JM (eds) *Estimating numbers of terrestrial birds*. Cooper Ornithological Society, pp 513–521
- Wiens JA, Rotenberry JT, Van Horne B (1987) Habitat occupancy patterns of North American shrubsteppe birds: the effect of spatial scale. *Oikos* 48:132–147