PREDICTING REGIONAL ABUNDANCE OF RARE GRASSLAND BIRDS WITH A HIERARCHICAL SPATIAL COUNT MODEL

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Abstract. Grassland birds are among the most imperiled groups of birds in North America. Unfortunately, little is known about the location of regional concentrations of these birds, thus regional or statewide conservation efforts may be inappropriately applied, reducing their effectiveness. We identified environmental covariates associated with the abundance of five grassland birds in the upper midwestern United States (Bobolink [*Dolichonyx oryzivorus*], Grasshopper Sparrow [*Ammodramus savannarum*], Henslow's Sparrow [*A. henslowii*], Sedge Wren [*Cistothorus platensis*], and Upland Sandpiper [*Bartramia longicauda*]) with a hierarchical spatial count model fitted with Markov chain Monte Carlo methods. Markov chain Monte Carlo methods are well suited to this task because they are able to incorporate effects associated with autocorrelated counts and nuisance effects associated with years and observers, and the resulting models can be used to map predicted abundance at a landscape scale. Environmental covariates were derived from five suites of variables: landscape composition, landscape configuration, terrain heterogeneity and physiognomy, climate, and human influence. The final models largely conformed to our *a priori* expectations. Bobolinks and Henslow's Sparrows were strongly sensitive to grassland patch area. All of the species except Henslow's Sparrows exhibited substantial negative relations with forest composition, often at multiple spatial scales. Climate was found to be important for all species, and was the most important factor influencing abundance of Grasshopper Sparrows. After mapping predicted abundance, we found no obvious correspondence in the regional patterns of the five species. Thus, no clearly defined areas exist within the upper midwestern United States where management plans can be developed for a whole suite of grassland birds. Instead, a larger, region-wide initiative setting different goals for different species is recommended.

Key words: abundance, Bobolink, Grasshopper Sparrow, Henslow's Sparrow, hierarchical model, Sedge Wren, Upland Sandpiper.

Predicción de la Abundancia Regional de Aves Raras de Pastizales Mediante un Modelo Espacial Jerárquico Basado en Conteos

Resumen. Las aves de pastizales forman uno de los grupos más amenazados de aves en Norte América. Desafortunadamente, se conoce poco acerca de la ubicación de las concentraciones regionales de estas aves, por lo que los esfuerzos regionales o estatales de conservación podrían estar siendo aplicados inadecuadamente, reduciendo su efectividad. En este estudio empleamos un modelo espacial jerárquico basado en conteos y ajustado mediante métodos de cadenas de Markov Monte Carlo para identificar las covariables ambientales asociadas con la abundancia de cinco especies de aves de pastizales (*Dolichonyx oryzivorus*, *Ammodramus savannarum*, *A. henslowii*, *Cistothorus platensis* y *Bartramia longicauda*) en la parte alta del medio oeste de los Estados Unidos. Los métodos de cadenas de Markov Monte Carlo son adecuados para este propósito pues tienen la habilidad de incorporar efectos asociados con conteos autocorrelacionados y efectos no deseados asociados con los años y los observadores. Además, los modelos resultantes pueden emplearse para mapear predicciones sobre la abundancia a la escala de paisaje. Las covariables ambientales fueron derivadas a partir de cinco grupos de variables: composición del paisaje, configuración del paisaje, heterogeneidad y fisonomía del terreno, clima e influencia humana. Los modelos finales se ajustaron estrechamente a nuestras expectativas planteadas *a priori*. Las especies *D. oryzivorus* y *A. henslowii* fueron bastante sensibles al área de los parches de pastizal. Todas las especies excepto *A. henslowii* presentaron relaciones negativas significativas con la composición del bosque, a menudo

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a varias escalas espaciales. El clima resultó ser importante para todas las especies y fue el factor que más fuertemente influenció la abundancia de *A. savannarum*. Luego de mapear las abundancias predichas, no encontramos correspondencia en los patrones regionales de las cinco especies. Por lo tanto, no existen áreas claramente definidas en la parte alta del medio oeste de los Estados Unidos en donde puedan desarrollarse planes de manejo para todo un conjunto de aves de pastizales. En cambio, se recomienda emprender una iniciativa mayor a nivel regional en la que se proponga alcanzar diferentes metas para las distintas especies.

INTRODUCTION

Grassland birds in the upper midwestern United States have exhibited pronounced declines in the last three decades (Knopf 1994, Herkert 1995, Peterjohn and Sauer 1999). Knutson et al. (2001) indicated no grassland bird species in the upper midwestern United States were increasing in abundance and most possessed prioritization scores indicative of high conservation importance. Concern over the status of grassland birds has elevated their priority for conservation (Rodenhouse et al. 1995, Sample and Mossman 1997). For instance, Rich et al. (2004) identified the Henslow's Sparrow (*Ammodramus henslowii*) as a species in need of immediate action for conservation and the Grasshopper Sparrow (*A. savannarum*) as in need of management in the Prairie Avifaunal Biome. The U.S. Fish and Wildlife Service (2004) considered the Upland Sandpiper (*Bartramia longicauda*), Sedge Wren (*Cistothorus platensis*), Grasshopper Sparrow, and Henslow's Sparrow to be Birds of National Conservation Concern, and the Bobolink (*Dolichonyx oryzivorus*) a Bird of Regional Conservation Concern for the region encompassing the upper midwestern United States.

Unfortunately, there is a paucity of data regarding the geographic patterns of grassland bird abundance in the upper midwestern United States, and as a consequence the application of conservation measures are often either constrained to federal lands or inconsistently applied regionally (Gerard 1995, Weber et al. 2002). Since federal lands only comprise ~1% of all lands in the upper midwestern United States, effective conservation of rare birds must address populations on nonfederal lands and must occur in areas where the effect of such conservation will be greatest (Wells and Rosenburg 1999, Thogmartin et al. 2004a). In light of this need, we modeled and mapped the predicted abundance of five grassland birds in the upper midwestern United States: Upland Sandpiper, Sedge Wren, Grasshopper Sparrow, Henslow's Sparrow, and Bobolink. While all of these five species are regarded as grassland obligates, their selection of grassland types varies. For instance, Upland Sandpipers require short grass environs, whereas Henslow's Sparrows and Sedge Wrens select taller, denser grasslands; and whereas Henslow's Sparrows do not use grassland until 2–3 years after a fire, Bobolinks, Grasshopper Sparrows, and Upland Sandpipers favor recently burned prairies (Herkert 1994a, Johnson et al. 2004).

We used data from the Breeding Bird Survey to model and map predicted abundance. Counts from surveys of this sort are often spatially correlated because of population-level effects (e.g., dispersal) and underlying environmental gradients that are also autocorrelated. In our particular example, bird counts were similar to each other to varying degrees because of temporal and spatial correlation and correlated observational error (Link and Sauer 2002, Thogmartin et al. 2004a), each of which created a level of correlated structure among survey counts. We used a hierarchical modeling approach that can accommodate this potential for autocorrelation to properly map predicted abundance. Our 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. This approach was hierarchical because multiple parameters in the model were related in a multilevel manner (i.e., a joint probability model for these interrelated parameters reflected the dependence among them; Gelman et al. 1995). Secondly, we evaluated the association of environmental parameters to bird counts at multiple, nested, spatial scales (Scott et al. 2002 and references therein, Lawler and Edwards 2006). Spatial scale is an integration of extent and resolution (grain). Most often, multiscale studies of avian-habitat asso-

ciations assess varying spatial extents; varying spatial resolution is assessed less often. Using our multiscale approach, we evaluated bird-habitat associations at three logarithmically related, nested, spatial extents representing spatial scales of ecological processes influencing avian population dynamics on the breeding grounds.

Hierarchical statistical models are applicable to modeling data from complex surveys in which data are collected from a clustered or multilevel sample design. In the example we describe, our approach accommodates known clustering, or correlation, among survey locations, observers, and years. Counts from an area are expected to be similar from one year to the next (temporal correlation), and counts in any one area are expected to be more similar to counts from neighboring areas than those from distant areas (spatial correlation). Another level in this complex hierarchy is that observers perceive bird songs differently, influencing the composition and number of birds they record. This hierarchy of observer-route-year affects the properties of the estimator used; for example, the variance of mean bird counts is different when counts are drawn as clustered samples (e.g., when routes are sampled over time) than when counts are selected by simple random sampling from a population. Failure to accommodate variation expressed over these multiple levels can result in improperly assessed relationships between variables and the response of interest (Bryk and Raudenbush 1992, Moerbeek et al. 2003).

METHODS

STUDY AREA AND MODEL DATA

We modeled avian abundance for populations occurring in the Prairie Hardwood Transition Bird Conservation Region (U.S. NABCI Committee 2000). The Prairie Hardwood Transition occupies 230 111 km^2, stretching from central Minnesota through centraland southern Wisconsin and Michigan, including small sections of northeastern Iowa and northern Illinois and Indiana; Lake Michigan bisects the region. The predominant land uses and land covers in this region are row crop agriculture (36%), agricultural grassland (27%), and deciduous forest (21%; WET, unpubl. data). 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, transitions 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 (Host et al. 1995).

We used 1840 counts collected in the Prairie Hardwood Transition area by the North American Breeding Bird Survey (BBS) as the response variable in our models (Thogmartin et al. 2004a). Each BBS route contains 50 evenly spaced roadside survey locations (stops) at which an observer counts all birds seen or heard in a 3-min period. We used the sum of counts from the 50 stops in one year's survey as an index of abundance along the route for that year. The 1840 counts we used for model building were collected by 310 observers over 140 routes between 1981 and 2001. We used 1991, the midpoint of the time series, for scaling results so as to coincide with the 1990s National Land Cover Dataset (Vogelmann et al. 2001). An additional 376 counts were reserved for model evaluation; these included randomly selected counts collected between 1981 and 2001 and all counts collected in 2002.

MODELING APPROACH

We adopted a Bayesian framework for inference and prediction, implemented with Markov chain Monte Carlo (MCMC) methods (Gibbs sampling; Link et al. 2002). Markov chain Monte Carlo is a generic term describing a collection of methods for simulating from complex multivariate distributions, and, in particular, from distributions having probability density functions that are analytically intractable (Gelman et al. 1995, Diggle et al. 1998, Royle et al. 2002). The posterior distribution of this function (i.e., the distribution of the expected response given the data and prior information) can be obtained through simulation using Bayes' Theorem, yielding means, variances, and credibility intervals for the parameters of interest. Implementing this approach enables uncertainty to be incorporated

because parameters in both the systematic (e.g., predicted abundance) and stochastic (e.g., regression coefficients) components of the model are estimated. The effect of parameter uncertainty can be substantial, especially when modeling a spatially varying process such as avian abundance (Diggle et al. 1998, Banerjee et al. 2004). This is another reason the Bayesian framework is preferred over an alternative frequentist approach.

Link et al. (2002) provided a thorough synopsis of MCMC methods and Thogmartin et al. (2004a) outlined the particular methodology we used in modeling avian abundance. To briefly reiterate, we modeled avian counts as a loglinear function of explanatory variables describing habitat, spatial relatedness, and individual effects of observer and year. The model is an overdispersed Poisson regression with fixed and random effects. We conducted model fitting in WinBUGS (Spiegelhalter et al. 2003), a statistical package conducting Bayesian inference with MCMC.

Effects of observer and year were accommodated in the model in a way that minimized bias in the parameter estimates (Link and Sauer 2002). Adjustment for observer effects was twofold: observations from novice observers were deleted in their first year and a term was included in the model to accommodate an expected improvement in observer quality over time (Sauer et al. 1994, Kendall et al. 1996). Route-regression methods suggested all of the species we modeled with the exception of Sedge Wrens exhibited substantial declines in the Prairie Hardwood Transition between 1981 and 2001 (JRS, unpubl. data). A year effect was included to remove this linear trend, revealing a temporally unbiased estimate of counts.

Because we suspected spatially adjacent counts would be more similar to each other than those separated by large distances (Legendre 1993), we included a measure of potential correlation among BBS route counts. Spatial relatedness among route counts was included as a conditional autoregression (Best et al. 1999, Banerjee et al. 2004, Thogmartin et al. 2004a). Conditional autoregression assumes that the probability of observing a particular count on a given survey route depends on the values of the expected counts in the neighborhood around the survey route.

The final spatial conditional autoregressive model can thus be written as follows:

$$Z(s_i) = \mu(s_i) + \sum_{k=1}^{n} c_{ik}[(Z(s_k) - \mu(s_k)] + \omega_k(s) + \eta I(s) + \gamma_k(s) + \varepsilon(s_k)$$

where s_i are location coordinates for route i; $\mu(s_i)$ is the large-scale trend surface that may depend on covariates (independent environmental variables); c_{ik} are the spatial dependence parameters, and $i,k = 1,..., n$, where the dependence is symmetric and pair-wise dependence occurs only between neighboring survey locations; and $\varepsilon(s_k)$ are the independent error terms with zero mean and constant variance τ^2. Random observer and year effects are ηI (novice), ω (observer experience), and γ (year). Diffuse or noninformative priors and hyperpriors were assigned to each parameter to represent an initial null expectation of the variables on bird counts (Appendix A).

For each model, we iterated the Markov chain an additional 3000 iterations past convergence, which occurred at 15 000 iterations (Gilks et al. 1996). This chain creation was conducted five times to create replicate chains for the Gelman-Rubin diagnostic (Brooks and Gelman 1998, Spiegelhalter et al. 2003), which compares within-chain and between-chain variability.

Gelman et al. (1995) described a goodness-of-fit procedure using a posterior predictive check that compares parameter sets derived from the original data with parameter sets derived for a replicate data set. As in Link and Sauer (2002) and Thogmartin et al. (2004a), a replicate data set was generated following model specifications for each of the 15 000 sets of parameters (5×3000 iterations) sampled by simulation. The Gelman-Rubin diagnostic compares this replicate data set with the true data set. We also conducted a route-regression analysis (Geissler and Sauer 1990, Link and Sauer 1994) of data for the Prairie Hardwood Transition and plotted these results as a means of comparison against annual median abundance predicted from the hierarchical spatial count models.

We followed an information-theoretic approach to model building (Burnham and Anderson 2002) to identify relevant environmental covariates for consideration. We derived *a priori* models from published habitat associa-

tions of the five bird species (Martin and Gavin 1995, Vickery 1996, Herkert et al. 2001, 2002, Houston and Bowen 2001; Appendix B). Further, we tested associations between grassland birds and climate identified by Price (1995). Species experts reviewed each global *a priori* model. Some variables identified as important for consideration in our models (e.g., pasture and hay, small grains) were poorly mapped for the Prairie Hardwood Transition (Thogmartin et al. 2004b); in some cases, surrogates were derived (e.g., static wetness index for moist soil conditions; Appendix B).

Much of our knowledge of grassland bird-habitat associations is derived from studies conducted at a small spatial extent (i.e., that of a field), and few studies have identified important relationships at coarser scales. Thus, the forms of bird-habitat associations were unknown, though estimated effects were expected to be unimodal (for a species response to a gradient that is well within its niche boundaries) or monotonic (for a species response to a gradient that exceeds its niche boundaries). Interactions between variables were not considered unless suggested by previously published literature or by the opinion of a species expert. 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 approximately 800, 8000, and 80 000 ha, respectively. We standardized each environmental covariate by removing the mean and dividing by the standard deviation to increase the efficiency of the iteration process (Gilks and Roberts 1996) and to identify standardized model parameters.

Models were ranked according to the Deviance Information Criterion (DIC), where $DIC = \bar{D} + p_D$, which is the posterior mean of the deviance ($\bar{D}$) plus the effective number of parameters (p_D; Spiegelhalter et al. 2002). To assess the weight of models relative to each other in the best subset of models, DIC model weights were calculated as follows:

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum\limits_{i=1}^{R} \exp\left(-\frac{1}{2}\Delta_i\right)},$$

where Δ_i is the difference between DIC for model i and DIC for the best model. Model

averaging was conducted sensu Burnham and Anderson (2002).

We constrained inference and model averaging to only those models within five 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. We calculated the relative portion of the variance explained by each suite of variables to infer the relative contributions of environmental and spatial variables to explaining the variance in the response.

POST-HOC ANALYSES

Following an approach outlined in Thogmartin et al. (2004a), we supplemented our *a priori* models with variables identified through *post-hoc* exploration of various environmental variables within five suites. These suites of variables were landscape composition, landscape configuration, terrain heterogeneity and physiognomy, potential human disturbance, and mean climate conditions (Thogmartin et al. 2004a). The best potential landscape-scale variables for inclusion in the model were identified with a regression tree approach (De'ath and Fabricius 2000, O'Connor and Wagner 2004). These *post-hoc* variables were retained if the resulting model exhibited a reduction in DIC and the 95% Bayesian credibility intervals about the slope parameters did not include zero. The aim of this *post-hoc* exploration was to remove residual spatial autocorrelation structure in bird counts.

MAPPING OF PREDICTED ABUNDANCE

We mapped the statistical models by combining geographic information systems (ArcGIS 8.0 and 9.x, EnvironmentalSystems Research, Inc., Redlands, CA) grid layers of model variables based on their model-averaged slope coefficients. Because we standardized the environmental variables in fitting our models, we also standardized the environmental grid layers before multiplying them by their slope coefficients in the ArcGIS Spatial Analyst map calculator. These weighted grid layer were then summed, producing the final grid layer of predicted abundance. The mapping process is described more fully in Thogmartin et al. (2004b). Final map resolution was 1 ha.

TABLE 1.   Summary statistics for annual Breeding Bird Survey route counts collected 1981–2001 for five grassland bird species in the Prairie Hardwood Transition of the upper midwestern United States. Mean count is the mean number of the species observed from all routes. Count sum is the number of birds counted over the period. Zero counts is the sum of the routes in which the species was not observed. Nonzero mean is the mean count from only those routes in which the species was observed, and thus does not include the instances in which the species was not counted.

Species	Mean count	Variance	Count sum	Total zero counts (%)	Nonzero mean	Nonzero variance
Upland Sandpiper	0.4	2.0	803	1540 (84)	2.7	6.2
Sedge Wren	2.8	44.7	5149	1095 (60)	6.9	81.9
Grasshopper Sparrow	0.8	9.8	1410	1503 (82)	4.2	39.2
Henslow's Sparrow	0.1	0.6	218	1739 (95)	2.2	7.0
Bobolink	9.7	140.1	17 821	274 (15)	11.4	145.3

MODEL EVALUATION

We used Breeding Bird Survey data that were not used for model creation and point counts conducted on public lands to preliminarily assess the validity of the models and maps we developed. The point counts were conducted at 17 locations within the Prairie Hardwood Transition (Thogmartin et al. 2004a) and were available from the National Bird Point Count Database (Wimer et al. 2003). We buffered each point count location by 1.5 km, derived the mean count, and mapped the standardized difference between the predicted count and the observed count at the survey point. The buffer was set at 1.5 km because there is some concern that an area smaller than 10 km^2 is too fine a scale given errors within the National Land Cover Dataset 1992 (J. Hollister, University of Rhode Island, pers. comm.; C. Homer, U.S. Geological Survey Earth Resources Observation Systems Data Center, pers. comm.).

RESULTS

Of the five species we studied, Bobolinks were most commonly counted and Henslow's Sparrows were least commonly counted (Table 1). Distributions of all species counts were highly kurtotic, resulting in high premodeling overdispersion for each species. Models of abundance indicated a substantial influence of environmental variables for all species except Upland Sandpiper (which is described more fully below). Most species conformed to our *a priori* notions of their habitat associations, though there were exceptions.

Unlike the other four species, the null model for Upland Sandpipers was superior to all of the models with environmental covariates (Table 2). However, considerable model uncertainty existed, with four models within four DIC units of the best (null) model. The average model for Upland Sandpipers revealed influences of grassland patch size and forest composition at each of the three scales we studied (Table 3). Grassland patch size and forest composition were most influential at the intermediate scale. The contribution of sandy soil composition, in conjunction with grassland patch size, indicated a selection for drier, grassland sites. Because the null model was the best-performing model, the map of predicted abundance showed little effect of variation in environmental factors (not shown).

Five models of Sedge Wren abundance, including the null model, were relevant for purposes of inference (Table 2). Disjunct core area in wetlands, a *post-hoc* addition to the models, was the only variable occurring in each model (Table 3). Disjunct core area of wetlands was the median area of wetlands >100 m from the patch edge. The average model derived from the subset of best models was the model among the five species with the fewest environmental covariates ($k = 5$ environmental covariates). Like the other species, a climatic term, mean temperature in January, exhibited the greatest influence on abundance. This species was primarily influenced by environmental variables measured at the finest scale (800 ha). Mucky soils, a correlate of moist grasslands, were positively associated with abundance of this species. Sedge Wrens were predicted to occur in many hot spots of abundance throughout eastern and central Wisconsin, small parts of central Minnesota, and in a few locations in central Michigan (Fig. 1).

TABLE 2.   Parameter estimates for the best subset of models fitted to 1981–2001 Breeding Bird Survey route counts for five grassland bird species in the Prairie Hardwood Transition of the upper midwestern United States. The Null model, included for comparison, is in each case a model with observer, year, and potential spatial correlation, but without environmental explanatory variables. Scales of explanatory variables are 800 ha, 8000 ha, and ~80 000 ha, respectively. pD is the effective number of parameters, and is given by the posterior mean of the deviance minus the deviance of the posterior means. DIC is Deviance Information Criterion. See text for details. ΔDIC is the difference between the best model and the model of interest. w_i is the model weight, as described in the text. The evidence ratio is the model weight of the best model divided by the weight for the model of interest. Variables are described in Appendix B.

Best subset model	Explanatory variable$_{Scale}$	pD	DIC	ΔDIC	w_i	Evidence ratio
Upland Sandpiper						
Null		230.41	1797.35	0.00	0.38	1.00
1	Grass patch size$_{80\ 000}$, Forest$_{80\ 000}$, Spring temperature	216.98	1798.01	0.66	0.28	1.39
2	Grass patch size$_{8000}$, Forest$_{8000}$, Sandy soil$_{8000}$, Spring temperature	215.97	1798.89	1.54	0.18	2.16
3	Grass patch size$_{8000}$, Forest$_{80\ 000}$, Sandy soil$_{8000}$, CV Summer precipitation, Spring temperature	217.41	1799.80	2.45	0.11	3.40
4	Grass patch size$_{800}$, Forest$_{800}$, CV summer precipitation, Spring temperature	217.70	1801.33	3.98	0.05	7.32
Sedge Wren						
1	Forest$_{800}$, Mucky soils$_{800}$, Disjunct core area of wetlands$_{8000}$	581.08	4454.50	0.00	0.38	1.00
2	Forest$_{800}$, Mucky soils$_{800}$, Mean temperature in January, Disjunct core area of wetlands$_{8000}$	579.73	4454.98	0.48	0.30	1.27
3	Mucky soils$_{800}$, Disjunct core area of wetlands$_{8000}$	580.85	4456.10	1.60	0.17	2.23
4	Grass$_{800}$, Disjunct core area of wetlands$_{8000}$	578.91	4456.34	1.84	0.15	2.51
Null		581.02	4456.94	2.44	0.11	3.39
Grasshopper Sparrow						
1	Forest$_{800}$, Wetness$_{800}$, Temperature during the warmest quarter, Range in growing season temperature, Mean and Variation in summer precipitation, Mean and Variation in autumn precipitation	320.60	2024.16	0.00	0.93	1.00
2	Grass$_{800}$, Forest$_{800}$, Temperature during the warmest quarter, Wetness$_{800}$, Mean autumn precipitation	324.81	2029.35	5.19	0.07	13.40
Null		328.32	2037.78	13.62	0.00	906.87
Henslow's Sparrow						
1	Grass patch size$_{8000}$, Forest$_{8000}$, Temperature during the driest season, Warm season precipitation, CV annual precipitation, Simpson's diversity, Grass-forest interaction	149.06	729.84	0.00	0.93	1.00

TABLE 2.   Continued.

Best subset model	Explanatory variable$_{Scale}$	pD	DIC	ΔDIC	w_i	Evidence ratio
2	Grass patch size$_{8000}$, Forest$_{8000}$, Grass-forest interaction	147.87	735.00	5.16	0.07	13.22
Null		188.06	762.61	32.77	0.00	1.3×10^6
Bobolink						
1	Grassland patch size$_{800}$, Forest$_{800}$, Temperature during coldest quarter, Grass-forest interaction, Grass patch shape$_{8000}$	1074.67	9153.83	0.00	0.33	1.00
2	Grassland patch size$_{8000}$, Forest$_{8000}$, Temperature during coldest quarter, Grass-forest interaction, Grass patch contiguity$_{8000}$	1077.25	9154.13	0.30	0.28	1.16
3	Grassland patch size$_{800}$, Forest$_{80\,000}$, Temperature during coldest quarter, Grass-forest interaction, Grass patch shape$_{8000}$, Grass patch contiguity$_{8000}$	1076.67	9154.40	0.57	0.25	1.33
4	Forest$_{8000}$, Temperature during the coldest quarter, CV precipitation, Grass patch contiguity$_{8000}$	1077.68	9155.52	1.69	0.14	2.33
Null		1520.29	9621.41	467.58	0.0	3.4×10^{101}

Virtually no uncertainty existed in the best model for Grasshopper Sparrow abundance, with the best model possessing a model weight of 93% (Table 2). Grasshopper Sparrows were predicted to be most abundant in southeastern Wisconsin and southern Michigan. Concentrations of abundance occurred in southern Michigan, just east of Lake Michigan, in a line from Three Oaks to Holland (Fig. 1). The Grasshopper Sparrow was the only species of the five we studied that did not retain a grassland covariate in the average model. The best model with the proportion of land cover in grassland possessed a model weight of only 7%. After the inclusion of environmental covariates, the residual spatial correlation in route counts was insufficient to be described with conditional autoregression. Grasshopper Sparrow abundance was most influenced by climatic variables rather than environmental variables, potentially obviating the need to describe large-scale correlations in abundance (Table 3).

The best subset of models for Henslow's Sparrows also showed virtually no model uncertainty, with the best model possessing a model weight of 93% (Table 2). *Post hoc* addition of climatic variables and the land cover type diversity term resulted in significant improvement over a reduced model containing only grassland patch size, the proportion of the landscape in forest, and their interaction (Table 3). Henslow's Sparrow abundance was closely associated with the interaction of grass patch size with the proportion of the landscape in forest, with higher abundances predicted in grasslands surrounded by forest; variation in precipitation was also important for Henslow's Sparrows. Henslow's Sparrows were rare everywhere, but predicted to occur most abundantly (0.04 birds expected per route) in southwestern Wisconsin (Fig. 1).

Four models of Bobolink abundance were superior to the null model (Table 2), however, considerable model uncertainty occurred because of the highly interrelated nature of the variables in each model. The best-performing models suggested Bobolink abundance was sensitive to grassland patch size at fine (800 ha) and intermediate (8000 ha) landscape scales. The average model suggested a positive association with larger grassland patches at the coarser scale but a marginally negative association at the finer scale (Table 3). A significant interaction between grassland patch size and

TABLE 3. Median and lower (LCL) and upper (UCL) credibility limits of the posterior distribution of standardized explanatory variable slopes for an average model derived from the Kullback-Leibler best subset of models for five grassland bird species in the Prairie Hardwood Transition of the upper midwestern United States. The explanatory variables are ordered by importance, which is the sum of the model weights for those models in which the variable of interest occurred. Variables are described in Appendix B.

| Species Explanatory variable	Scale (ha)	Median	95% CL	Variable importance
Upland Sandpiper				
Spatial conditional autoregression		−3.26	−3.27, −3.26	1.00
30-yr mean spring temperature (°C)		−0.97	−0.98, −0.96	0.62
Total forest (%)	80 000	−0.88	−0.90, −0.87	0.39
Area-weighted mean grassland patch size (ha)	8000	0.71	0.70, 0.72	0.29
Sandy soil (%)	8000	0.55	0.54, 0.56	0.29
Area-weighted mean grassland patch size (ha)	80 000	0.58	0.57, 0.59	0.28
Total forest (%)	8000	−0.97	−0.98, −0.96	0.18
Coefficient of variation in mean spring precipitation		0.41	0.40, 0.42	0.17
Total forest (%)	800	−0.58	−0.60, −0.57	0.05
Area-weighted mean grassland patch size (ha)	800	0.27	0.26, 0.28	0.05
Sedge Wren				
Spatial conditional autoregression		−1.22	−1.22, −1.21	1.00
Mucky soils (%)	800	0.39	0.38, 0.39	0.90
Disjunct core area of wetlands	8000	0.36	0.36, 0.37	0.90
Total forest (%)	800	−0.46	−0.46, −0.45	0.61
Mean temperature in January		−0.93	−0.95, −0.90	0.27
Grassland (%)	800	0.53	0.53, 0.54	0.14
Grasshopper Sparrow				
Total forest (%)	800	−1.16	−1.18, −1.14	1.00
Static wetness index	800	−1.05	−1.06, −1.03	1.00
Temperature during the warmest quarter		2.87	2.82, 2.92	1.00
Range in growing season temperature		−1.24	−1.27, −1.21	1.00
Mean summer precipitation		−1.83	−1.85, −1.80	1.00
Variation in summer precipitation		−1.18	−1.20, −1.16	1.00
Mean autumn precipitation		1.27	1.25, 1.29	1.00
Variation in autumn in precipitation		1.54	1.51, 1.58	1.00
Intercept		−4.25	−4.27, −4.23	1.00
Henslow's Sparrow				
Area-weighted grass patch size (ha)	8000	0.70	0.69, 0.71	1.00
Total forest (%)	8000	0.13	0.11, 0.14	1.00
Total Forest (%) * Grass patch size	8000	0.55	0.54, 0.56	1.00
Spatial conditional autoregression		−5.39	−5.42, −5.36	1.00
Mean temperature during the driest season		−1.13	−1.18, −1.09	0.93
Total warm season precipitation		0.25	0.23, 0.28	0.93
Coefficient of variation in annual precipitation		−1.39	−1.44, −1.34	0.93
Modified Simpson's diversity index	800	0.23	0.21, 0.24	0.93
Bobolink				
Temperature during the coldest quarter		−0.88	−0.89, −0.86	1.00
Spatial conditional autoregression		1.18	1.17, 1.18	1.00
Total Forest (%) * Grass patch size	8000	0.29	0.29, 0.30	0.86
Coefficient of variation in grass patch contiguity	8000	−0.39	−0.39, −0.38	0.67
Area-weighted grass patch size (ha)	800	−0.02	−0.02, −0.01	0.58
Total forest (%)	8000	−0.54	−0.54, −0.53	0.42
Total forest (%)	800	−0.54	−0.55, −0.54	0.33
Area-weighted grass patch size (ha)	8000	0.32	0.32, 0.33	0.28
Total forest (%)	80 000	−0.37	−0.38, −0.36	0.25
Coefficient of variation in annual precipitation		−1.15	−1.17, −1.12	0.14
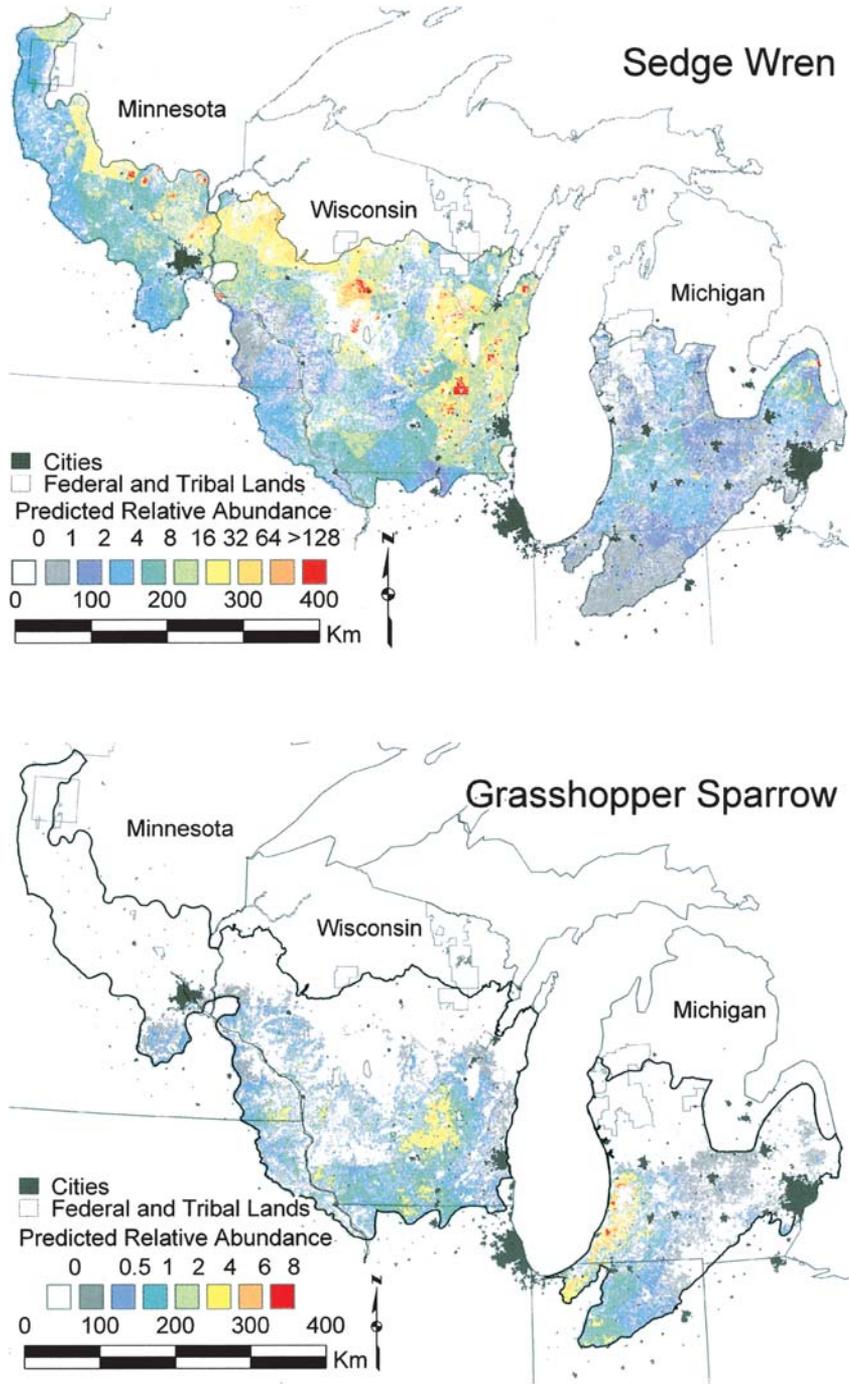
FIGURE 1.   Maps of predicted relative abundance for four grassland bird species in the Prairie Hardwood
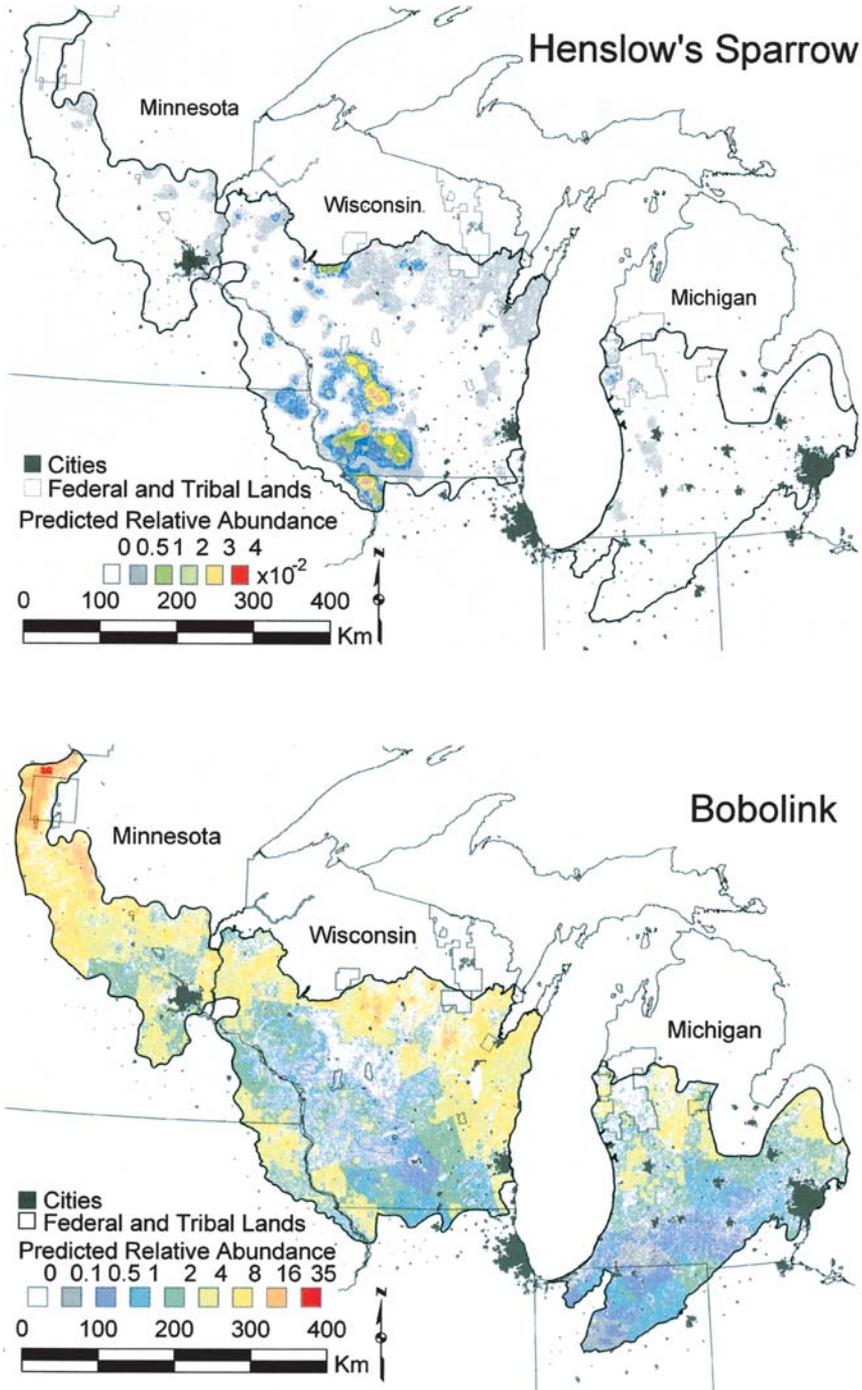
FIGURE 1.   (Continued.) Transition of the upper midwestern United States. Note the different abundance scales for each species.

TABLE 4.   Relative proportional contributions of environmental determinants to explaining the variance of rare bird abundances in the Prairie Hardwood Transition of the upper midwestern United States. Human disturbance (e.g., road density, population density) was not identified as an important contributor to explained variance in counts for any of the species.

Species	Land cover configuration	Land cover composition	Climate	Terrain heterogeneity and geomorphology	Spatial structure
Upland Sandpiper	0.17	0.27	0.15	0.06	0.36
Sedge Wren	0.09	0.26	0.24	0.10	0.31
Grasshopper Sparrow	0.00	0.11	0.90	0.00	0.00
Henslow's Sparrow	0.12	0.04	0.28	0.00	0.55
Bobolink	0.20	0.27	0.34	0.00	0.20

the proportion of the landscape in forest indicated that Bobolinks were more abundant in grasslands surrounded by forest when grassland patches were large. Abundance of Bobolinks was strongly associated with variation in annual precipitation, surpassed in strength of association only by the residual spatial correlation in route counts, but variation in annual precipitation occurred in only one of the top four models. In comparison, spatial structure (i.e., spatial correlation in route counts) was included in all four top models and the grass patch*forest composition interaction term occurred in three of these models. Mapping of the average model suggested Bobolinks occur most abundantly in western portions of the Prairie Hardwood Transition, in central Minnesota, with decreasing abundance moving east (Fig. 1).

For the five species we examined, we found land-cover composition provided the greatest contribution to the explained variance in counts for two of the five species (Sedge Wren and Upland Sandpiper), climate provided the greatest contribution for two species (Bobolink and Grasshopper Sparrow), and residual spatial correlation between route counts was most important for one species (Henslow's Sparrow; Table 4). Relative to the combined effects of land-cover configuration and composition, climate was most important only for Grasshopper Sparrows.

The Breeding Bird Survey data withheld from model construction and used to test our models suggested decent fit for Sedge Wren (Spearman's rank correlation: $r_s = 0.42$), Upland Sandpiper ($r_s = 0.19$), Grasshopper Sparrow ($r_s = 0.38$), and Bobolink ($r_s = 0.29$; Fig. 2). Considerable variation existed around the mean observed count for each species,

which was anticipated given that the mean expectation was an integration of counts across years and did not accommodate the random effects associated with observer, year, and route in the test data. Too little variation existed in the expected counts for Henslow's Sparrows (not shown), so it is unclear how well the models performed for this species.

Point counts provided additional inference concerning model performance, suggesting considerable areas of correspondence for each of the five grassland bird species (Fig. 3). The map for Bobolinks appeared to overpredict numbers for central Minnesota (with expected numbers higher than counts) and underpredict numbers for central Wisconsin. The map for Grasshopper Sparrows had the reverse pattern, with expected abundance lower than observed abundance for the western portion of the Prairie Hardwood Transition and expected abundance higher than observed abundance for the central portion. The map for Henslow's Sparrows appeared to underpredict abundance at one location along the Wisconsin-Minnesota border and overpredict abundance along the Iowa-Minnesota border; for this species, the effects may be because of study-specific point count methodology (e.g., differences in time at point counts) rather than model-specific predictions. No apparent geographic pattern existed for the other two species, but it appeared that compared with point count data the model consistently underpredicted abundance for Sedge Wrens. The main difficulty in comparing the point count data with our predicted abundance maps was that the point count data set was relatively sparse compared to 20 years of BBS data, was not randomly distributed over the ecoregion, and contained all of the spatial, observer, and temporal bias expected from any
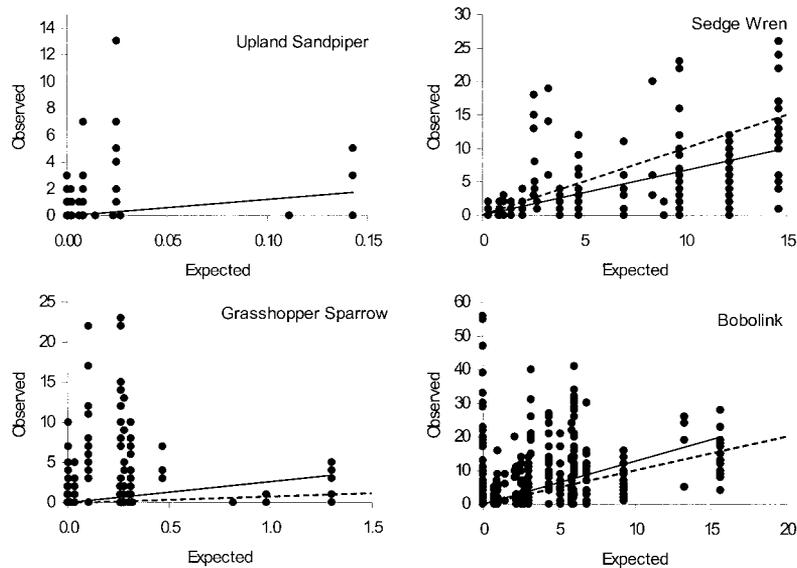
FIGURE 2.   Observed Breeding Bird Survey counts withheld from model construction for four grassland birds in the Prairie Hardwood Transition of the upper midwestern United States fitted to expected countswith least-squares regression (solid line). The dotted line is the line of one-to-one correspondence. Sample size was $n = 376$ for all species, except Sedge Wren ($n = 356$, 20 counts from Horicon National Wildlife Refuge were removed as outliers; observed abundance at this location was ~1/3 of the expected abundance).

similar data set. However, we retained this comparison because it was the only source of independent data available and provided a sense of spatial fit for the models.

DISCUSSION

We quantified and mapped relationships between the abundances of five grassland birds and their landscape-level environmental associations. Given that most of the models conformed to our *a priori* expectations, which were borne from fine-scale studies of these species, we can be fairly confident our results captured relevant ecological processes structuring regional abundances of these birds. However, for all of these species, a moderate degree of uncertainty remains. For three of the five species, considerable model uncertainty existed because of ambiguity in either the variables or in the spatial scale at which these variables were measured or both. Further, for four of the five species we studied, extensive structuring related to the spatial autocorrelation term remained unaccounted for by relevant ecological factors, suggesting that regional-level factors contributing to patterns in bird abundance were not identified. Ideally, our *post-hoc* exploration

would have removed the spatial autocorrelation term.

We suggest three sources of residual spatial structure. First, we may have incorrectly identified the appropriate scales at which to assess the relationship between grassland bird abundance and environmental factors (Thogmartin et al. 2004a). Despite our attempt to bound the relevant biological processes within three logarithmically related spatial extents, the environmental covariates we examined may be important to grassland birds at either finer or coarser scales. This is certainly true at spatial scales finer than that which we examined; effects at too fine a scale, however, would likely not translate to correlation in regional abundance unless they themselves were correlated and observable at coarser scales, and thus within the perspective of our study. Second, errors in the classification of remotely sensed data (Thogmartin et al. 2004b) would preclude finding close associations between the abundance of a species and environmental variables even if these relationships existed. Third, behavioral factors may have created this correlation in regional abundance. For instance, effects of natal philopatry may preclude
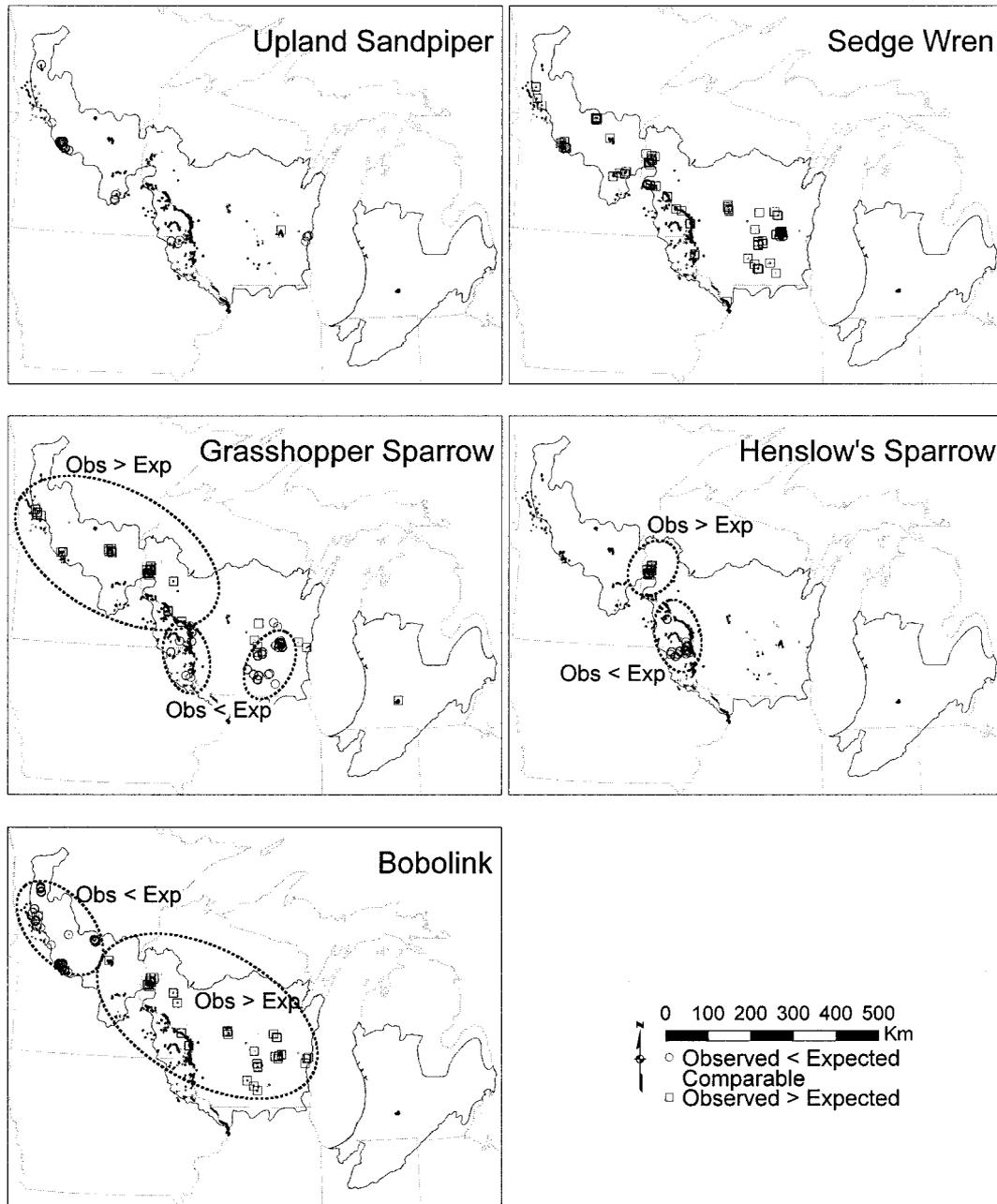
FIGURE 3. Standardized residuals resulting from comparison of hierarchical spatial count model predictions (expected) of grassland bird abundance with point counts (observed) collected on 17 federal lands in the Prairie Hardwood Transition of the upper midwestern United States. Standardized residuals >|2| are shown as circles and squares. Dashed ellipses encircle areas of consistent under- or overcounting.

occupancy of otherwise suitable habitat or dictate occurrence in what is otherwise marginal habitat, although available evidence seems to argue against this (Weatherhead and Forbes 1994). Conspecific (Stamps 1988, Ward and Schlossberg 2004) or heterospecific attraction (Mönkkönen et al. 1997, Forsman et al. 1998) among grassland birds may cause patterns in

abundance that are unexplained by effects of the environment alone. However, neither attraction has been demonstrated for the grassland species we studied. Despite these uncertainties in variables and scales, preliminary evaluation of these models against independent data suggested robust findings with regard to patterns of abundance.

Few *a priori* land-cover variables were associated with Upland Sandpiper abundance and our *post-hoc* exploration did not postulate any environmental associations. In general, Upland Sandpipers are most numerous on large blocks of idle or lightly grazed short grassland (Houston and Bowen 2001). Our results concur, suggesting an association with larger grassland patches at all the scales we examined. Similar to Bobolinks and Sedge Wrens, Upland Sandpipers were negatively associated with the proportion of the landscape in forest. Given the prominence of the null model among the subset of models used for inference, the average model should be interpreted with circumspection. The effect of the null model on the average model was to act as a grand mean, adjusted for observer, year, and autocorrelation effects, adjusted by a weight equal to the null model weight ($w_i = 0.38$). This weighting of the average model toward the contribution of the null model dampened the influence of the land-cover variables, leading to a map with little variation between areas of high and low abundance of sandpipers (this also occurred to a lesser extent with Sedge Wrens).

We did not find Sedge Wrens to be sensitive to grassland patch area, concurring with Herkert (1994b) but contrary to Johnson and Igl (2001). Breeding habitat of Sedge Wrens includes tall sedges and grasses in wet meadows, and sphagnum bogs, and on the margins of ponds and marshes, in the absence of woody vegetation (Sample 1989, Herkert et al. 2001). This fine-scale selection for moist grass environs and avoidance of woody vegetation is evident within our average model, as the proportions of the landscape in mucky soils and grassland were positively related, and the proportion of the landscape in forest was negatively related, to Sedge Wren abundance. Sedge Wren association with disjunct core area of wetlands suggests Sedge Wrens are more abundant in landscapes in which the number

and size of wetland patches is high (disjunct core area was highly correlated with total wetland area, $r = 0.7$) and is consistent with results from the Prairie Pothole region in Iowa (Fairbairn and Dinsmore 2001).

Models of Grasshopper Sparrow abundance that included the proportion of the landscape in grassland or grassland patch area were not among the best subset of models, contrary to many reports of area-sensitivity in this species (Herkert 1994b, Vickery et al. 1994, Bollinger 1995, Johnson and Igl 2001, Herkert et al. 2003). At the field scale, Grasshopper Sparrows in the midwestern United States typically select relatively short and sparse vegetation (Wiens 1969). At the landscape level, Ribic and Sample (2001) indicated Grasshopper Sparrows were positively associated with dry grasslands situated in diverse landscapes and negatively associated with distance from hedgerows, with highest abundances occurring in pasture, prairie, alfalfa, and fallow fields (Best et al. 1995). We may have been unable to identify relationships between Grasshopper Sparrow abundance and grassland because our data precluded us from distinguishing among these grassland types (Thogmartin et al. 2004b). However, because the proportion of the landscape in forest was negatively associated with the combined cover of row crops and grasslands ($r = -0.64$), the negative relationship of Grasshopper Sparrows to forest composition suggests Grasshopper Sparrows were more abundant in landscapes with a greater herbaceous content. That this combined effect of row crop and grassland did not reveal itself in the final subset of models suggests some effect of forest cover over and above the effect of herbaceous land cover. Saab (1999) suggested the composition and configuration of the matrix surrounding habitat patches may have a greater influence on some birds than the habitat within patches, presumably because of an overriding influence on habitat quality by the surrounding matrix. Predation and brood parasitism are two mechanisms potentially allowing the surrounding matrix to exert an overriding influence on the habitat patch, and rates of predation and brood parasitism on Grasshopper Sparrow nests are higher near woodlands and brush fields because of increased exposure to predators and Brown-headed Cowbirds (*Molothrus ater*, Johnson

and Temple 1990, Vickery 1996, Herkert et al. 2003).

Area-sensitivity of Henslow's Sparrows is a common finding (Burhans 2002, Herkert et al. 2002). However, we predicted this species to occur most abundantly in landscapes of large grassland patches interspersed with forest, as opposed to alternative matrix land covers such as agriculture. This finding is seemingly contrary to results of field-level studies (Sample 1989, O'Leary and Nyberg 2000), which have suggested Henslow's Sparrows avoid grassland habitat adjacent to or containing an abundance of trees. Unlike the other four species, we found Henslow's Sparrows were positively associated with the proportion of the landscape in forest, albeit at a strength 5.6 times lower than their association with grassland patch size. This apparent contradiction between field-level studies and our landscape-level assessment indicates habitat relationships do not necessarily translate linearly between spatial scales (Wiens et al. 1987). The positive association with forest suggested by the models could be a result of the types of grasslands found in landscapes with more forest. At least in southwestern Wisconsin, areas with more forest tend to have greater topographical relief, less agriculture, and more idle and Conservation Reserve Program grasslands (L. Murray, University of Wisconsin-Madison, pers. comm.).

Numerous studies of Bobolinks have indicated area-sensitivity for this species (Herkert 1994b, Vickery et al. 1994, Bollinger 1995, Johnson and Igl 2001, Fletcher and Koford 2003), including this one. In their study of grassland birds in southwestern Wisconsin, Ribic and Sample (2001) indicated Bobolink densities were solely influenced by landscape-level, rather than field-level, habitat factors. They found that Bobolink densities were highest in landscapes with lower cover-type diversity, lower forest area, and fewer forest patches; the low-diversity landscapes where Bobolinks were most abundant were characterized by large amounts of hay and grassland. Similarly, we found Bobolink abundance negatively associated with forest cover. Further, we found area-sensitivity in grassland patch size to be mediated by the proportion of the landscape in forest. Helzer (1996) and Fletcher and Koford (2003) reported similar findings, demonstrating avoidance of woody edges by Bobolinks.

Compared with the large number of studies of associations between birds and land-cover types (Repasky 1991, Price 1995, 2000a, 2000b, Lloyd and Palmer 1998, Venier et al. 1999), only a few studies have examined relationships between climate and bird occurrence, distribution, and abundance at regional scales. Our results are largely in agreement with associations first identified by Price (1995) for birds in the Great Plains of the United States. O'Connor et al. (1999) found climate of greater importance than agricultural variables for Bobolinks, but not for Grasshopper Sparrows and Upland Sandpipers. We found similar results, with the relative proportional contribution of climate compared to land-cover composition greater for Bobolinks and smaller for Upland Sandpipers; our results for Grasshopper Sparrows differed, however, in that we predicted a much greater contribution from climate than land-cover composition at the scales we examined. O'Connor et al. (1999) reported equivocal results for Henslow's Sparrows, whereas we found climate contributed more to predicting abundance. Although some of the climatic effects reported by Price (1995), O'Connor et al. (1999), and this study are similar, marked differences indicate some degree of uncertainty in the proper identification of relevant climatic variables.

It is also unclear how climatic variables influence bird abundance. Undoubtedly, the effects are both direct and indirect. Direct effects include climatic factors influencing the energetics of individual birds (Root 1988a, 1988b). Any direct effects on abundance must be related to climatic aspects during the breeding season when these birds are present in the upper midwestern United States. Indirect effects may include the influence of climate on food availability, cover or escape habitat, or predator and competitor distribution. Temperature during the coldest quarter (Bobolink) and mean temperature in January (Sedge Wren) must have indirect effects, as Bobolinks and Sedge Wrens overwinter in the pampas of South America and the coastal states of the southern United States, respectively (Martin and Gavin 1995, Herkert et al. 2001); the particular mechanisms responsible for this indirect correlation with climate are unknown for these species.

No obvious correspondence existed in the patterns of abundance among the five species

we studied, suggesting these species are not clustered in any particular portion of the Prairie Hardwood Transition. Thus, no clearly defined area within the region exists where management plans could be developed for rare grassland birds as a whole. Instead, a larger, region-wide initiative setting different goals for different species in each area is warranted (Wells and Rosenberg 1999, Knutson et al. 2001).

Our maps of predicted abundance identify concentrations of each species, providing a context for future monitoring and a focus for conservation efforts. Threats to these areas exist, especially conversion of grassland to row crops (O'Leary and Nyberg 2000). Native grasslands are among North America's most endangered ecosystems (Samson and Knopf 1994, Noss et al. 1995), with <0.1% of native prairie remaining in some areas. However, despite the threats to the habitat of these birds, regional conservation of grassland birds must occur within the overarching context of climate. Since climate is beyond the control of management, region-wide initiatives will be most successful in landscapes where climate is conducive to abundant populations of grassland birds. Given the presently limited occurrence of grassland, particularly native grassland, the strong associations of these species with mean climatic conditions places them at particular risk of local extirpation in the context of global climate change if new habitat is not made available. For instance, models of species occurrence relative to likely scenarios of climate change suggest extirpation of Bobolinks and Sedge Wrens from the Prairie Hardwood Transition within this century (Price 2000a, 2000b).

Our approach is a means by which to determine relationships between the abundances of species and environmental covariates, while controlling for a known hierarchy (observer-route-year) resulting from a complex survey design. Further, we demonstrate one method (model averaging) by which species-habitat relationships can integrate results over multiple spatial scales. Our data provide more insight into factors such as climate, spatial autocorrelation, and landscape characteristics dictating regional geographic patterning in bird abundance. Lastly, maps resulting from these species-habitat associations may be useful in focusing bird conservation efforts to specific landscapes within the region.

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APPENDIX A. Prior distributions 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 $(0.0, 1 \times 10^{-6})$[b]
Z	Spatial relatedness	Random	Flat (for the conditional autoregression-related intercept)[c] $\tau_{\text{Space}} \sim$ Gamma $(0.5, 0.0005)$
ω	Observer experience effect	Random	Normal $(0.0, \tau_{\text{Observer}})$ $\tau_{\text{Observer}} \sim$ Gamma $(0.001, 0.001)$
η	Novice observer effect	Fixed	Normal $(0.0, 1 \times 10^{-6})$
y	Year effect	Random	Normal $(0.0, \tau_{\text{Year}})$ $\tau_{\text{Year}} \sim$ Gamma $(0.001, 0.001)$
ε	Error	Random	Normal $(0.0, \tau_{\text{Noise}})$ $\tau_{\text{Noise}} \sim$ Gamma $(0.001, 0.001)$

[a] Precision rather than variance is described; precision = 1/variance.
[b] Essentially a flat or noninformative prior distribution.
[c] See Thomas et al. (2002) for details regarding flat prior relating to the conditional autoregression implemented in WinBUGS.

APPENDIX B.   Environmental covariates included in initial (global) models of habitat associations for five grassland birds in Bird Conservation Region 23, the Prairie Hardwood Transition. Variables considered *a priori* are denoted by species; the unattributed variables were evaluated *post hoc* for all five species.

Environmental suite	Environmental variables	Species
Landscape composition		
	Percent composition of landscape in forest	Henslow's Sparrow
	Cover type diversity	Sedge Wren, Henslow's Sparrow, Grasshopper Sparrow, Bobolink
	Percent composition of landscape in agriculture	Henslow's Sparrow, Bobolink
	Percent composition of landscape in emergent herbaceous wetlands	Sedge Wren
	Percent composition of landscape in forage crops (pasture or hay)	
	Percent composition of landscape in herbaceous land cover (grassland)	Sedge Wren, Henslow's Sparrow, Upland Sandpiper, Grasshopper Sparrow, Bobolink
	Percent composition of landscape in row crop	Bobolink
Landscape configuration		
	Mean patch size of grassland	Sedge Wren, Henslow's Sparrow, Upland Sandpiper, Grasshopper Sparrow, Bobolink
	Interspersion and juxtaposition or proximity index or connectedness of grassland	Grasshopper Sparrow
Terrain heterogeneity and physiognomy		
	Percent composition of the landscape described as moist, as indexed by a measure of wetness potential	Sedge Wren, Henslow's Sparrow, Upland Sandpiper, Grasshopper Sparrow, Bobolink
	Percent of landscape in sandy parent material	Upland Sandpiper
	Stream density	Henslow's Sparrow
Climate[a]		
	Range in annual precipitation	Henslow's Sparrow, Upland Sandpiper
	Mean temperature in January	Sedge Wren
	Minimum temperature during the coldest quarter of the year	Grasshopper Sparrow
	Mean temperature during the coldest quarter of the year	Bobolink
	Variability in temperature during the coldest quarter of the year	Bobolink
	Mean precipitation during the coldest quarter of the year	Upland Sandpiper
	Variability in mean spring precipitation	Bobolink
	Mean number of growing days	Sedge Wren
	Mean temperature during the wettest quarter of the year	Grasshopper Sparrow
	Mean spring precipitation	Bobolink
	Mean spring temperature	Upland Sandpiper
	Mean summer precipitation	Grasshopper Sparrow, Upland Sandpiper
	Variability in mean summer precipitation	Grasshopper Sparrow
	Maximum temperature during the hottest quarter of the year	Grasshopper Sparrow
	Mean temperature during the driest quarter of the year	Henslow's Sparrow
	Mean precipitation during the hottest quarter of the year	Henslow's Sparrow, Upland Sandpiper
	Variability in precipitation during the hottest quarter of the year	Upland Sandpiper

APPENDIX B.   Continued.

Environmental suite	Environmental variables	Species
	Variability in temperature during the hottest quarter of the year	Grasshopper Sparrow
	Mean autumn precipitation	Grasshopper Sparrow
	Variability in mean autumn precipitation	Grasshopper Sparrow
Other		
	Interaction of stream density and percent grassland	Sedge Wren
	Interaction with grass measures and percent composition of the landscape in forest	Henslow's Sparrow, Upland Sandpiper, Bobolink
	Interaction between percent grassland and percent moist land	Henslow's Sparrow, Bobolink
	Interaction of sandy parent material and percent landscape in grassland	Upland Sandpiper

[a] Climate variables constitute 30-year mean conditions (http://www.glfc.cfs.nrcan.gc.ca/landscape/climate_models_e.html [9 November 2005]).