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A HIERARCHICAL SPATIAL MODEL OF AVIAN ABUNDANCE WITH APPLICATION TO CERULEAN WARBLERS

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Abstract. Surveys collecting count data are the primary means by which abundance is indexed for birds. These counts are confounded, however, by nuisance effects including observer effects and spatial correlation between counts. Current methods poorly accommodate both observer and spatial effects because modeling these spatially autocorrelated counts within a hierarchical framework is not practical using standard statistical approaches. We propose a Bayesian approach to this problem and provide as an example of its implementation a spatial model of predicted abundance for the Cerulean Warbler (*Dendroica cerulea*) in the Prairie–Hardwood Transition of the upper midwestern United States. We used an overdispersed Poisson regression with fixed and random effects, fitted by Markov chain Monte Carlo methods. We used 21 years of North American Breeding Bird Survey counts as the response in a loglinear function of explanatory variables describing habitat, spatial relatedness, year effects, and observer effects. The model included a conditional autoregressive term representing potential correlation between adjacent route counts. Categories of explanatory habitat variables in the model included land cover composition and configuration, climate, terrain heterogeneity, and human influence. The inherent hierarchy in the model was from counts occurring, in part, as a function of observers within survey routes within years. We found that the percentage of forested wetlands, an index of wetness potential, and an interaction between mean annual precipitation and deciduous forest patch size best described Cerulean Warbler abundance. Based on a map of relative abundance derived from the posterior parameter estimates, we estimated that only 15% of the species' population occurred on federal land, necessitating active engagement of public landowners and state agencies in the conservation of the breeding habitat for this species. Models of this type can be applied to any data in which the response is counts, such as animal counts, activity (e.g., nest) counts, or species richness. The most noteworthy practical application of this spatial modeling approach is the ability to map relative species abundance. The functional relationships that we elucidated for the Cerulean Warbler provide a basis for the development of management programs and may serve to focus management and monitoring on areas and habitat variables important to Cerulean Warblers.

Key words: abundance mapping; Bayesian; CAR; Cerulean Warbler; conditional autoregression; count data; Dendroica cerulea; *Markov chain Monte Carlo; MCMC; North American Breeding Bird Survey; spatial autocorrelation.*

INTRODUCTION

Much of the focus of contemporary wildlife research is on monitoring populations over large areas (Pollock et al. 2002). The North American Breeding Bird Survey (hereafter NABBS; Peterjohn et al. 1996) is one of the most important, long-term monitoring efforts in avian conservation. Counts provided by the NABBS can be regarded as indices to population size and used to estimate spatial and temporal patterns in relative population abundance (Link and Sauer 1998). Link and Sauer (2002) provided a robust framework for the examination of temporal patterns in NABBS counts. There are, however, few analyses of spatial patterning in NABBS counts (Villard and Maurer 1996, Wikle 2002), largely because the proper accommodation of spatial and nuisance effects is not practical using standard statistical (i.e., frequentist) approaches.

We consider this modeling problem from a hierarchical perspective, modeling avian counts as Poisson, conditional on a spatially varying intensity process. Link and Sauer (2002) proposed an objective Bayesian hierarchical model for estimating trends in avian counts. Their generalized linear mixed model was of the form

$$Y_i \mid \mu_i \sim \mathrm{Poiss}[E_i \exp(u_i)]$$

where Y_i denoted avian counts, E_i the expected count

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in area i, after adjusting for possible confounding factors, and μ_i was the log-relative mean for area i. The μ_i may be replaced by a linear combination of covariate and random effects so as to explain patterns in model residuals.

When counts are expected to be spatially correlated (Koenig 1999, 2001, Lichstein et al. 2002*a*, *b*), geographical proximity may be specified a priori, forming a Bayesian smoothing model (Best et al. 1999). Thus,

$$\mu_i = x_i\beta + Z_i + \eta_i$$

where x_i denotes a vector of covariates associated with area i, β the vector of associated parameters, and Z_i and η_i are random effects (intercepts) associated with spatial similarity and excess heterogeneity (i.e., overdispersion, extra-Poisson variation), respectively. To model spatial similarity, Z_i, a conditional autoregressive (CAR) structure may be used (Besag et al. 1991, Cressie 1993, Best et al. 1999).

We present a hierarchical spatial model with environmental covariates for regional prediction of avian abundance from NABBS data, and fit the model to data with Markov chain Monte Carlo methods (MCMC). Hierarchical Bayesian models are well-suited to the analysis of complicated spatial problems (Wikle et al. 1998). The model that we present is a spatial version of the objective Bayesian hierarchical model presented by Link and Sauer (2002), with effects of spatial autocorrelation and environmental covariates included for modifying predicted mean counts. As an application of the procedure, we predicted avian counts for the Cerulean Warbler (*Dendroica cerulea*) from NABBS data for the Prairie–Hardwood Transition ecoregion in the upper midwestern United States.

The Cerulean Warbler is a small (8–10 g), Neotropical migratory songbird experiencing substantial declines in abundance throughout its range (Sauer et al. 2002). For this reason, it is considered a Species of Concern in the midwestern United States by the U.S. Fish and Wildlife Service (Salveter 2002). This species was once one of the most common forest birds in eastern North America (Hamel 2000*a*), but is now one of the rarest. Cerulean Warblers nest and raise their young in large tracts of deciduous hardwood forests consisting of tall, large-diameter trees over an open understory. Gaps in the forest canopy, or forest openings, are also considered important habitat components (Hamel 2000*a*). Cerulean Warblers nest almost exclusively in broad-leaved deciduous forests in uplands, wet bottomlands, and moist slopes of mountains. The capability to model and map abundances of high-priority species like the Cerulean Warbler over large regions is useful for managers; maps can be used to identify and prioritize habitats for conservation actions and future monitoring (Donovan et al. 2002). Results of the habitat modeling that we describe may also be used as a basis for evaluating threats to breeding habitats.

METHODS

Study area

The focus of our modeling effort was Bird Conservation Region 23 (hereafter BCR23), the Prairie–Hardwood Transition (Fig. 1).[4]

This BCR is virtually identical to Partners-in-Flight Physiographic Area 16 (Upper Great Lakes Plain).[5] The BCR23 occupies 230 111 km^2, 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. This region was chosen because of its diverse land uses, both historical and current. The predominant land uses/land covers in this region are row crop agriculture (36%), 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). BCR23, 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 from northwest to southeast, with climatic differences being most pronounced east of Lake Michigan.

Response data

There are 124 NABBS routes in BCR23, with an additional 80 routes within 50 km of the study area. We included these additional routes to minimize the influence of edge effects when predicting abundance at the edges of the region. Each NABBS route contains 50 evenly spaced 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 a year's route survey as an index of abundance along the route for that year. We used counts collected from 1981 to 2001 to coincide temporally with our land cover data, derived from satellite imagery taken in the late 1980s and early 1990s (Vogelmann et al. 2001), but unlike Link and Sauer (2002), we also included routes where Cerulean Warblers were never sighted because these routes are important for identifying the distributional boundary of this species. In total, we used 1840 counts in constructing the model; these route- and year-specific counts were produced by 310 observers over 140 routes between 1981 and 2001 (64 routes were withheld; see *Model evaluation*).

Hierarchical model

Model formulation.—To identify unbiased relationships between environmental covariates and avian abundance, we implemented a flat-prior Bayesian model (Gelman et al. 1995, Gilks et al. 1996, Spiegelhalter

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[4] ⟨http://library.fws.gov/Bird_Publications/na_birdconservation_regdescrip00.pdf⟩

[5] ⟨http://www.blm.gov/wildlife/plan/pl_16_10.pdf⟩

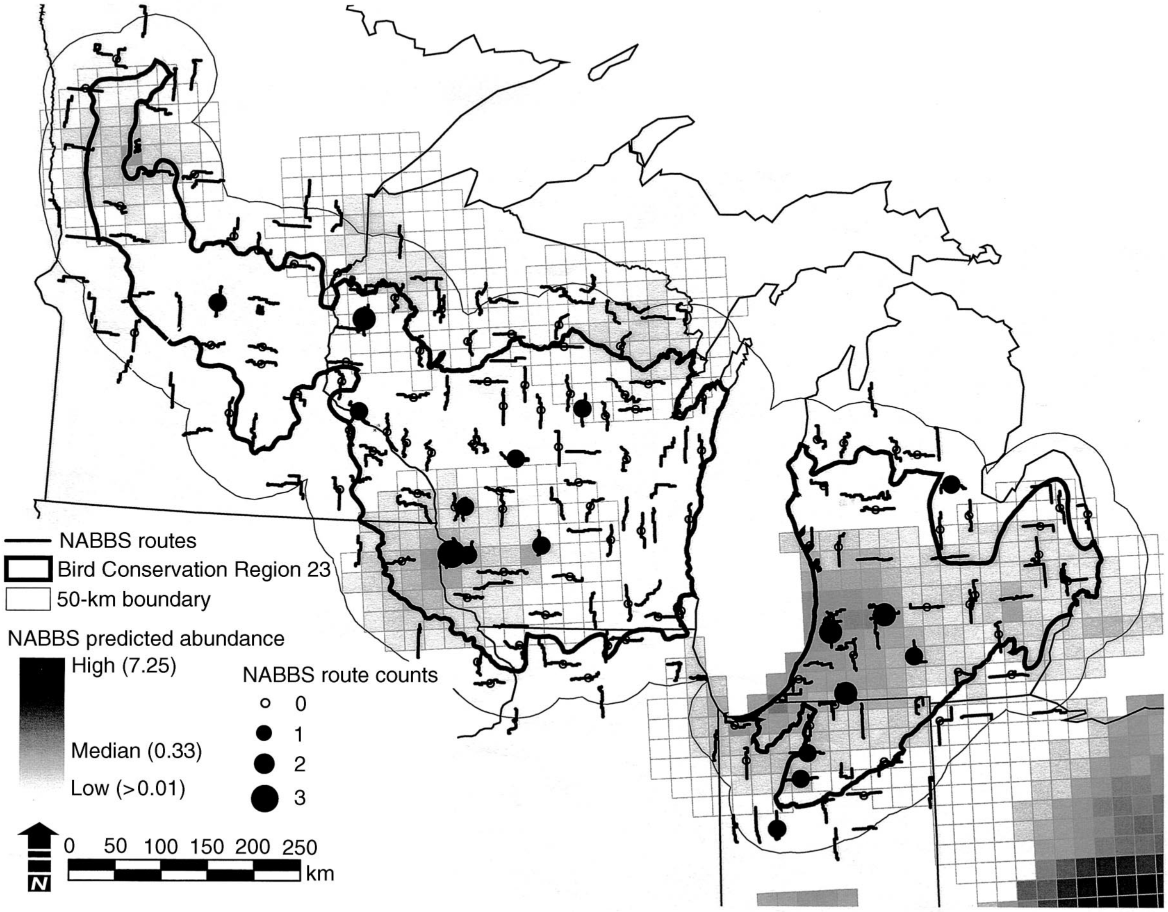

FIG. 1. North American Breeding Bird Survey (NABBS) counts from 1981 to 2001 and predicted Cerulean Warbler abundance across Bird Conservation Region 23 (BCR23), the Prairie–Hardwood Transition.

et al. 2000) accounting for space, environmental covariates, and count structure. Poisson models are a natural starting point for modeling count data because counts are ''discrete, positive valued, and [typically] exhibit strong mean-variance relationships'' (Royle et al. 2002:625). The general spatial Poisson model was specified as

$$\log[\lambda(s)] = \mu(s) + Z(s) + \eta(s)$$

where $Z(s)$ and $\eta(s)$ are random effects, and $\mu(s) = \Sigma_{j=1}^{p} \beta_j x_j(s)$, with $x_j(s)$ as spatially indexed covariates such as landscape descriptors, and β_j determining change in abundance (on the log scale) per unit change in covariate j (Royle et al. 2002). The index s is in geographic coordinates. The random effects $Z(s)$ and $\eta(s)$ control for spatial relatedness of counts and nuisance effects (i.e., variation between observer, novice, route, and year), respectively. Environmental covariates are treated as fixed effects, under the assumption that they are measured without error.

Spatial effects $[Z(s)]$ were included by applying a Gaussian conditional autoregressive (CAR) prior distribution on the spatial neighborhood of routes (Besag et al. 1991, Spiegelhalter et al. 2000). A neighborhood is defined by areas sharing a common boundary, a common definition in Bayesian mapping. Determination of the proper spatial neighborhood is critical for proper parameter estimation. We delineated a spatial neighborhood on an irregular lattice by tessellating the sample routes (Fig. 2), and from this neighborhood structure derived an adjacency matrix of first-order neighbors. The tessellation of routes was performed in ArcView 3.3 (ESRI 2002*a*). Neighborhood weights were set to 1 for areas sharing a common boundary and 0 otherwise (Besag et al. 1991). This weighting scheme assumes that the spatially structured random effect for a given area, relative to all other areas, has mean equal to the average of the random effects for the immediate neighboring areas and precision proportional to the number of neighboring areas. The resulting spatial model thus depends only on the neighborhood structure, and not, for instance, on the distance between areas.

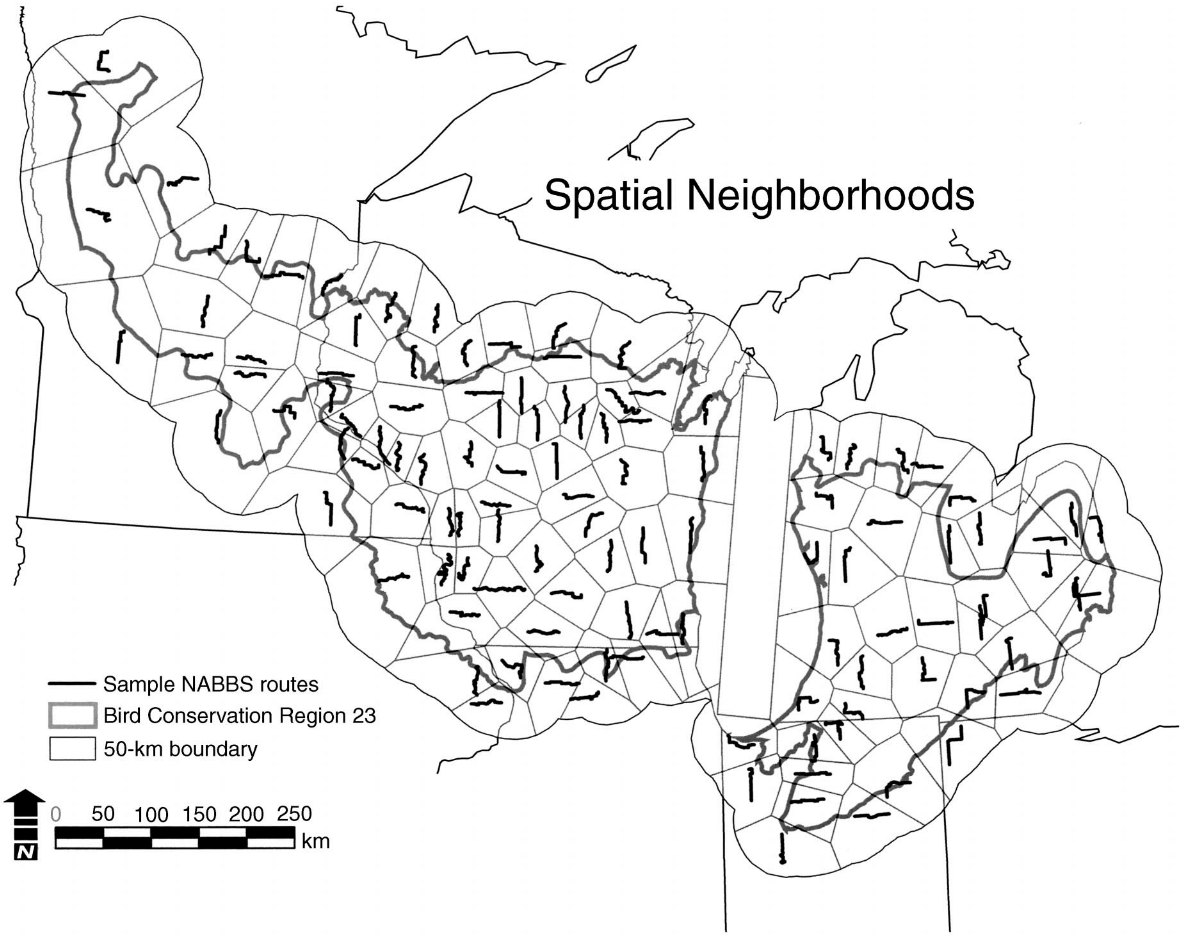

FIG. 2. Delineation, by tessellation, of the spatial neighbors of North American Breeding Bird Survey routes occurring within the Prairie–Hardwood Transition. Only nearest (first-order) neighbors were used in modeling the structure of spatial correlation in counts. Lake Michigan was assumed to act as a barrier.

To accommodate observer biases in $\eta(s)$, we included a random effect, ω, for observers and a random effect, $\eta\mathbf{I}$, to indicate the first year of service for an observer, where $\mathbf{I}$ is an indicator variable (0, 1) (Link and Sauer 2002). We also included a year effect (γ), while extra-Poisson dispersion was accounted for by overdispersion effects (ϵ_k). The final model then is

$$\log[\lambda(s)] = \sum_{k=1}^{p} \beta_k x_k(s) + Z_k(s) + \omega_k(s) + \eta\mathbf{I}(s) + \gamma_k(s) + \varepsilon_k$$

where k is year-specific counts indexed over space (s). In effect, the model is an overdispersed Poisson regression with fixed and random effects, with the counts modeled as a loglinear function of explanatory variables describing habitat, spatial relatedness, and nuisance effects.

Because there is no closed-form expression for the parameter estimates, the model must be fitted by iterative simulation (Royle et al. 2002). We conducted model fitting in WinBUGS 1.3 (Speigelhalter et al. 2000; Supplement), a statistical package conducting Bayesian inference with MCMC methods (Gibbs Sampling) (Link et al. 2002), following specific methodology described by Royle et al. (2002:630–631).

A necessary initial consideration in a Bayesian analysis is whether prior distributions are informed (Link et al. 2002). Given little empirical support for one distribution over another, we modeled with non-informative, or flat, priors (Link and Sauer 2002). Year (γ), observer (ω), and overdispersion (ϵ) effects were specified as having mean zero normal distributions (as in Link and Sauer 2002). The hyperparameters β, Z, and η were given diffuse (essentially flat) normal distributions with mean of 1 and variance equal to 1000 (Thomas et al. 2002).

Model selection.—Variables relevant to Cerulean Warblers were chosen a priori (Table 1) after a review of literature (primarily the Birds of North America account, Hamel [2000*a*], and references therein) and expert opinion (Tom Will, U.S. Fish and Wildlife Ser-

TABLE 1. Fixed-effects habitat variables measured at three spatial scales (800, 8000, and ~80 000 ha) describing Cerulean Warbler habitat in the upper midwestern United States.

Variable	Description
Area-weighted median deciduous forest patch size†	sum of patch area divided by number of deciduous forest patches (ha), buffered from extremes by area-weighting
Proportion of landscape in forested wetlands†	proportion of landscape devoted to permanently inundated forested wetlands
Proportion of oak and elm	proportion of landscape devoted to oak (*Quercus* spp.) and elm (*Alba* spp.) forest
Easting	Universal Transverse Mercator coordinate for longitudinal location
Northing	Universal Transverse Mercator coordinate for latitudinal location
Static wetness potential†	ln(catchment area/tan(slope angle))
Mean annual precipitation‡	30-yr mean precipitation (cm)

† A priori variable retained after post hoc modeling.
‡ Variables identified through exploratory classification regression trees.

vice). These variables and others considered in our analysis were those that could be measured by way of remote sensing across the region, including land use composition and configuration, climate, terrain, and human influence (Appendix A). Each variable was assessed at three logarithmically related scales, 800, 8000, and 80 000 ha (these extents correspond to the mean product of buffers of 0.1, 1, and 10 km, respectively, placed about each NABBS route). This range of scales should adequately encompass both the ecology of the Cerulean Warbler on the breeding ground and the range of landscape processes impinging upon this ecology.

Variables were standardized to have zero mean and unit variance to improve MCMC performance (Gilks and Roberts 1996) and to assess the comparative value of each model covariate. Because of the cumbersome nature of iterative simulation and our multiscale approach, we conducted variable selection analogous to a backward selection from a global model. Models were created with variables measured at a common scale and then were combined to create a multiscale model. Interaction and quadratic terms were assessed only if published habitat associations warranted their inclusion.

A properly parameterized model (i.e., a model with the correct covariates) would reduce the need for the CAR spatial structure (B. D. Ripley, *comment* in Besag et al. [1991]). To assess the relative contributions of the spatial (Z) and nuisance (η) random effects (structured and unstructured components, respectively), we calculated the posterior distribution of the quantity $\psi = \text{var}_Z/(\text{var}_Z + \text{var}_\eta)$, where var_Z and var_η are the empirical marginal variances of Z and η, respectively (Best et al. 1999). As ψ approaches 0, spatial variation becomes negligible.

We compared the Deviance Information Criterion (DIC) between models with spatial structure and models without spatial structure; DIC is an information criterion analogous to Akaike's Information Criterion (AIC), with the most parsimonious model possessing the smallest DIC (Speigelhalter et al. 2002). We calculated model weights akin to the method suggested by Burnham and Anderson (1998, 2002) for AIC weights:

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

where Δ_i is the difference between the DIC from model i and the DIC possessed by the most parsimonious model (the model possessing the minimum DIC).

Model critique.—We assessed model goodness of fit by comparing model fit to the fit of replicate data (Gelman et al. 1995). Fit was calculated as

$$P = \sum_k \frac{(Y_k - \lambda_k)^2}{\lambda_k}.$$

The frequency to which the fit of the original data exceeded the fit of replicate data is the Bayesian P value; this measures the proportion of simulations in which the replicate quantity exceeds the realized quantity. Good fit occurs with $P = 0.5$, whereas major failures of the model occur at $P < 0.01$ or >0.99 (Gelman et al. 1995:173).

Post hoc exploration.—Ideally, spatial structuring ($Z_k(s)$) in the model would be unnecessary, given the inclusion of a proper set of environmental covariates defining the spatial relatedness between counts. Thus, in the situation in which our a priori set of environmental variables failed to obviate the spatial structuring of the model, we conducted a post hoc examination for additional potential explanatory variables. We employed a regression tree approach (De'ath and Fabricius 2000) whereby we evaluated the relative influence on Cerulean Warbler counts of 28 climate, 25 landscape composition, 27 landscape configuration, two human disturbance, and 15 terrain variables measured for several land cover types at each of the three spatial scales (Appendix A). Many of these variables were related, measuring various aspects of landscape composition and configuration. For example, deciduous forest edge density, deciduous core area, and deciduous patch interspersion and juxtaposition measure some aspect of forest edge, but none by itself provides a complete context to the phenomenon. The advantage of using a regression tree approach was to allow the data to identify the most appropriate variables.

Calculations of regression trees occurred with CART4.0 (Breiman et al. 1984, Steinberg and Colla 1997). The regression tree was split based on least squares minimization for $\log_{10}$-transformed Cerulean Warbler counts. Tree size was defined by the one-standard-error rule, whereby the smallest tree was chosen that minimized the estimated error rate to within one standard error of the minimum error rate (De'ath and Fabricius 2000). Tenfold cross validation was used to test the validity of the resulting tree (De'ath and Fabricius 2000). The final variables selected for inclusion in post hoc models were based on their importance value across the tree. We chose importance value as a means of identifying the relevant suite of variables for possible inclusion rather than simply those occurring as primary node splitters because the importance score measures the ability of a variable to mimic the chosen tree and to act as a surrogate to primary splitter variables. By including these surrogates, we reduced the potential for spurious associations. We introduced the final suite of post hoc variables to the a priori model for consideration; these variables were retained if they reduced the variance explained by the model's spatial structure or replaced an a priori surrogate.

Model evaluation.—We evaluated the model against three independent sources of data. The first evaluation data set was NABBS counts collected over all routes in 2002 plus those counts collected between 1981 and 2001 from the 64 NABBS routes (of the 204 total routes) that we withheld from model construction ($n = 396$ route counts, 25 counts >0). These routes were randomly selected, except for a few that were excused from model creation because they partially overlapped the boundary of the study area or were inadequately run between 1981 and 2001.

Additional sources of independent model assessment included the use of point counts of Cerulean Warblers collected at 17 locations within the study area (7151 point counts, 292 recording at least one Cerulean Warbler) and data provided by the Cerulean Warbler Atlas project ($n = 303$ surveys; Rosenberg et al. 2000). The point counts used in our model assessment were largely collected on federal lands for purposes independent of this analysis (Appendix B). The Atlas data only included known Cerulean Warbler locations and, thus, did not provide insight into how well the model predicted areas of absence. For each route, point count, or atlas location used in the evaluation, we calculated a mean predicted abundance as determined by the final model and related the observed independent counts against this predicted abundance with simple linear regression. The intercept was allowed to vary because we assumed that different methodologies would yield differences in scale; the slope was evaluated as the measure of agreement between the model and observations.

Because our modeling approach integrates >20 years of counts, we are able to calculate temporal trends that are unbiased by the nuisance effects previously outlined. As a demonstration of this ability, we plotted standardized model estimates against standardized estimates obtained from estimating equations (Link and Sauer 1994), a common method for determining trend in NABBS counts.

Mapping issues

Translating a statistical model into a mapped model is largely an ad hoc process. The approach that we took was to apply the final model function across the study region, integrating map layers according to the model coefficients with the Spatial Analyst extension of ArcGIS 8.0 (ESRI 2002*b*). Resolution of the map layers for the environmental variables was consistent with the scale identified by the model (e.g., 800 ha for Static Wetness Potential, 8000 ha for Area-weighted Median Deciduous Forest Patch Size; Thogmartin et al. 2004). We filtered this map by allowing model predictions only for areas conducive to Cerulean Warbler occurrence, i.e., forested environs. Urban and agricultural areas were masked out of the prediction (although these areas generally predicted only extremely few Cerulean Warblers anyway). Final map resolution was 0.25 ha because of the urban and agricultural filter.

RESULTS

The distribution of Cerulean Warbler counts was highly kurtotic, with 90.2% and 2.9% of counts occurring as zeros and ones, respectively; nine was the maximum count. Overdispersion prior and post modeling was estimated as 1.4 and 0.4, respectively.

Our a priori expectation of an association between Cerulean Warbler abundance and the percentage of the landscape in oak and elm was not confirmed. However, our other a priori expectations were largely correct, with percentage of forested wetlands, mean deciduous patch size, and the static wetness index being retained. Post hoc analysis suggested replacing northing by easting with mean annual precipitation in the interaction with deciduous patch size. Our final model, then, consisted of the percentage of the landscape in forested wetlands, an index of wetness, and an interaction of deciduous forest patch size with mean annual precipitation (Table 2). The model weight (w_1) was 0.448 whereas competing models had $w_j < 0.151$. The nearest competing models were similar in their variables but differed in the scale at which they were measured, indicating a degree of uncertainty in the scales of the final model. However, useful inference about the importance of environmental variables can be restricted to this single final model because, based on DIC $\Delta_i \geq 2.18$, the competing models had considerably less sup-

TABLE 2. Posterior distributions of median standardized model parameters and diagnostics, with 95% credibility intervals.

Parameter	β_{Median}	2.5%	97.5%
Year	−0.080	−0.182	0.008
Observer	1.263	−0.069	2.919
Area−weighted median deciduous forest patch size (8000 ha)	0.199	−0.935	1.247
Proportion of landscape in forested wetlands (8000 ha)	1.254	0.356	2.482
Static Wetness Potential (800 ha)	−1.176	−2.435	−0.270
Mean annual precipitation	1.487	−0.112	3.277
Interaction of forest patch and precipitation	1.733	0.127	3.661
Spatial structure (μ†)	−8.537	−11.830	−6.180

Note: Distributions were computed from chain values of length 25 000 after discarding the first 10 000 values.
† Residual spatial structure unaccounted for by environmental covariates.

port than the final chosen model (Burnham and Anderson 2002:170). The evidence ratio ($w_{\text{best}}/w_{\text{2nd best}}$) for the nearest competing model was 2.97.

In the final model, deciduous forest patch size and the percentage of forested wetlands were included at the intermediate scale (8000 ha), whereas the wetness index was included at the finest scale (800 ha). Cerulean Warblers increased in abundance as the percentage of the landscape in forested wetlands increased, but within a context of forested wetlands, Cerulean Warblers decreased as potential soil moisture increased. In other words, Cerulean Warblers were found at drier locations within landscapes that included forested wetlands. Further, Cerulean Warblers decreased in abundance as forest patches and precipitation decreased. Cerulean Warblers were relatively abundant in small deciduous patches if mean precipitation was high; conversely, small, dry deciduous patches had fewer Cerulean Warblers.

We were unable to explain the spatial structuring that resulted from the autocorrelation in counts with the environmental variables as we measured them. Despite our interest in removing this correlation structure through a post hoc exploratory analysis, there was considerable remaining spatial structuring in the final model ($\psi = 0.86$). Spatial structuring due to autocorrelation in counts explained 1.5 times that of the combined effect of all of the environmental variables.

Mapping of the model indicated that Cerulean Warblers were predicted to achieve their greatest densities in Allegan and Barry State Game Areas of southern Michigan (Fig. 3). The model predicted that Allegan State Game Area possessed 2% of the predicted population, whereas Barry State Game Area had 0.7% of the population. Cerulean Warblers were also predicted to be in relatively high abundance in the Driftless Area of western Wisconsin and in central Wisconsin. Although Cerulean Warblers have been encountered on NABBS routes in BCR23 in central Minnesota, we predicted their abundance to be comparatively low there.

Overlaying a GIS layer of lands under federal management indicated that 15.1% of the estimated Cerulean Warbler population occurred on federal lands (Table 3), with Manistee National Forest (in Michigan) and Menominee Indian Reservation (in Wisconsin) holding the largest populations, 10.5% and 2.1% of the total population, respectively. Both Manistee National Forest and Menominee Indian Reservation are located along the largely forested northern border of the Prairie–Hardwood Transition.

Model evaluation.—NABBS data withheld from model construction suggested a roughly positively linear relationship between observed and predicted abundances, although this relationship was driven exclusively by a small number of counts from routes in Allegan and Barry counties, Michigan, where Cerulean Warblers were predicted to be at their greatest abundance. In general, the model appeared to overpredict abundance (Fig. 4A).

Point counts collected from federal lands were highly variable relative to the predicted abundance (Fig. 4B). Despite the array of methodological differences between NABBS route counts and refuge point counts, the median count was roughly equal to the predicted relative abundance, at least up to counts of four Cerulean Warblers. The single instance in which six Cerulean Warblers were counted at one point count location in one year (1997) was contrary to the predicted abundance, which was zero; in other years at this same location, zero or one Cerulean Warblers were counted.

In concordance with the other two assessment data sets, comparison with Cerulean Warbler Atlas data suggested that the model overpredicted abundance at the high end of the predicted abundance and underpredicted at the low end of predicted abundance (Fig. 4C). Of the Cerulean Warbler sightings, 41% occurred in locations where the model predicted zero abundance (median = 1, maximum estimated as 25–40 at one location). However, inspection of the maps indicated that many of these sightings occurred in nonforested habitats adjacent to forested habitat where Cerulean Warblers were predicted to occur. Because our maps predicted the species to occur only in forested habitat, these errors could be because of simple inaccuracy in the survey location. In addition, there is some probability of not detecting a Cerulean Warbler even when it is present.

Annual model estimates of relative Cerulean Warbler abundance in BCR23 were in good agreement with estimates derived from estimating equations (Fig. 5).

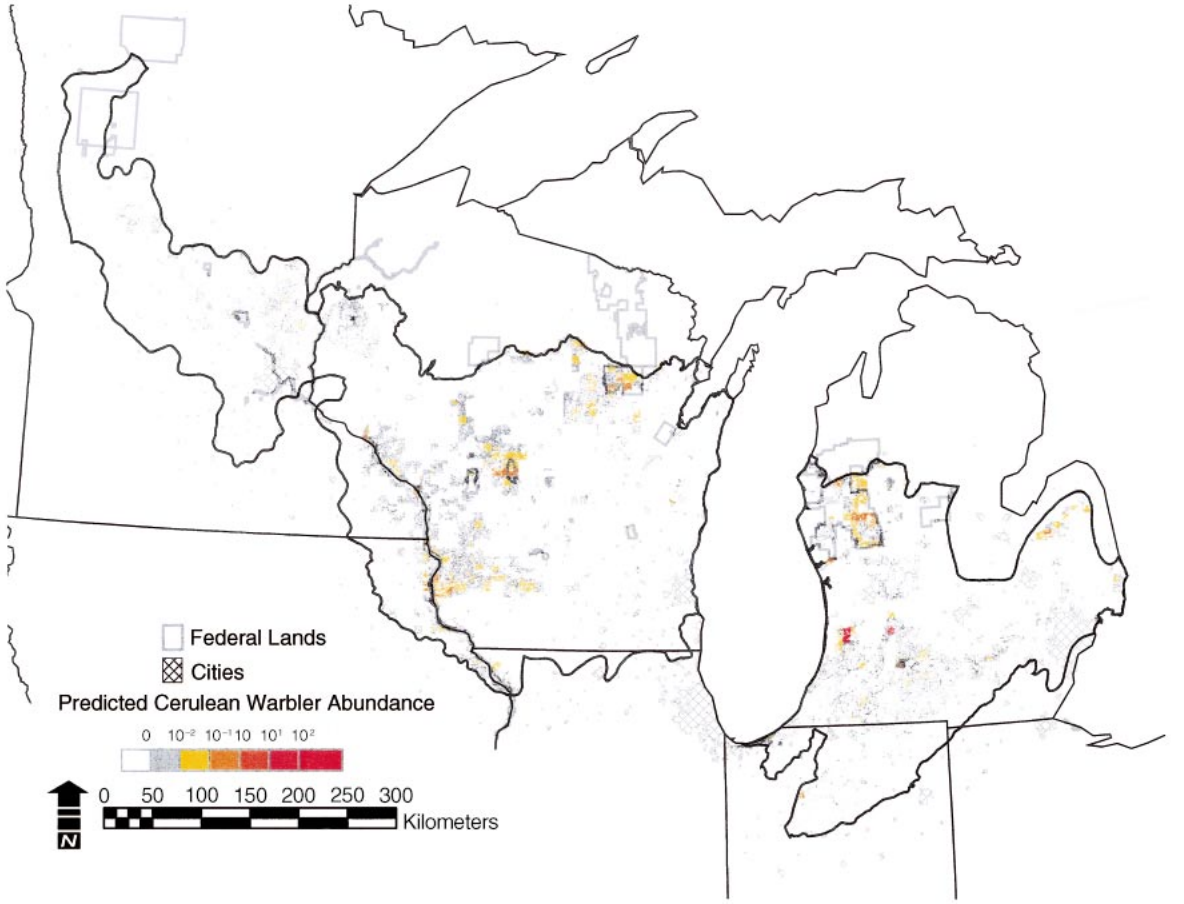

FIG. 3. Model predictions of spatial patterning in Cerulean Warbler abundance across the upper-Midwestern Prairie–Hardwood Transition. For any given location, the predicted abundance is the median expectation, given replication of the North American Breeding Bird Survey.

TABLE 3. Percentage of the estimated Cerulean Warbler population occurring on U.S. federal lands in the Prairie–Hardwood Transition (BCR23).

Name	Authority	State	Area (km^2)†	Percentage of population
Savanna Army Depot	DOD	IL	53	0.02
Sherburne National Wildlife Refuge	FWS	MN	133	0.05
Chequamegon National Forest	FS	WI	28	0.06
Saint Croix National Scenic Riverway	NPS	MN–WI	131	0.06
Indiana Dunes National Lakeshore	NPS	IN	32	0.09
Custer Reserve Forces Training Area	DOD	MI	32	0.23
Fort McCoy	DOD	WI	241	0.37
Necedah National Wildlife Refuge	FWS	WI	153	0.38
Stockbridge Indian Reservation	BIA	WI	86	0.41
Upper Mississippi River Wildlife And Fish Refuge	FWS	IL–IA–MN–WI	765	0.54
Menominee Indian Reservation	BIA	WI	871	2.1
Manistee National Forest	FS	MI	3779	10.5
Total			6304	15.1

Notes: Authorities are as follows: DOD, Department of Defense; FWS, Department of Interior, Fish and Wildlife Service; FS, Department of Agriculture, Forest Service; NPS, Department of Interior, National Park Service; and BIA, Department of Interior, Bureau of Indian Affairs. States are: IL, Illinois; MN, Minnesota; WI, Wisconsin; IN, Indiana; MI, Michigan; IA, Iowa.

† The areas reported for each federal land unit may be less than the total area associated with the management unit as some federal lands occurred only partially within the boundary of BCR23.

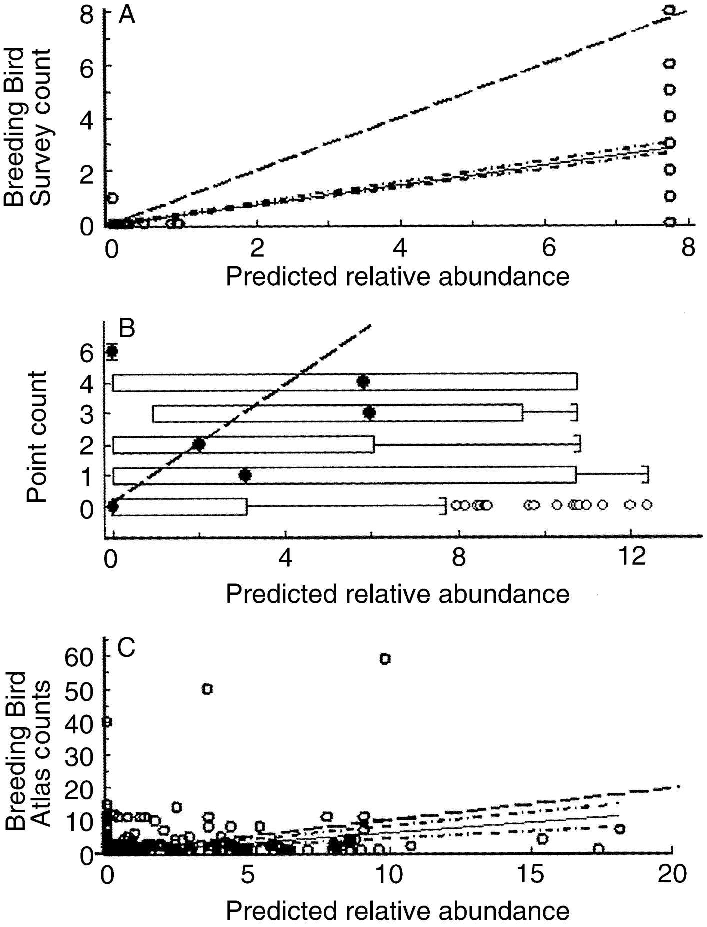

FIG. 4. Performance of the model relative to independent data. (A) Scatter plot, with best-fit line and 95% confidence limits, of observed vs. predicted North American Breeding Bird Survey counts of Cerulean Warblers in the Prairie–Hardwood Transition. The figure includes both counts withheld from modeling and counts from 2002. The dashed line represents one-to-one correspondence between observed and predicted responses. (B) Whisker plot [median (solid circles); lower and upper quartiles, 1.5× interquartile brackets; and outliers (open circles)] of point counts from federal lands relative to predicted abundance. The dashed line represents one-to-one correspondence between observed and predicted responses. (C) Scatter plot, with best-fit line and 95% confidence limits, of observed Cerulean Atlas counts vs. predicted abundance. Because Atlas counts are ≥ 1, they do not reflect locations where Cerulean Warblers were not observed. The dashed line represents one-to-one correspondence between observed and predicted responses.

From the estimating equation used by the NABBS, Cerulean Warblers exhibited an annual mean decline of 11.2% per year ($n = 11$ NABBS routes, $P = 0.024$) in the Prairie–Hardwood Transition; our modeling largely concurred, predicting an annual mean decline equaling 8.0% (95% credibility interval = -18.2 to $+0.8$%).

DISCUSSION

The approach that we have outlined overcomes three challenges to modeling and mapping avian counts over space: that is, extra-Poisson dispersion, nuisance effects associated with count data collection, and spatial autocorrelation. Singly, each of these challenges can be met successfully with standard (i.e., frequentist) statistical approaches, but there is currently no means for considering these challenges conjointly. Failure to accommodate any one of these three challenges would have prevented the unbiased assessment of environmental covariates associated with counts. In this regard, we have improved upon the model of Link and Sauer (2002) by extending its applicability to spatial domains of inference.

The aggregate of independent data suggests that the model we developed generally predicts patterns in Cerulean Warbler abundance, although with each evaluation data set we found that the model overpredicted abundance. This is not surprising, given the rarity of this species, which is only infrequently encountered on NABBS routes. Any count-based evaluation of a model is likely to produce low counts relative to model predictions, because counts are biased estimates of actual population sizes. The extent of undercounting was not estimated for any of our evaluation data sets, but the hierarchical model accommodated some forms of undercounting. Alternatively, the model for the counts may also influence fit, and formulations of the model to accommodate an inflation of the zero counts, such as a zero-inflated negative binomial approach, may result in less overprediction, but at the cost of increased model complexity.

We acknowledge that our modeling approach has other shortcomings that deserve refinement. Our inability to replace the spatial autocorrelation structure with appropriate environmental covariates may be due, in part, to differences in the scales at which these two elements were measured and to a failure to accommodate underlying biological processes not directly associated with environmental variables. The neighborhood structure that we chose was much coarser than

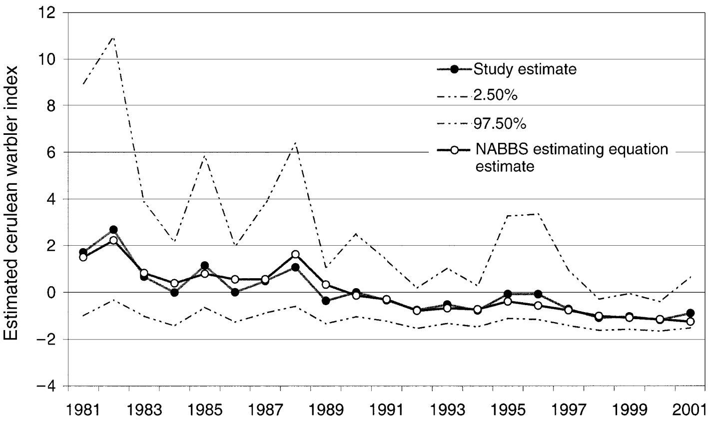

FIG. 5. Comparison of standardized North American Breeding Bird Survey (NABBS) estimating equation and standardized hierarchical estimates of annual abundance for Cerulean Warblers in the Prairie–Hardwood Transition, 1981–2001. Hierarchical estimates include 95% credibility intervals.

the coarsest scale we examined. Further, biological processes relating to predation, competition, and mate-finding, for instance, may only imperfectly coincide with environmental variables.

Methodologically, the normal assumption for the CAR is susceptible to outliers, leading to local over-smoothing of avian counts (Best et al. 1999). For instance, Cerulean Warblers were only counted on two routes in Minnesota, leading to some overestimation of their abundance in this area. Despite this potential bias, Best et al. (1999) found that the particular treatment of the spatial effects had little effect on final model inferences, indicating that the model framework is robust to spatial effects. In other contexts, however, a more appropriate spatial model might include a conditional autoregression on a regular grid rather the irregular grid that we used (Andy Royle, *personal communication*) or geostatistical interpolation between route counts, which is now available in the most recent version of WinBUGS (Diggle et al. 1998, Wikle 2002). Kelsal and Wakefield (2001) suggested that correlation structures between neighboring areas are more realistic when derived from an underlying continuous surface.

Another potential problem is that chance patterns within the counts of Cerulean Warblers may result in regression trees dominated by spurious variables (Breiman et al. 1984, Anderson et al. 2001). By using regression tree analysis to supplement our a priori models, we tried to avoid models with spurious variables. With this approach, we found that precipitation acted as a strong surrogate for the Easting × Northing interaction in our a priori model. Across the Prairie–Hardwood Transition, there exists a gradient in precipitation from the northwest, where it is drier, to the southeast, where it is wetter. It is conceivable that precipitation is erroneously included in the model. However, the hypothesis that precipitation contributes to the spatial structuring of this species in the Prairie–Hardwood Transition and elsewhere across the range of this species should be tested. Our use of a post hoc exploratory approach was warranted because there has been little explicit testing of large-scale habitat associations for this and most other bird species reported in the literature. Habitat observations are generally limited to a few specific study areas and tend to focus on local habitat conditions rather than landscape composition and configuration factors measured remotely over large regions.

The spatial structuring of this species appears to be due, in part, to area sensitivity to forest patch size. Our model concurs with much of the literature in this regard. In a review by Hamel (2000*a*), Cerulean Warblers required minimum forest tract sizes of 10 ha in Ontario, 20–30 ha in Ohio, 700 ha in the Mid-Atlantic states, and >1600 ha in the Mississippi alluvial valley. These studies suggested great variability in area sensitivity over the range of the Cerulean Warbler. Rosenberg et al. (2000) cautioned that because studies of range size come mainly from the Mid-Atlantic and southeastern United States, ‘‘rangewide assumptions of extreme area sensitivity may be exaggerated.’’ Our results indicate, however, that even in the northwestern portion of the range of the Cerulean Warbler, where populations are small, area sensitivity appears to occur.

The mechanism of this area sensitivity has not been determined (Hamel 2000*a*). Response by Cerulean Warblers to habitat fragmentation may relate to factors varying concurrently with fragment size rather than a particular behavioral aversion to small patch size. For instance, some research has suggested that area sensitivity is a function of intensity of predation and Brown-headed Cowbird (*Molothrus ater*) parasitism (Robinson et al. 1995).

Our model suggests a correlate, if not a mechanism, for the great variability in area sensitivity, in that the area sensitivity was mediated by precipitation. The greatest Cerulean Warbler abundance occurred in areas where precipitation and forest patch size were coincidentally greatest. This culminated in very high predicted abundance in the Prairie–Hardwood Transition east of Lake Michigan, probably as a consequence of elevated lake-effect precipitation and large remaining

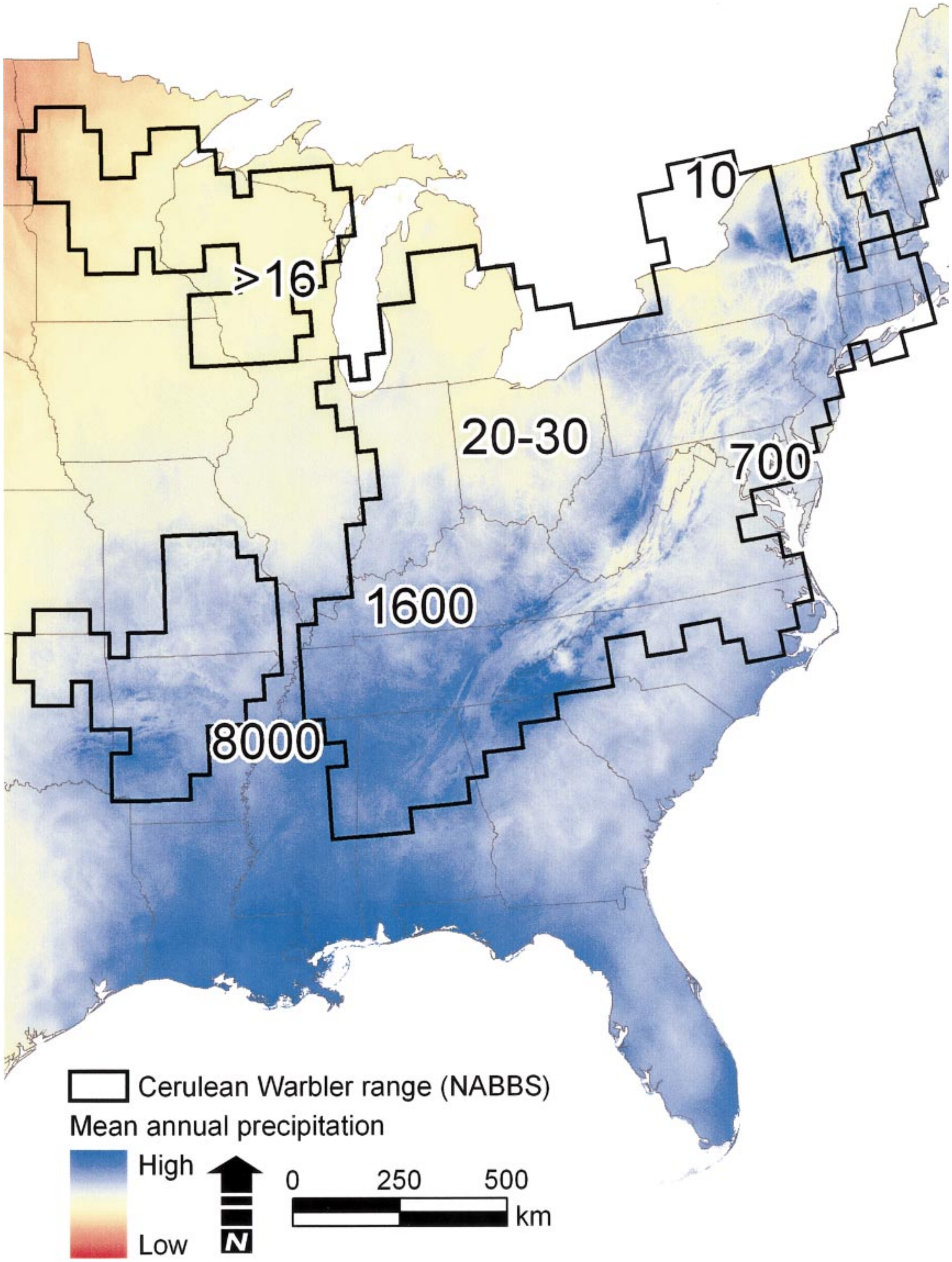

FIG. 6. Mean annual precipitation in the eastern United States and published patterns in observed area sensitivity (in hectares) in the Cerulean Warbler. Area sensitivity in this species may correspond to precipitation.

tracts of forest. This coincidence of area sensitivity with regional precipitation is also observed across the range of the species (Fig. 6).

Perhaps the greatest conundrum among Cerulean Warbler researchers is in explaining the dichotomy of occupied habitats (reviewed in Hamel 2000*b*:12–14). For instance, Barker and Rosenberg (1998:9) wrote:

‘‘Cerulean Warblers were found in two very different types of habitat: in upland sites such as dry ridge slopes and moist cove forests and in bottomland sites, including riparian areas, swamp forests, and river islands. Oaks of various kinds dominated most of the upland sites, whereas the bottomland sites contained a variety of trees, including red and silver maples, oaks, sycamores, cottonwoods, and white ash.’’

We believe that our results are concordant with this apparent dichotomy of habitat associations. We predicted Cerulean Warblers to be most abundant within large, dry, upland forests embedded within a larger matrix of forested wetlands, and it was the scale of these associations that accommodated these apparent differences. Dry (i.e., upland) areas influenced abundance at the finest scale (800 ha), whereas the forested wetlands were important at a coarser scale (8000 ha). In simplistic terms, Cerulean Warblers chose forested uplands within a matrix of moist bottomland forest. Paul Hamel, an expert on the ecology of this species, indicated that his field observations generally concurred with these model predictions (P. Hamel, *personal communications*, 19 December 2002).

Implications

Our approach identified large areas of potential Cerulean Warbler habitat, the vast majority residing in non-public ownership. This result has important consequences for conservation of this species in the upper Midwest. Conservation partnerships with private landowners will be critical to conserving the majority of Cerulean Warbler habitat. Federal and state land management agencies will be able to use the maps to identify locations where such conservation partnerships may be most fruitful.

Data from the NABBS suggested a decline in abundance between 1980 and 2001 in the Driftless Area and Great Lakes Plain physiographic areas of BCR23 (Sauer et al. 2002). Our annual estimates of these same data concur, indicating a decline of ~8.5% per year between 1981 and 2001. Robbins et al. (1992) indicated that loss of mature deciduous forest, especially within riparian corridors, contributed to these declines. However, deciduous forest acreage and stand age have substantially increased in Minnesota, Michigan, and Wisconsin in the last three decades, especially on federal land (Haugen and Mielke 2002, Leatherberry 2002, Vissage 2002); this change in deciduous forest ostensibly increases the quality of habitat for Cerulean Warblers. Thus, it seems that loss of deciduous forest is not associated with the decline of the species in this BCR.

Even though mature deciduous forests may have been stable or increasing, forested wetlands in the region have been declining in area and structural diversity (Abernethy and Turner 1987, Knutson et al. 1996, Knutson and Klaas 1998). Wetland forests in the north-central United States have declined in area (Mitsch and Gosselink 1993), with their greatest decline (-0.7% annually) occurring between 1940 and 1980 (Abernethy and Turner 1987). Coincidental changes have occurred in tree species composition along large rivers, tending toward a monoculture of silver maple (*Acer saccharinum*) in some areas (Knutson and Klaas 1998, Sparks et al. 1998). In BCR23, we found that the strength of the association of Cerulean Warblers to forested wetlands was six times greater than the association with deciduous forest patch size. Thus, declines in wetland forest area would presumably have a much greater influence on regional abundance than increases in deciduous forest area.

The association between forested wetlands and Cerulean Warbler abundance may be unique to regions where forested wetlands are well-represented in the landscape. For instance, we would not expect the association of Cerulean Warbler abundance and forested wetlands to occur in the core of the species range, because such habitat is rare in the Cumberland Plateau (see Figs. 3–8 in Mitsch and Gosselink [1993]) where Cerulean Warblers are at their greatest abundance; we might, however, hypothesize that the dependence on deciduous forest should increase as the strength of the relationship to forested wetlands declines.

Summary

Spatial models such as that presented here can be used to investigate hypotheses about relationships between landscape pattern and ecological response when the response occurs as a count. In some respects, the species that we modeled was a worst case scenario; counts of this species were extremely low or zero at all locations. Given our success here, there is promise in using this approach on other rare taxa. Further, the functional relationships that we have elucidated can now be used to formulate regional management plans for the conservation of this species. For instance, management effort and monitoring can be focused on areas within the Prairie–Hardwood Transition where Cerulean Warblers are predicted to be at their highest abundance, rather than spread diffusely across the entire region. These models also provide testable hypotheses for the structuring of Cerulean Warblers in other parts of their range.

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APPENDIX A

Environmental covariates considered for hierarchical models of Cerulean Warbler habitat associations in the prairie–hardwood transition are available in ESA's Electronic Data Archive: *Ecological Archives* A014-035-A1.

APPENDIX B

Point counts from 17 locations within the prairie–hardwood transition, used in evaluating hierarchical count models, are available in ESA's Electronic Data Archive: *Ecological Archives* A014-035-A2.

SUPPLEMENT

WinBUGS code for modeling relative Cerulean Warbler abundance in the upper midwestern United States is available in ESA's Electronic Data Archive: *Ecological Archives* A014-035-S1.