



RESEARCH ARTICLE

Land use and climate affect Black Tern, Northern Harrier, and Marsh Wren abundance in the Prairie Pothole Region of the United States

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ABSTRACT

Bird populations are influenced by many environmental factors at both large and small scales. Our study evaluated the influences of regional climate and land-use variables on the Northern Harrier (*Circus cyaneus*), Black Tern (*Chlidonias niger*), and Marsh Wren (*Cistothorus palustris*) in the prairie potholes of the upper Midwest of the United States. These species were chosen because their diverse habitat preference represent the spectrum of habitat conditions present in the Prairie Potholes, ranging from open prairies to dense cattail marshes. We evaluated land-use covariates at three logarithmic spatial scales (1,000 ha, 10,000 ha, and 100,000 ha) and constructed models a priori using information from published habitat associations and climatic influences. The strongest influences on the abundance of each of the three species were the percentage of wetland area across all three spatial scales and precipitation in the year preceding that when bird surveys were conducted. Even among scales ranging over three orders of magnitude the influence of spatial scale was small, as models with the same variables expressed at different scales were often in the best model subset. Examination of the effects of large-scale environmental variables on wetland birds elucidated relationships overlooked in many smaller-scale studies, such as the influences of climate and habitat variables at landscape scales. Given the spatial variation in the abundance of our focal species within the prairie potholes, our model predictions are especially useful for targeting locations, such as northeastern South Dakota and central North Dakota, where management and conservation efforts would be optimally beneficial. This modeling approach can also be applied to other species and geographic areas to focus landscape conservation efforts and subsequent small-scale studies, especially in constrained economic climates.

Keywords: abundance maps, Bayesian, hierarchical models, Markov chain Monte Carlo, North American Breeding Bird Survey, Prairie Pothole Region, wetland birds

El uso de la tierra afecta la abundancia de *Chlidonias niger*, *Circus cyaneus* y *Cistothorus palustris* en la región de Prairie Pothole, Estados Unidos

RESUMEN

Las poblaciones de aves son influenciadas por muchos factores ambientales a escalas grandes y pequeñas. Nuestro estudio evaluó la influencia de variables del clima regional y del uso de la tierra sobre *Circus cyaneus*, *Chlidonias niger* y *Cistothorus palustris* en la región de Prairie Pothole de la parte alta del centro-oeste de los Estados Unidos. Estas especies fueron escogidas debido a que sus diversas preferencias de hábitat representan el espectro de hábitats presentes en el área, que abarca desde praderas abiertas hasta pantanos con alta densidad de cortaderas. Evaluamos covariables del uso de la tierra en tres escalas espaciales logarítmicas (1000 ha, 10000 ha, y 100000 ha) y construimos modelos *a priori* usando información de publicaciones sobre asociaciones de hábitat e influencias climáticas. Las variables que tuvieron una influencia más fuerte sobre la abundancia de cada una de las tres especies fueron el porcentaje de área de humedal a través de las tres escalas espaciales y la precipitación en el año anterior al que se realizaron los censos de aves. Aún entre escalas que abarcan tres órdenes de magnitud, la influencia de la escala espacial fue pequeña, dado que los modelos con las mismas variables expresadas a diferentes escalas estuvieron frecuentemente en el subconjunto de los mejores modelos. La evaluación de los efectos de variables ambientales a gran escala en aves de humedal elucidó relaciones que se han pasado por alto en muchos estudios a pequeña escala, como la influencia de las variables climáticas y del hábitat a escala del paisaje. Dada la variación espacial en la abundancia de nuestras especies focales dentro de la región de estudio, las predicciones de nuestro modelo son especialmente útiles para identificar localidades donde el manejo y los esfuerzos de conservación traerían óptimos beneficios, como el nororiente de Dakota del Sur y el centro de Dakota del Norte. Esta aproximación por modelamiento también puede ser aplicada en otras especies y áreas geográficas para enfocar los esfuerzos de

conservación del paisaje y los subsecuentes estudios a pequeña escala, especialmente en climas económicamente restringidos.

Palabras clave: aves de humedal, bayesiano, cadenas de Markov Monte Carlo, censo norteamericano de aves reproductoras, mapas de abundancia, modelos jerárquicos, región de Prairie Pothole

INTRODUCTION

Avian habitat studies are commonly used to assess how one or more species of bird responds to environmental factors. Many studies examining bird–habitat relationships have been conducted at small scales focusing on microhabitats (e.g., Murkin et al. 1997, Vierling 1999). Often, results from these site-intensive studies are extrapolated to a regional level because little information about bird–habitat relationships is available at larger scales. Unfortunately, extrapolating small-scale study results to a landscape scale can overlook influences emergent at larger scales (Thogmartin 2007).

The effects of environmental variables on birds can differ as scale varies, becoming pronounced at some scales and inconsequential at others (Tozer et al. 2010). Saab (1999) found strong bird–habitat relationships at landscape, microhabitat, and macrohabitat scales, with landscape-scale features being the most important. Landscape-scale features also were found to be more influential on Northern Bobwhite (*Colinus virginianus*) populations than site-specific variables, especially in areas with moderate amounts of habitat (Duren et al. 2011). Thogmartin et al. (2004b, 2006, 2007) noted that Cerulean Warblers (*Setophaga cerulea*), American Woodcocks (*Scolopax minor*), and grassland birds also were influenced differently by landscape factors at varying scales. The variable influence of scale in landscape analyses underscores the importance of examining landscape effects at multiple scales so that important relationships are not overlooked (Urban 2005, Thogmartin 2007). In this study, landscape effects refer to the influences of environmental variables at scales ranging from 1,000 ha to 100,000 ha (Forcey et al. 2011).

A relatively new approach to avian habitat studies is to examine environmental influences beyond the landscape scale at a more regional level encompassing one or more Bird Conservation Regions (Fitzgerald et al. 2008). Bird Conservation Regions have been identified as ecologically unique areas with similar avian communities, and are used to foster a large-scale approach to bird conservation and management (NABCI 2005). Sauer et al. (2003) examined North American Breeding Bird Survey (NABBS) data over the whole of North America and found Bird Conservation Regions to be useful strata for analyses of avian population trends. Bird Conservation Regions were also found to be effective strata for mapping the predicted abundances of five species of grassland bird as a function of land-use and

climate variables (Thogmartin et al. 2006), as well as for modeling the distribution of waterbird species in the prairie potholes (Forcey et al. 2011). In addition to species distributional modeling, the Bird Conservation Region scale can also be used for mapping and directing large-scale management and monitoring efforts (LeBrun et al. 2012).

Regional spatial models and their mapped abundance predictions can be used to identify important geographic areas where management efforts can be focused to be optimally beneficial. This spatial targeting is especially important when allocating scarce monies and conservation resources. Thogmartin and Rohweder (2008) used spatial models to understand the distributions of grassland and forest songbirds across preferred habitats on public and private lands. Thogmartin and Rohweder (2007) also used modeled abundance predictions to assess the relative contribution of public and private land to American Woodcock habitat conservation. Understanding the degree at which preferred habitat occurs on private land can better inform conservation and management planning for species of concern. Spatial models and abundance predictions are also particularly applicable to the U.S. Fish and Wildlife Service's Strategic Habitat Conservation philosophy, which dictates that conservation practices are evaluated and delivered in a strategic manner (Thogmartin et al. 2011). While not a panacea, spatial models and associated abundance predictions are one tool that can be developed and applied in a repeatable and scientifically justified manner for the purposes of allocating often scarce conservation resources and directing management efforts (Thogmartin and Rohweder 2008).

We evaluated the influence of large-scale land-use and climatic variables on wetland-breeding populations of Northern Harrier (*Circus cyaneus*), Black Tern (*Chlidonias niger*), and Marsh Wren (*Cistothorus palustris*) in the United States portion of Bird Conservation Region 11 (BCR11), the Prairie Potholes. Both the Black Tern and Northern Harrier are listed as focal species in the Plains and Prairie Potholes Landscape Conservation Cooperative; the Marsh Wren is listed as a priority species (USFWS 2009). Additionally, more than 50% of the continental population of Black Terns occurs in the prairie potholes during breeding (Niemuth 2005), and the breeding range of Northern Harriers and Marsh Wrens overlaps entirely with this region (Kroodsma and Verner 1997, Smith et al. 2011). Thus, BCR11 represents an ideal location to study all three of these wetland species. These three species also

encompass a variety of taxa that inhabit a wide range of habitats from open prairies to dense cattail marshes, which reflects the spectrum of conditions found in the prairie potholes. Modeling a variety of taxa with different habitat preferences allowed us to test the ability of the models to predict abundance under a wide range of conditions of species detectability, environmental covariates, and habitat preferences.

We used bird abundance data from the NABBS (Sauer et al. 2012), land-cover data from the National Land Cover Dataset (NLCD; Vogelmann et al. 2001), and climate data from the National Climatic Data Center (National Climatic Data Center 2012) to model relative bird abundance as a function of environmental variables at three different spatial scales: 1,000 ha, 10,000 ha, and 100,000 ha. Environmental covariates included habitat and climate variables that were hypothesized a priori to influence abundance based on a literature review of our focal species. Our aims were to provide insight into the influence of land-use and climatic factors on our focal species at a regional scale and to predict relative abundances within BCR11. Abundance predictions can be used as a starting point for focusing conservation resources at specific locations.

METHODS

Study Area

Bird Conservation Region 11 (BCR11) covers >715,000 km² across five states and three provinces. We examined the portion of BCR11 within the United States (Figure 1) because of a lack of continuous and thematically consistent land-cover data across international boundaries. The landscape of BCR11 was formed approximately 12,000 years ago when glaciers melted and left behind depressions and potholes, which collect rain and snowmelt (Leitch 1989). Vegetation composition varies widely across BCR11 because of large fluctuations in hydrologic regimes. Submergent vegetation dominates in locations deep enough to have standing water during the dry season. Central zones within wetlands that periodically dry out contain medium-height and tall emergents. Vernal potholes primarily support grasses, sedges, and forbs (Kantrud 1989). Before European settlement, the region consisted of approximately 10% wetland habitat (Mitsch and Gosselink 2000); however, it is estimated that more than half of preexisting wetlands have been drained for agriculture (Leitch 1989). The remaining wetlands are heavily impacted by agriculture-induced sedimentation, nutrients, and agricultural chemical input (Euliss et al. 1999).

The climate of BCR11 is characterized by both precipitation and temperature extremes. The region is typically colder and wetter to the north and east, and warmer and drier to the west and south (Kantrud 1989).

Water balance is variably negative throughout BCR11, with evaporation exceeding precipitation by 60 cm in south-western Saskatchewan, but only by 10 cm in Iowa (Winter 1989). Temperatures in BCR11 are generally cold, with mean daily temperatures at or below 0°C for five months of the year. Air temperatures in the winter can drop below -60°C, but can exceed 40°C during the summer (Euliss et al. 1999).

Historical Datasets

We collected data for this study from several existing, large-scale datasets. We obtained bird abundance data from North American Breeding Bird Survey (NABBS) routes within BCR11 (Sauer et al. 2012), and acquired climate data for the United States from the National Climatic Data Center (National Climatic Data Center 2012). We took land-cover data for the United States from the U.S. Geological Survey National Land Cover Dataset (NLCD; U.S. Department of the Interior 1992, Vogelmann et al. 2001). We used these datasets in conjunction with a hierarchical spatial count model to predict relative bird abundance as a function of environmental covariates.

The NABBS is a long-term survey to monitor bird population trends at a continental scale (Sauer et al. 2012). Breeding bird surveys are performed annually along roadsides across North America during late May and June. Each route is 39.4 km in length, with 50 stops every ~0.8 km along the route. At each stop, an observer conducts a 3-min point count and records all birds seen or heard within a 402-m radius. Individual routes are surveyed by the same observer each year, when possible, using a consistent method and only under suitable weather conditions (i.e. low wind and minimal precipitation) during which bird detection probabilities are less likely to be affected. Attempts to minimize variability in NABBS data ensure that data are as unbiased as possible and that real variation in trends can be detected over time. We used NABBS data between the years 1980 and 2000 because this timeframe centrally overlaps the time when land-cover data were derived from satellite imagery during the early 1990s (Vogelmann et al. 2001). In addition, the 20-year period (as opposed to shorter periods) allowed us to better estimate an average effect of land use, smoothing over the year-to-year variability in the changing landscape, much in the same way that a broader period allowed for estimation of an average effect of climate less influenced by decadal-varying global climate processes. In BCR11, there were 95 routes for which data were used in this study (Figure 1); data from 77 routes were used to create spatial models, while data from 18 randomly selected routes were withheld for validation.

We derived land-use information and metrics from the NLCD 1992 distributed by the U.S. Geological Survey. Land-use data from the NLCD are available as 30-m grids

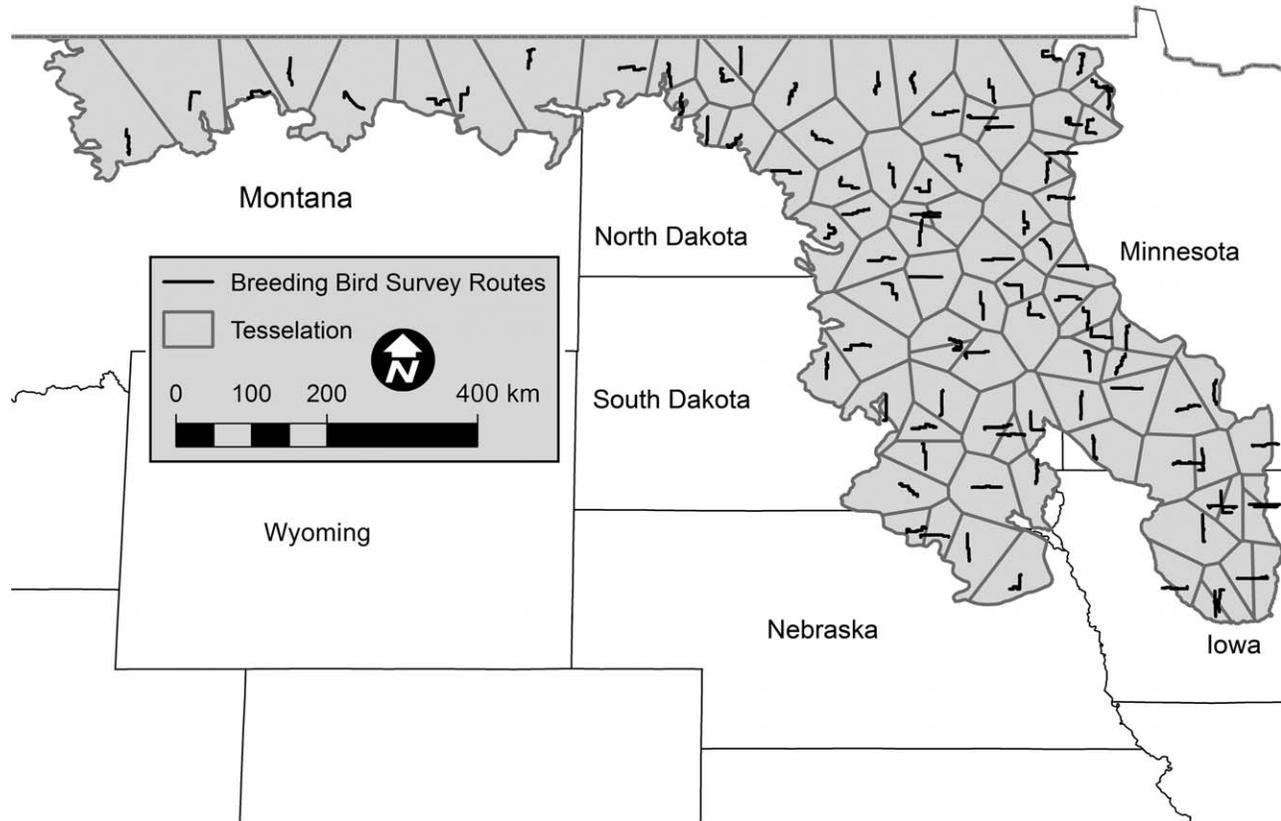


FIGURE 1. Distribution and tessellation (created to account for spatial autocorrelation in counts) of 95 North American Breeding Bird Survey routes in the U.S. portion of Bird Conservation Region 11.

and represent conditions in the United States in the early 1990s. We evaluated land-use patterns at three spatial scales by creating three buffer sizes—0.1 km (~1,000 ha), 1 km (~10,000 ha), and 10 km (~100,000 ha)—around each 39.4-km NABBS route (Brennan and Schnell 2007). We quantified land-use patterns within each buffer size around each route using ArcGIS version 9.1 Geographic Information System software (ESRI 2005) and FRAGSTATS version 3 (McGarigal et al. 2002). We reclassified the NLCD from Anderson level two classes into a modified Anderson level one classification (Anderson et al. 1976) to reduce potential errors in land-use classification that may occur at finer levels. We used raster algebra to multiply the NLCD reclassifications by each size of buffer; the resulting grid contained only land-use data within each buffer surrounding each route. We calculated land-use metrics within each buffer zone surrounding NABBS routes using FRAGSTATS (Table 1; McGarigal et al. 2002).

We acquired weather data from 245 recording stations across BCR11 in both the United States and Canada. Weather data from both countries were used so that interpolations would span country borders and so that the maximum number of data points were available to

interpolate (Forcey et al. 2007). Total precipitation was calculated as follows:

$$\text{Total precipitation} = \text{Rainfall} + (0.1 \times \text{Snowfall})$$

This equation approximates the amount of liquid precipitation as one-tenth of the amount of snowfall, which is a common conversion factor (Akinremi et al. 1999). We used the kriging function of the Spatial Analyst extension of ArcGIS version 9.1 (ESRI 2005) to create a continuous surface for each climate variable from 1980 to 2000 over BCR11. Surface interpolations use information from known points to estimate values on a grid where information is absent. This allowed estimation of climate variables around NABBS routes from the information recorded at surrounding weather stations. We averaged grid cell values within each 10-km buffer surrounding each NABBS route to compute a value for each weather variable for each route for each year. Resolution of climate interpolations was 1,000 m.

Statistical Analyses

We modeled total bird abundance per route per year from the NABBS as a function of nuisance effects associated

TABLE 1. A priori environmental variables included in suites of candidate models to predict abundance of three wetland bird species in the Prairie Potholes Region of the United States. All covariates were standardized with a mean of 0 and a standard deviation of 1.

Type of variable	Variable	Variable description	Species modeled ^a
Climate	Previous year precipitation	Total precipitation from the year prior to when bird abundance was measured	NOHA, BLTE, MAWR
	Previous year spring temperature	Mean spring temperature from the spring prior to when bird abundance was measured	NOHA, BLTE, MAWR
	Yearly precipitation	Total precipitation from the same year that bird abundance was measured	NOHA
	Spring temperature	Mean spring temperature from the same year that bird abundance was measured	NOHA
Patch-level land cover	Herbaceous planted largest patch index (%) ^b	Percentage of the total landscape comprising the largest patch of herbaceous plants	NOHA
	Herbaceous upland largest patch index (%) ^b	Percentage of the total landscape comprising the largest patch of herbaceous upland	NOHA
	Shrubland (%)	Percentage of shrubland in the landscape (includes woody vegetation <6 m tall)	MAWR
	Water (%)	Percentage of open water in the landscape	BLTE
	Water interspersed and juxtaposition index ^c	Percentage of land use types that are adjacent to open water	MAWR
	Water largest patch index (%) ^b	Percentage of the total landscape comprising the largest patch of open water	BLTE
	Wetland (%)	Percentage of vegetated wetland in the landscape	NOHA, BLTE, MAWR
	Wetland largest patch index (%) ^b	Percentage of the total landscape comprising the largest patch of vegetated wetland	NOHA, BLTE
Landscape-level land cover	Contagion ^d	Aggregation of different patch types in the landscape (low contagion indicates many land uses in the landscape)	NOHA, MAWR
	Patch richness density	Number of different land uses present per 100 ha	MAWR

^a Species abbreviations: NOHA = Northern Harrier, BLTE = Black Tern, and MAWR = Marsh Wren.

^b 'Largest patch index' equals the area of the largest patch of a particular land use divided by the total landscape area, multiplied by 100.

^c 'Interspersion and juxtaposition' is ~0 when a particular land-use type is adjacent to only 1 other land-use type. 'Interspersion and juxtaposition' equals 100 when a particular land-use type is equally adjacent to all other land-use types.

^d 'Contagion' is ~0 when every grid cell is a different land-use type. The contagion index equals 100 when the landscape consists of a single land-use type. This metric is similar to 'interspersion and juxtaposition,' except that 'contagion' is based on cell adjacencies and not land-use type adjacencies.

with survey design, land-use variables, and climatic influences using a hierarchical modeling approach within a Bayesian framework. Hierarchical models are useful for modeling NABBS data because they acknowledge correlation among multiple observational units. Temporal correlation in counts is present among years and spatial correlation is present among routes. Temporal correlation occurs when count similarity is tied to survey chronology; spatial correlation arises when count similarity is tied to geographical proximity. We used a Bayesian framework to fit hierarchical models because with this method all unknown quantities are treated as random variables and it therefore provides a natural approach to this type of analysis (Link and Sauer 2002). Modeling within a Bayesian framework can accommodate Poisson-distributed counts, nuisance effects such as those associated with the NABBS, and spatial autocorrelation that may be present in the data.

We used data from 1,212 NABBS counts conducted by 145 observers during 1980–2000 to model bird abundance as a function of environmental covariates in BCR11. The response variable in the models was the total number of birds for each species across the entire route for each year. We incorporated nuisance effects into the models at three levels in the model hierarchy. We included a year effect and a trend term to account for inherent temporal variation in bird abundance which occurs as populations naturally fluctuate. We included two observer effects in the model: One accounted for differences in surveying abilities among observers (Sauer et al. 1994) and the other accounted for inexperience (a first-time observer effect). The first-time observer effect was a binary variable which was "0" if it was an observer's first time surveying a given route and "1" if the observer had surveyed the route previously. The first-time observer effect accounted for improvements in observer bird identification over time, increased surveying

efficacy, and associating certain species with individual stops (Kendall et al. 1996). We accounted for spatial autocorrelation in counts by using a spatial conditional autoregressive (CAR) prior distribution on the route effect (Banerjee et al. 2004). We derived an adjacency matrix (Lawson et al. 2003) within BCR11 by creating an irregular lattice from a tessellation of NABBS routes within BCR11 (Figure 1; Hooge and Eichenlaub 1997). Spatial autocorrelation was accounted for when routes shared a common boundary in the tessellation; distances among routes were not taken into account, though this is possible in other applications (Thogmartin et al. 2004b).

We used Poisson regression to model bird abundance as a function of environmental covariates in BCR11 because counts are typically discrete positive values and are often Poisson-distributed. We fit models using Markov chain Monte Carlo (MCMC) techniques using Gibbs sampling (Link et al. 2002). Gibbs sampling is an algorithm used to sample the posterior distribution of a random variable (Gelman et al. 2004). Three MCMC chains were computed for each simulation, with different starting values for each chain to allow computation of the Gelman-Rubin test for convergence (Brooks and Gelman 1998). We ran MCMC simulations for 25,000 iterations, including a 20,000-iteration burn-in period required for convergence. Convergence represents the point beyond which the data do not influence the posterior distribution and dependence on the prior distribution is minimized. We fitted spatial count models using WinBUGS 1.4.1, which provides a means to run MCMC simulations using Gibbs sampling (Spiegelhalter et al. 2003).

One unique aspect of Bayesian analyses is the inclusion of prior beliefs or information which may influence the final outcome. This prior information (hereafter, priors) can be either vague or specific. Because little is known about how environmental variables influence wetland birds at the regional level, we assigned vague prior distributions to parameters in the model (Link and Sauer 2002). Counts, environmental fixed effects (v_k), and nuisance effects all occurred across space (s). Lambda (λ) represents the count of a species on a route for a given year (sample size $k = 1$ to n). Year (γ_k) and observer (ω) effects in counts were given mean zero normal distributions; beta parameters (β_k) and spatial effects (Z) were given normal distributions with a mean of 0 and a variance equal to 1,000 (Link and Sauer 2002, Thogmartin et al. 2004b). The first-time observer effect (η) was an indicator variable (0 or 1). The final model used was

$$\log(\lambda(s)) = \sum_{k=1}^n v_k(s) + Z_k(s) + \omega_k(s) \\ + \eta I(s) + \gamma_k(s) + \varepsilon_k$$

The number of environmental variables that can be measured through remote sensing is large relative to our sample size. Because of risks associated with finding spurious effects when examining a large number of covariates, variables that were thought to be important descriptors of bird abundance were selected a priori. We calculated Spearman's rank correlations for environmental covariates; covariates with a correlation coefficient >0.5 were not included in the same a priori model.

We evaluated the life histories of the Northern Harrier (Smith et al. 2011), Black Tern (Heath et al. 2009), and Marsh Wren (Kroodsmas and Verner 1997) to determine which environmental variables would likely have the most effect on their respective abundances (Table 1). We used these variables to construct a candidate set of models at each spatial scale for each focal species. The total number of models in each candidate set per species-scale combination were 16 for Northern Harrier, 9 for Black Tern, and 12 for Marsh Wren. While habitat preferences varied among our focal species, the metrics that characterized habitat were similar across species and included the percentage of relevant habitats, the amount of habitat edge, interspersions of a given habitat with other habitats, and the size of the largest contiguous habitat patch among others (Table 1). Land-cover types surrounding NABBS routes have been shown to be generally similar to land cover within Bird Conservation Regions as a whole (Niemuth et al. 2007, Veech et al. 2012), so our sampling process should be representative of habitats within BCR11.

We standardized all environmental variables to have a mean of 0 and a standard deviation of 1. This not only improves MCMC convergence (Gilks and Roberts 1996), but also allows comparison of the slopes in the model to assess the relative importance of each variable. We constructed models keeping covariates at a common scale because we did not have sufficient a priori information to warrant constructing multiscale models. We ranked models as to how well they fit the data by comparing the Deviance Information Criteria (DIC) among models and ranking them accordingly (Spiegelhalter et al. 2002), and constrained inference to models that were within 4 DIC units of the best model. This limitation approximates a 95% confidence set of best models (Burnham and Anderson 2002:170). We calculated model weights and variable importance measures to assess the relative importance of each model and variable, respectively. We also ran null models (which contained no environmental variables, only nuisance variables) to provide a reference point to ascertain the degree to which environmental variables improved model fit.

Model Evaluation

We withheld data from 18 NABBS routes in BCR11 (~20% of the total number of routes in the analysis) from model

construction so that known abundance information from these routes could be compared with estimated abundances generated from the best model. Estimated abundances calculated by WinBUGS from the best model were based on prior information, information in the data, and the value of the beta parameters in the model. We compared abundance values calculated for withheld routes with known data using simple linear regression. We evaluated our models using two aspects of model validation: discrimination and calibration. We assessed the ability of the model to predict abundance by comparing the slope of the regression line with a 1:1 correspondence line (calibration) and by examining the R^2 values of the regression line (discrimination). All regression analyses were performed using program R (R Development Core Team 2012).

Relative Abundance Mapping

We created maps of bird abundance across BCR11 for each species. We based the spatial models on the values of the model-averaged beta parameters in each model within the subset of best models (Burnham and Anderson 2002:151). We standardized (subtracted the mean and divided by the standard deviation) data layers in GIS before creating maps of bird abundance to make spatial layers in different units comparable when performing raster algebra and because the same covariates were standardized prior to MCMC simulation. We created three sizes of regular lattices over BCR11; the three sizes corresponded to the spatial extents examined in the study (1,000 ha, 10,000 ha, and 100,000 ha). For each bird species, we summarized environmental covariates in the lattice size at the scale(s) at which the covariate was determined to be important. Final maps of avian abundance had 1,000-m resolution and were computed using the raster calculator in the Spatial Analyst extension of ArcGIS version 9.1 (ESRI 2005).

RESULTS

Both landscape and climatic factors were important descriptors of wetland bird abundance in BCR11 (Table 2). The influence of scale was less pronounced, as models with the same predictor variables at different scales had similar DIC values across all focal species (Table 2). Slope coefficients for the same variable across scales were generally similar, further indicating a lesser importance of landscape scale (Table 3). Climatic variables contributed to predicting bird abundance for all species. None of the best models for any species lacked climatic variables; however, many 95% credibility intervals (Bayesian confidence intervals) overlapped zero, indicating some uncertainty about the influence of climate. Spatial correlation among route counts contributed strongly to predicting bird abundance, with this being the strongest effect for all

three of our study species (Table 3). We considered a variable as having a strong effect if its 95% credibility interval did not overlap zero.

There was moderate model uncertainty present in the best subset of models for predicting Northern Harrier abundance, with five models better than the null. The best model improved on the null model by 1.51 DIC units and had a model weight of 0.26. The small improvement of the best model over the null model suggests that environmental covariates may not be very informative for describing Northern Harrier abundance (Table 2). The most important predictors of Northern Harrier abundance were wetland area at the intermediate and coarsest scales and herbaceous upland largest patch index at the intermediate scale (Table 3). A map of Northern Harrier abundance showed abundance to be highest in central North Dakota and eastern South Dakota, with low abundance in the eastern portion of BCR11 (Figure 2A).

Models explaining Black Tern abundance in BCR11 had a moderate level of model selection uncertainty, with the three best models (which differed only in scale) having a combined model weight of 0.69 (Table 2). The effect of the previous year's precipitation on Black Tern abundance was relatively strong compared with the effects of other covariates, and the influence of temperature was much smaller. Wetland area at the intermediate and coarsest scale and wetland largest patch index at the finest and intermediate scales had the strongest effects on Black Tern abundance (Table 3). In BCR11, Black Tern abundance was most concentrated in central and northeastern North Dakota and in northeastern South Dakota. Lower abundances were predicted in other locations throughout BCR11 (Figure 2B).

Marsh Wrens had the highest degree of model selection uncertainty of our focal species, with the best model having a weight of only 0.14 (Table 2). Model selection uncertainty was the result of the effect of spatial scale and not predictor variables. The models in the best subset for predicting Marsh Wren abundance all contained similar predictor variables, but at different spatial scales (Table 2). Both the previous year's spring temperature and the previous year's precipitation were important climatic influences on Marsh Wrens, with precipitation having a stronger effect. The land-use covariates with the strongest effects were wetland area at the finest and intermediate scales; wetland area at the coarsest scale had a slightly weaker effect (Table 3). Maps of Marsh Wren abundance showed scattered high concentrations of abundance in eastern North Dakota and northeastern South Dakota; western Minnesota also had high predicted abundances of Marsh Wrens (Figure 2C).

In general, validation through discrimination showed that our models predicting wetland bird abundance in BCR11 had fair-to-good fit ($R^2 = 0.18\text{--}0.61$). The

TABLE 2. Explanatory variables, and the scale at which they were evaluated, from the best subset of models predicting abundance of three wetland bird species in the U.S. portion of Bird Conservation Region 11, the Prairie Potholes. Only models within 4 Deviance Information Criteria (DIC) units of the best model are included. The null model (a model without any environmental covariates) was included to serve as a comparison with models containing environmental variables.

Species	Model ^a	Scale (ha) ^b	Parameters ^c	Δ DIC ^d	w_i^e
Northern Harrier	SpringTemp + YearlyPrecip + HerbaceousPlantedLargestPatch + HerbaceousUplandLargestPatch + Contagion + WetlandLargestPatch	100,000	202.107	0.00	0.260
	HerbaceousPlantedLargestPatch + HerbaceousUplandLargestPatch + Contagion + Wetland(%)	100,000	200.331	0.73	0.180
	SpringTemp + YearlyPrecip + Wetland(%)	10,000	199.653	1.00	0.158
	PreviousYearSpringTemp + PreviousYearPrecip + Wetland(%) + Contagion	100,000	201.616	1.13	0.148
	SpringTemp + YearlyPrecip + Wetland(%)	100,000	201.197	1.36	0.132
Black Tern	Null	N/A	209.305	1.51	0.122
	PreviousYearSpringTemp + PreviousYearPrecip + WaterLargestPatch + WetlandLargestPatch	10,000	331.793	0.00	0.271
	PreviousYearSpringTemp + PreviousYearPrecip + WaterLargestPatch + WetlandLargestPatch	100,000	331.612	0.37	0.225
	PreviousYearSpringTemp + PreviousYearPrecip + WaterLargestPatch + WetlandLargestPatch	1,000	332.166	0.64	0.197
	PreviousYearSpringTemp + PreviousYearPrecip + Wetland(%) + Water(%)	100,000	331.984	0.67	0.194
Marsh Wren	PreviousYearSpringTemp + PreviousYearPrecip + Wetland(%) + Water(%)	10,000	332.321	1.75	0.113
	Null	N/A	338.553	12.18	<0.001
	PreviousYearSpringTemp + PreviousYearPrecip + Wetland(%) + PatchRichness	100,000	308.144	0.00	0.140
	PreviousYearSpringTemp + PreviousYearPrecip + Wetland(%) + PatchRichness + WaterInterspersion + Shrubland(%) + Contagion	10,000	309.227	0.07	0.135
	PreviousYearSpringTemp + PreviousYearPrecip + Wetland(%) + PatchRichness + WaterInterspersion + Shrubland(%) + Contagion	1,000	308.050	0.25	0.123
	PreviousYearSpringTemp + PreviousYearPrecip + PatchRichness + Contagion	1,000	308.435	1.11	0.080
	PreviousYearSpringTemp + PreviousYearPrecip + PatchRichness + Contagion	10,000	309.432	1.29	0.073
	PreviousYearSpringTemp + PreviousYearPrecip + Wetland(%) + PatchRichness + WaterInterspersion + Shrubland(%) + Contagion	100,000	309.045	1.41	0.069
	PreviousYearSpringTemp + PreviousYearPrecip + Wetland(%) + WaterInterspersion	10,000	308.534	1.61	0.062
	PreviousYearSpringTemp + PreviousYearPrecip + PatchRichness + Contagion	100,000	309.121	1.66	0.061
	PreviousYearSpringTemp + PreviousYearPrecip + Wetland(%) + PatchRichness	10,000	309.151	1.71	0.059
	PreviousYearSpringTemp + PreviousYearPrecip + Wetland(%) + WaterInterspersion	1,000	308.927	1.74	0.059
Marsh Wren	PreviousYearSpringTemp + PreviousYearPrecip + Wetland(%) + WaterInterspersion	100,000	308.233	1.77	0.058
	PreviousYearSpringTemp + PreviousYearPrecip	100,000	309.470	2.25	0.045
	PreviousYearSpringTemp + PreviousYearPrecip + Wetland(%) + PatchRichness	1,000	308.396	2.76	0.035
	Null	N/A	312.038	10.92	<0.001

^a Descriptions of model parameters can be found in Table 1.

^b The scale at which the variable was measured is presented in hectares. Null models have no scale associated with them.

^c The effective number of parameters is calculated by the posterior mean of the deviance minus the deviance of posterior means.

^d Δ DIC is the difference in DIC between the best model and the model for which the Δ DIC is given. DIC values for the best models are: Northern Harrier: 2124.84, Black Tern: 1846.72, and Marsh Wren: 1946.35.

^e Model weights provide a measure of support for the model relative to the others in the candidate set.

TABLE 3. Means and 95% lower and upper credibility limits (LCL and UCL; i.e. Bayesian confidence intervals) from posterior distributions of explanatory variables in the best subset of models for predicting abundance of three wetland bird species in the U.S. portion of Bird Conservation Region 11, the Prairie Potholes.

Species	Variable ^a	Mean ^b	95% LCL	95% UCL	
Northern Harrier	Previous year spring temperature	0.003	-0.017	0.023	
	Spring temperature	-0.013	-0.061	0.035	
	Previous year precipitation	0.007	-0.017	0.031	
	Yearly precipitation	-0.046	-0.104	0.012	
	*Herbaceous planted largest patch index 1,000	-0.009	-0.017	-0.001	
	Herbaceous planted largest patch index 10,000	-0.002	-0.042	0.038	
	Herbaceous planted largest patch index 100,000	0.053	-0.155	0.261	
	Herbaceous upland largest patch index 1,000	0.007	-0.003	0.017	
	*Herbaceous upland largest patch index 10,000	0.017	0.001	0.033	
	Herbaceous upland largest patch index 100,000	0.065	-0.051	0.181	
	Wetland largest patch index 10,000	0.004	-0.002	0.010	
	Wetland largest patch index 100,000	0.034	-0.020	0.088	
	*Wetland area (%) 1,000	0.060	0.024	0.096	
	*Wetland area (%) 10,000	0.111	0.055	0.167	
	*Wetland area (%) 100,000	0.125	0.023	0.227	
	Contagion 1,000	0.000	-0.004	0.004	
	Contagion 10,000	-0.010	-0.034	0.014	
	Contagion 100,000	-0.160	-0.320	0.000	
	*Spatial conditional autoregressive	-0.939	-1.221	-0.657	
	Black Tern	Previous year spring temperature	-0.077	-0.411	0.257
		*Previous year precipitation	1.024	0.628	1.420
		*Wetland area (%) 10,000	0.153	0.089	0.217
		*Wetland area (%) 100,000	0.249	0.093	0.405
Water area (%) 10,000		0.020	-0.036	0.076	
Water area (%) 100,000		-0.052	-0.164	0.060	
Water largest patch index 1,000		0.070	-0.036	0.176	
Water largest patch index 10,000		-0.026	-0.134	0.082	
Water largest patch index 100,000		-0.122	-0.268	0.024	
*Wetland largest patch index 1,000		0.144	0.036	0.252	
*Wetland largest patch index 10,000		0.290	0.100	0.480	
Wetland largest patch index 100,000		0.173	-0.037	0.383	
*Spatial conditional autoregressive		-2.605	-3.153	-2.057	
Marsh Wren		Previous year spring temperature	0.169	-0.057	0.395
		*Previous year precipitation	0.488	0.206	0.770
	Shrubland (%) 1,000	-0.156	-0.364	0.052	
	Shrubland (%) 10,000	-0.152	-0.358	0.054	
	Shrubland (%) 100,000	-0.103	-0.247	0.041	
	Water interspersion and juxtaposition 1,000	-0.002	-0.110	0.106	
	Water interspersion and juxtaposition 10,000	0.002	-0.132	0.136	
	Water interspersion and juxtaposition 100,000	-0.083	-0.177	0.011	
	*Wetland area (%) 1,000	0.239	0.107	0.371	
	*Wetland area (%) 10,000	0.285	0.109	0.461	
	Wetland area (%) 100,000	0.189	-0.025	0.403	
	Contagion 1,000	-0.028	-0.168	0.112	
	Contagion 10,000	-0.055	-0.217	0.107	
	Contagion 100,000	-0.076	-0.174	0.022	
	*Patch richness density 1,000	0.171	0.039	0.303	
Patch richness density 10,000	-0.011	-0.263	0.241		
Patch richness density 100,000	0.048	-0.142	0.238		
*Spatial conditional autoregressive	-2.586	-3.130	-2.042		

^a An asterisk indicates a strong effect, i.e. the credibility interval did not overlap zero.

^b The mean represents a model-averaged value of the beta parameter based on the values of the beta parameter in each model and the corresponding weight (w_i) of each model (Burnham and Anderson 2002:152).

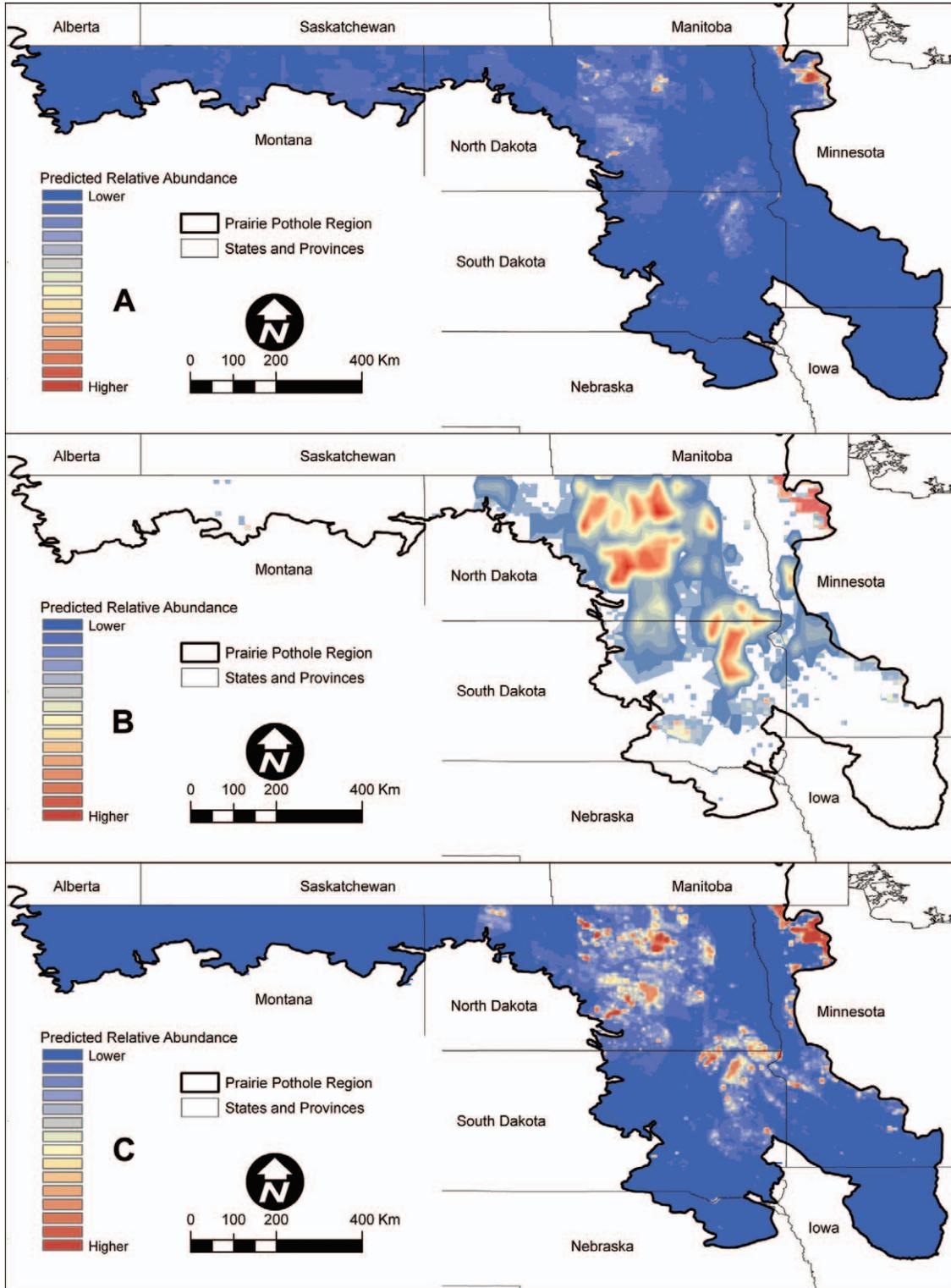


FIGURE 2. Predicted relative abundance from the best model (Table 2) for (A) Northern Harrier, (B) Black Tern, and (C) Marsh Wren in Bird Conservation Region 11, the Prairie Potholes. Color shades are equivalent among maps.

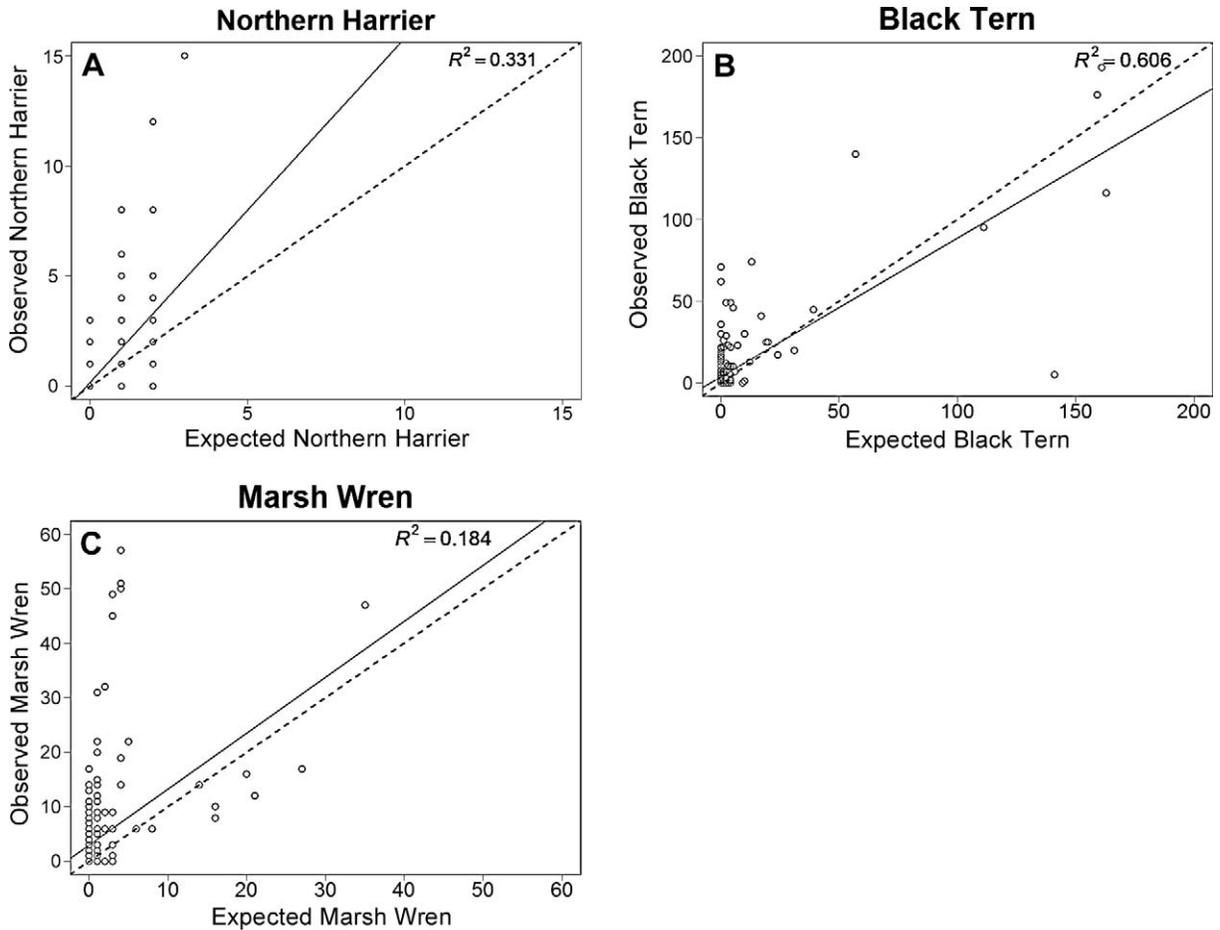


FIGURE 3. Simple linear regression plots of expected and observed species counts validating spatial models for predicting abundance of (A) Northern Harrier, (B) Black Tern, and (C) Marsh Wren in the U.S. portion of Bird Conservation Region 11. The solid line represents the regression line and the dotted line represents a 1:1 correspondence line. The units represent the total number of birds per route.

calibration component of our validation showed that models generally underpredicted bird numbers at the higher range of observed abundances and overpredicted bird abundance when observed bird numbers were low. Generally, the models best predicted abundance when observed numbers were in the middle of the abundance range observed for each species (Figure 3). Zero values made up approximately half of the observed abundances for all three focal species. Of the validation routes where zero birds were observed, our models correctly predicted zero Black Terns 83% of the time, zero Marsh Wrens 81% of the time, and zero Northern Harriers 85% of the time.

DISCUSSION

Our focal species were influenced by both land-cover and climatic variables at all three spatial extents that we examined (1,000 ha, 10,000 ha, and 100,000 ha), with no

particular spatial extent having a predominant effect on bird abundance. Our three study species showed consistent relationships with environmental variables over two orders of magnitude difference in spatial scale.

We included wetland area as a covariate a priori in all candidate models because all focal species utilize wetland areas to some extent within BCR11. Our hypotheses regarding positive relationships with wetland area were confirmed, with all three species showing a strong positive relationship with this variable at one or more spatial scales. Including climatic covariates notably improved model fit for all species except the Northern Harrier, for which inclusion of climatic predictors made only a small improvement. This finding agrees with the results of other studies including that of Venier et al. (2004), who found that adding climatic variables to models with land-cover covariates improved all models in a study of forest songbird distribution in the Great Lakes Basin. Their

finding suggests that climate captured the majority of the variation in species distribution in their study region. Cerulean Warbler, Upland Sandpiper (*Bartramia longicauda*), Grasshopper Sparrow (*Ammodramus savannarum*), and Henslow's Sparrow (*Ammodramus henslowii*) abundance has also been shown to be affected by temperature and precipitation variables, although the strength of the effects varied among species (Thogmartin et al. 2004b, 2006). While climate has proven to be a good predictor of bird abundance and distribution in our study and in others, climatic effects in our study may be more pronounced because we treated the climatic data as a time series covariate rather than as an average over many years as has been done in other studies.

Climate and land cover appeared to have less impact on Northern Harrier populations at larger spatial extents, with the exception of the percentage of wetland area and herbaceous upland largest patch index at the intermediate scale. The positive relationship between Northern Harriers and the percentage of wetland in the landscape was not surprising, given that this species breeds primarily in wetland habitats in the Midwestern United States (Smith et al. 2011). The lack of strong effects of the largest patch index for herbaceous vegetation was unexpected given the area sensitivity of this species (Johnson and Igl 2001, Ribic et al. 2009) and its tendency to nest in old fields and pastures (Smith et al. 2011). Given the lack of a strong relationship, our study results agree more with those of Herkert et al. (1999) and Walk and Warner (1999), who suggested that Northern Harriers are not heavily influenced by the size of grassland tracts as long as the grassland size is larger than ~100 ha.

Strong positive associations were found between Black Tern abundance and precipitation from the previous year, wetland area, and wetland largest patch index. These results were expected, as Naugle et al. (2000) found both total wetland area and wetland size to be important for Black Tern habitat suitability. Our study did not reveal strong effects of water area or water largest patch index, which was unexpected as Black Terns commonly forage over large water bodies (Heath et al. 2009). Our results suggest that Black Terns may be more influenced by the presence of emergent wetland for nesting than by the availability of open water for foraging.

All environmental covariates strongly associated with Marsh Wren abundance were positively related, and included the previous year's precipitation, wetland area at the finest and intermediate spatial scales, and patch richness density at the finest scale. These findings suggest that Marsh Wrens are most affected by landscape variables at smaller scales, especially the presence of edges and the abundance of habitat patches. Our study did not identify any strong associations with shrubland vegetation, which is occasionally used for nesting (Kroodsmas and Verner 1997).

Preferred nesting substrate likely varies across the Marsh Wren's geographic range, and the abundance of cattail marshes in BCR11 probably reduces the likelihood of nesting in shrubs. The coarse classifications in the land-use data also may have precluded the ability to discern strong effects relating to shrubland vegetation (Thogmartin et al. 2004a).

Despite our findings, there are several possible limitations of our study that may have reduced our ability to discern relationships between bird abundance and environmental covariates. Many environmental variables cannot be measured by remote-sensing techniques. For example, many prairie pothole bird species have been shown to benefit greatly from the presence of land set aside by the Conservation Reserve Program (CRP; Johnson and Igl 1995), and cattails provide valuable habitat for many wetland-dwelling birds (Linz et al. 1996). Cattail coverage and CRP lands likely have some effect on wetland birds in BCR11, but spatial data for these variables is lacking. Classification inaccuracies using land-use data from Thematic Mapper imagery can also occur, especially for rare cover types and for smaller ephemeral wetlands (Thogmartin et al. 2004a, Gallant 2009). Thus, we reclassified the NLCD 1992 into broader land-use categories similar to the Anderson level one classification system (Anderson et al. 1976) to reduce classification inaccuracies in our study. Temperature and precipitation interpolations are also imperfect and reduced our ability to find relationships between climate and wetland birds. However, interpolation errors would be most pronounced in geographic areas with low densities of weather recording stations and at small scales. We had a large sample of weather recording stations ($n = 245$); thus, large-scale errors over BCR11 are unlikely, and microvariation in climatic variables at small scales is not relevant for regional-scale modeling efforts.

A final concern with our modeling approach involves using time-series climatic data with static land-cover data. The lack of a time series of land-cover data reduced the amount of information present and prevented evaluation of how bird populations responded to land-cover change over time. Incorporation of time-series land-cover data would likely have improved our ability to detect effects of changes in these variables on bird populations. Despite this lack of temporally relevant data, we were able to elucidate effects of mean land-cover conditions on wetland birds in BCR11, and the strength of these effects were, in some instances, greater than annually varying climatic influences. This is likely because land cover more directly dictates nesting and foraging suitability than climatic variables.

Climatic conditions, especially the amount of annual precipitation, were important predictors of bird abundance. Annual precipitation directly influences wetland availability (Johnson et al. 2010), also an important variable

for predicting abundances of our study species. These findings point to the synergistic effects of climate and land use in the prairie potholes, and the importance of understanding the consequences of a changing climate on resulting land cover. Most models of future climatic conditions in the prairie potholes suggest an increase in mean temperature of nearly 4°C, but only small shifts in mean annual precipitation (–5% to +10%; Johnson et al. 2010). These predictions would perhaps suggest that our focal species will be largely unaffected by a changing climate. However, the hydrologic cycle is expected to intensify, leading to increased frequencies of droughts and floods (Ojima and Lockett 2002, Johnson et al. 2004), which would in turn have huge ramifications for these species through the effects on wetland availability. The models we developed could be used in conjunction with climate models to forecast potential consequences.

Results from both discrimination and calibration validation showed that our models predicted the withheld data with fair-to-good ability ($R^2 = 0.18\text{--}0.61$). Despite a lower R^2 value for Marsh Wrens, mapping the models is still useful as long as the results from model validation are considered when interpreting the maps. In general, models underpredicted bird abundance when observed abundance was high. Low-to-intermediate abundance within each species was generally accurately predicted or overpredicted. Both observations suggest the possibility of a social dimension that we did not incorporate in our models (Thogmartin et al. 2004b). We may have overpredicted abundance in areas where birds were not present because their conspecifics also were not present for reasons of philopatry, conspecific attraction, or other aspects of social organization. This would be especially true for Black Terns, which tend to forage in small flocks (Heath et al. 2009). We suggest that over- or under-prediction of abundance is not a serious issue for two reasons: 1) The absolute abundance prediction is of lesser importance than the relative prediction, and the models generally did predict higher expected counts when observed numbers were also higher and vice versa; and 2) The model validation exercise that we performed identified how the models performed under a variety of input values, and this knowledge can be applied when interpreting the model outputs or when using the models as a predictive tool with a given range of input values. Our maps of relative abundance for wetland birds in BCR11 should be interpreted with these caveats in mind, and should only be used when evaluating the relative abundance of birds across the wider breadth of the region. Abundance maps should be supplemented with ancillary field data before any conservation or management decisions are made in order to validate the presence and relative abundance of the species of interest (LeBrun et al. 2012).

With the conversion of wetlands and grasslands to agriculture, conservation of birds in regions such as BCR11 will continue to remain a priority for biologists and land managers. Application of hierarchical spatial count models to wetland bird conservation and management serves two purposes: 1) Models provide information on how wetland birds are affected by climate and land-use patterns at varying spatial scales; and 2) Maps of predicted relative abundance suggest locations where conservation and management efforts should be focused in order to most efficiently affect habitats that favor (or disfavor) the species of interest. Given the spatial variation in abundance of our focal species within the Prairie Potholes, our predictions are especially useful for targeting locations such as northeastern South Dakota and central North Dakota where management and conservation efforts would be optimally beneficial. Our predictions are based on model-based estimates, and have much finer resolution than interpolations of abundance data from bird surveys alone. While climate is not a factor easily amenable to management, it is possible to manage land-use patterns to aid in the conservation and management of wetland birds in BCR11 (Howell et al. 2008). Further, understanding the relationships of these birds with climate may allow predictions of the effect of climate change on future patterns of distribution and abundance. The ability to model and predict abundance from environmental covariates is one tool that can be applied to regional conservation planning in a repeatable and scientifically justified manner.

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