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Research Article

Spatially Explicit Modeling of Blackbird Abundance in the Prairie Pothole Region

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ABSTRACT Knowledge of factors influencing animal abundance is important to wildlife biologists developing management plans. This is especially true for economically important species such as blackbirds (Icteridae), which cause more than $100 million in crop damages annually in the United States. Using data from the North American Breeding Bird Survey, the National Land Cover Dataset, and the National Climatic Data Center, we modeled effects of regional environmental variables on relative abundance of 3 blackbird species (red-winged blackbird, *Agelaius phoeniceus*; yellow-headed blackbird, *Xanthocephalus xanthocephalus*; common grackle, *Quiscalus quiscula*) in the Prairie Pothole Region of the central United States. We evaluated landscape covariates at 3 logarithmically related spatial scales (1,000 ha, 10,000 ha, and 100,000 ha) and modeled weather variables at the 100,000-ha scale. We constructed models a priori using information from published habitat associations. We fit models with WinBUGS using Markov chain Monte Carlo techniques. Both landscape and weather variables contributed strongly to predicting blackbird relative abundance (95% credibility interval did not overlap 0). Variables with the strongest associations with blackbird relative abundance were the percentage of wetland area and precipitation amount from the year before bird surveys were conducted. The influence of spatial scale appeared small—models with the same variables expressed at different scales were often in the best model subset. This large-scale study elucidated regional effects of weather and landscape variables, suggesting that management strategies aimed at reducing damages caused by these species should consider the broader landscape, including weather effects, because such factors may outweigh the influence of localized conditions or site-specific management actions. The regional species distributional models we developed for blackbirds provide a tool for understanding these broader landscape effects and guiding wildlife management practices to areas that are optimally beneficial. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS bayesian, blackbirds, climate, crop damage, hierarchical models, landscape, MCMC, North American Breeding Bird Survey, Prairie Pothole Region, relative abundance, weather.

Avian habitat studies are commonly used to assess the influence of environmental factors on species presence and abundance, which can be used to inform management decisions. In the past, results from small-scale habitat studies that focus on microhabitats (e.g., Clark and Weatherhead 1986, Murkin et al. 1997, Vierling 1999) were often extrapolated to a regional level, because little information about bird-habitat relationships was available at larger scales (Thogmartin 2007, Thogmartin and Knutson 2007). Although small-scale habitat studies are still common, the number of large-scale (or regional) habitat studies and models is growing because of the wide availability of readily accessible data via the internet, powerful geographic information system (GIS) software, and software for Bayesian analysis (Calder et al. 2003, Link and Sauer 2002, Thogmartin et al. 2004*b*). Regional spatial models and their abundance predictions can be used to identify important geographic areas where management efforts can be focused to be optimally beneficial (Thogmartin et al. 2014). This spatial targeting is especially important when

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allocating scarce management resources across the landscape. Although spatial modeling will not replace traditional management approaches, models can be developed and applied in a repeatable and scientific manner (Thogmartin and Rohweder 2008, LeBrun et al. 2012).

An additional benefit of regional spatial modeling is the ability to evaluate the influence of scale on relative abundance. Scale of covariate analysis can affect the degree to which a given environmental variable affects the presence or abundance of a bird, and its influence can vary widely among studies (Tozer et al. 2010). For example, Saab (1999) found strong bird–habitat relationships at multiple scales including landscape, microhabitat, and macrohabitat; variables measured the landscape level were the most influential factors on abundance. Thogmartin et al. (2004*b*, 2006, 2007) found that cerulean warblers (*Setophaga cerulea*), grassland songbirds, and American woodcock (*Scolopax minor*) were also influenced differently by landscape factors at varying scales. Despite the strong influences found in these studies, other research has found little influence of the spatial scale of variables on the abundance of birds (e.g., Forcey et al. 2011, 2014). The wide-ranging influence of spatial scale on bird-habitat relationships underscores the importance of considering the analysis scale of landscape covariates in modeling efforts (Thogmartin 2007).

Understanding the hierarchical nature of the environmental influences on animal abundance is especially important for species that can have deleterious economic impacts. For example, blackbirds collectively cause more than $100 million in crop damages in the United States each year, with most of this damage occurring in the Prairie Pothole region (Linz et al. 1996, 2011; Klosterman et al. 2013). The economic costs of blackbird damage have led to a variety of management programs including the development of perennial sunflower for foods plots (Hagy et al. 2008, Linz et al. 2014) and herbicide treatments of blackbird nesting vegetation (Linz and Homan 2011), which mostly occur at smaller scales. To date, there is little information on landscape-level influences on blackbird populations. An understanding of how environmental factors are associated with blackbird abundance beyond the local scale, or how such factors behave across scales, could aid in the management of these species. Minimizing crop damage caused by blackbirds also has additional benefits for wildlife management, because agricultural crops are widely used by other species of conservation interest such as migratory songbirds (e.g., Hagy et al. 2010).

We evaluated the influence of landscape composition and configuration along with weather variables on red-winged blackbird (*Agelaius phoeniceus*), yellow-headed blackbird (*Xanthocephalus xanthocephalus*), and common grackle (*Quiscalus quiscula*) relative abundance in the Prairie Pothole Region of the United States, where these species are responsible for the majority of the sunflower crop damage (Peer et al. 2003). Our objectives were to 1) identify the most important attributes of landscape composition and configuration, and weather factors influencing blackbird relative abundance and determine how these factors relate to relative abundance across a gradient of spatial scales, and 2) use the derived spatial models to produce maps predicting the relative abundance of blackbirds across the study region so that the most optimal areas for management can be identified.

STUDY AREA

The Prairie Pothole Region (Bird Conservation Region 11; BCR11), covers over 715,000 km^2 across 5 states and 3 provinces (North American Bird Conservation Initiative 2005). We examined only the portion of BCR11 within the United States because of a lack of continuous and thematically consistent land use data across international boundaries. Vegetation is highly variable across BCR11 because of large differences in hydrology across the region. The economy in BCR11 is largely driven by agriculture, which has greatly affected the region ecologically (Euliss et al. 1999). Historically BCR11 consisted of around 10% wetland (Mitsch and Gosselink 2000); however, over half of preexisting wetlands have been drained for agriculture (Leitch 1989). Although farms are continuing to increase in size and urban areas are expanding, the human population is generally sparse (Leitch 1989).

The climate of BCR11includes precipitation and temperature extremes with the area being typically colder and wetter to the north and east and warmer and drier to the west and south (Kantrud 1989); however, all locations within BCR11 have a negative water balance. Mean daily temperatures in BCR11 remain at or below 0° C for 5 months of the year. Air temperatures can drop below −60° C in the winter and can exceed 40° C during the summer (Euliss et al. 1999). Annual average precipitation nearly triples from 300 mm/year to 900 mm/year from west to east in the region (Millett et al. 2009).

METHODS

We focused our study on 3 species: red-winged blackbird, yellow-headed blackbird, and common grackle. We chose these species because they represent a variety of blackbird taxa, their behaviors are conducive to representation by the North American Breeding Bird Survey (NABBS), and because they are the 3 species most responsible for agricultural damage in BCR11.

Data Acquisition and Processing

Because of the spatial extent of the study, and the impracticality of collecting field data over BCR11, we used data from existing large-scale datasets to model relative blackbird abundance as a function of landscape and weather variables with the goal of predicting relative abundance across BCR11. We used bird abundance data from NABBS routes within BCR11 (Sauer et al. 2014; Fig. 1), land use data from the United States Geological Survey National Land Cover Dataset (NLCD; U.S. Department of the Interior 1992, Vogelmann et al. 2001), and weather data from the National Climatic Data Center (National Climatic Data Center 2014).

The NABBS monitors bird population trends at an international scale (Sauer et al. 2014). Breeding bird survey

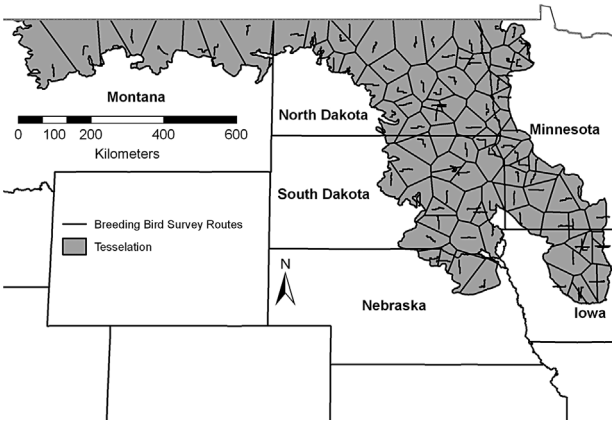

Figure 1. Distribution and tessellation of 95 North American Breeding Bird Survey routes in the United States region of Bird Conservation 11, 1980–2000.

routes are randomly assigned along roadsides across North America and are surveyed every year during late May and June. Each route is 39.4 km in length, and an observer performs 50 counts approximately every 0.8 km along the route. Each count consists of a 3-minute point count, and all birds seen or heard within a 402-m radius are recorded. The same observer surveys each route every year, when possible, with the same method and only under ideal weather conditions (i.e., low wind and minimal precipitation), so there is minimal impact to bird detection rates. The NABBS survey is designed to minimize sampling and detection error so that variance in trends can be detected over time. Despite efforts to maximize detection probabilities within and among NABBS counts, detection probabilities of <1 are present and thus abundance data should be considered relative in nature. We used data from 95 routes in BCR11 for this study; we fit models using data from 77 routes and withheld data from 18 randomly selected routes for model evaluation. We used NABBS data collected from each year between 1980–2000 because this period overlaps the early 1990s when land use data were derived from NLCD satellite imagery (Vogelmann et al. 2001). The long 20-year period (as opposed to shorter periods) allowed us to smooth over the annual variability in the changing landscape and better estimate average effect of land use, much in the same way that a longer time period allows for estimation of an average effect of climate (Hurrell and Loon 1997).

The 1992 NLCD data represent conditions in the United States in the early 1990s and are available in 30-m resolution (Vogelmann et al. 2001). We evaluated landscape variables at 3 spatial scales by creating 3 sizes of buffers—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 reclassified the NLCD from Anderson Level II into a modified Anderson Level I (Anderson et al. 1976) to smooth small-scale variation in land use and reduce potential errors in land use classifications that may occur at finer levels. We calculated landscape variables within each buffer zone using FRAGSTATS 3 (McGarigal et al. 2002). Although habitat preferences vary among the 3 blackbird species, the metrics that characterize habitat were similar across species and included the percentage of relevant habitats, edge density, interspersion of a particular habitat with other habitats, and the size of the largest contiguous habitat patch (Table 1). Land use types surrounding NABBS routes have been shown to be generally similar to land use within BCRs as a whole (Niemuth et al. 2007, Veech et al. 2012), so the sampling methodology should be representative of habitats within BCR11.

We used weather data from 245 recording stations across BCR11 in both the United States and Canada. We used data from Canada with those from the United States as part of another study to evaluate bird-environment relationships in the Canadian region of BCR11 (Forcey et al. 2007). We calculated total precipitation as follows (Akinremi et al. 1999):

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

We used the Spatial Analyst extension of ArcGIS 9.1 (Environmental Systems Research, Inc. [ESRI] 2005) along with the kriging function to create a continuous surface for each weather variable for each year from 1980 to 2000 over BCR11. This allowed us to estimate weather variables around NABBS routes from the information at nearby weather stations. Within each 10-km buffer surrounding each NABBS route, we averaged the grid cell values to compute a value for each weather variable for each route for each year. Resolution of weather interpolations was 1,000 m.

Abundance Modeling

We modeled total blackbird relative abundance per route per year from 1,212 NABBS counts (surveyed by 145 observers from 1980–2000) as a function of nuisance effects associated with the survey design, landscape variables, and weather variables. We used a hierarchical Poisson regression model for several reasons. Hierarchical models can be crafted to acknowledge correlation among multiple observational units, which are present in the survey design. Poisson regression counts are typically discrete positive values. In a Bayesian framework, all unknown quantities are treated as random variables and therefore they provide a natural approach to this type of analysis (Link and Sauer 2002). Modeling in a Bayesian framework simultaneously accommodated the Poisson-distributed counts, nuisance effects associated with the NABBS, and spatial autocorrelation present in the data.

We fit models using Markov chain Monte Carlo (MCMC) techniques using Gibbs sampling (Link et al. 2002, Gelman et al. 2004). We computed 3 MCMC chains 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 substantively influence the posterior distribution and dependence on the prior distribution is minimized. We

Table 1. A priori weather and landscape variables included in suites of candidate models for predicting relative abundance of red-winged blackbirds (RWBL), yellow-headed blackbirds (YHBL), and common grackles (COGR) in the United States region of Bird Conservation Region 11 in the Prairie Potholes based on survey data from 1980 to 2000. All covariates were standardized with a mean of 0 and standard deviation of 1.

Type of variable	Variable	Variable description	Species that variable was modeled[a]
Weather	Previous year precipitation	Total precipitation from the year prior to when bird abundance was measured	All species
	Previous spring temperature	Mean spring temperature from the spring prior to when bird abundance was measured	All species
	Yearly precipitation	Total precipitation from the same year bird abundance was measured	All species
	Yearly temperature	Mean yearly temperature from the same year bird abundance was measured	YHBL
	Spring temperature	Mean spring temperature from the same year bird abundance was measured	All species
Patch-level landscape	Developed (%)	Percentage of developed area in the landscape (includes roads, buildings, etc.)	YHBL, COGR
	Forest edge density	Amount of forest edge per hectare	YHBL, COGR
	Herbaceous planted (%)	Percentage of herbaceous planted in the landscape (includes cropland, fallow, and, pasture)	RWBL
	Herbaceous upland (%)	Percentage of herbaceous planted in the landscape (includes grasses and forbs)	RWBL
	Wetland (%)	Percentage of vegetated wetland in the landscape	All species
	Wetland largest patch index	Percentage of total landscape comprised by the largest patch of wetland	YHBL
	Wetland interspersion and juxtaposition index[b]	Percentage of land use types that are adjacent to vegetated wetland	RWBL, YHBL
Total landscape	Contagion[c]	Aggregation of different patch types in the landscape (low contagion indicates many land uses in the landscape)	All species
	Patch richness density	Number of different land uses present per 100 ha	All species
	Simpson's diversity[d]	Diversity of land uses in the landscape	RWBL, COGR

[a] Detailed review of life history and justification for including variables for each species can be found in Forcey (2006).
[b] Interspersion and juxtaposition is approximately 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.
[c] Contagion is approximately 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.
[d] Simpson's diversity index represents the chance that any 2 grid cells selected at random would be different land use types.

fitted the spatial Poisson models using WinBUGS 1.4.1 (Spiegelhalter et al. 2003).

We included temporal, spatial, and observer variables to account for nuisance effects in the variation among counts so we could look at unbiased trends in relative abundance. Temporal correlation in bird counts was present among years, spatial correlation was present among routes, and observers have varying degrees of birding acumen, which can influence detections. We included a year effect and a trending term to account for temporal variation in bird relative abundance that occurs as populations naturally fluctuate over time. We included a spatial conditional autoregressive (CAR) prior distribution on the route effect to account for spatial autocorrelation present in the data (Banerjee et al. 2004). We derived an adjacency matrix (Lawson et al. 2003) within BCR11 by using a tessellation of NABBS routes within BCR11 and creating an irregular lattice (Hooge and Eichenlaub 2000; Fig. 1). We accounted for spatial autocorrelation when routes shared a common boundary in the tessellation; we did not consider distances among routes, although this is possible in other applications (Thogmartin et al. 2004*b*). We included 2 observer covariates in the model. The first observer variable accounted for differences in surveying abilities among observers (Sauer et al. 1994) as well as improvements in observer bird identification over time through experience, increased surveying efficacy, and associating certain species with individual stops (Kendall et al. 1996). The second observer effect was a 0 or 1 and accounted for inexperience (a first-time observer effect).

Because little information is known about how environmental variables influence blackbirds at the regional level, we assigned vague prior distributions to parameters in the model (Link and Sauer 2002). Counts, environmental covariates (v_k), and nuisance effects all occurred across space (s). Lambda (λ) represents the expected or mean count of a species on a route for a given year (sample size $k = 1$ to n). We gave year (γ_k), observer (ω_k), and overdispersion (ε_k) effects in counts mean zero normal distributions; we gave beta parameters (β_k), and spatial effects (Z_k) normal distributions with mean of 0 and variance equal to 1,000. The first-time observer effect (η) was an indicator variable (0 or 1; Link and Sauer 2002, Thogmartin et al. 2004*b*). The final model equation used was

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

Given the large number of environmental variables that can be measured through remote sensing and concomitant risks associated with finding spurious effects when examining a large number of covariates, we selected variables that we thought to be important descriptors of each blackbird species a priori before fitting models. We reviewed published habitat associations and life histories for blackbirds to determine which environmental variables would be likely to have the

most effect on relative abundance (Table 1); a detailed review of life history for each species can be found in Forcey (2006). We used these variables to construct a candidate set of models at each spatial scale for each species. We constructed all candidate model sets at a common scale because sufficient a priori information was not available to warrant constructing multi-scale models. 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 created a Spearman's rank correlation matrix for our environmental covariates and excluded covariates from the same a priori model that had a correlation coefficient of >0.5.

We ranked models as to how well they were supported by the data by comparing the Deviance Information Criterion (DIC) among models (Spiegelhalter et al. 2002). We constrained our inferences to models within 4 DIC units of the best model, which approximates a 95% confidence set of best models (Burnham and Anderson 2002:170). We calculated model weights to assess the relative importance of each model and determined the strength of each variable by evaluating its credibility interval. We considered a variable as having a strong effect if its 95% credibility interval did not overlap 0. We also fitted null models (which contained no environmental variables, only nuisance variables) to compare to models with environmental covariates to determine the extent that model fit was improved.

We compared abundance information from the withheld routes with predicted relative abundances from the best model. Estimated counts 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 from withheld routes to predicted values using simple linear regression. We evaluated model performance using calibration and discrimination. We evaluated the each model's ability to predict abundance by comparing the slopes of the regression line to a 1:1 correspondence line (calibration) and by examining the R^2 values of the regression line (discrimination). We performed all regression analyses using *R* (R Development Core Team 2012).

We created maps of relative predicted bird abundance across BCR11 for each blackbird species in this study by calculating output grids based on the model-averaged beta parameters in each model within the subset of best models (Burnham and Anderson 2002:151). We standardized all data layers in the GIS before calculating the modeled prediction, because the same covariates were standardized prior to MCMC simulation. Standardization also made all the layers dimensionless thereby providing consistent units across variables. We created 3 sizes of fishnet grids over BCR11 corresponding to the spatial extents examined in the study (1,000 ha, 10,000 ha, and 100,000 ha). For each bird species, we calculated the values of environmental covariates in a lattice size equaling the scale(s) at which it was determined to be important. Final maps of avian relative abundance had a 1,000-m resolution and were computed using the Spatial Analyst extension of ArcGIS 9.1 (ESRI 2005).

RESULTS

Landscape and weather variables were both important in predicting spatial patterns of blackbird abundance. Counts of red-winged and yellow-headed blackbirds were both positively associated with precipitation in the previous year and the amount of wetland habitat (Table 2). A 1 standard deviation increase (207 mm) in previous year precipitation increased red-winged blackbird abundance by 2.6% and yellow-headed blackbirds by 7.9%. A 1 standard deviation increase in the percentage of wetland habitat at the finest scale (2.7%) increased red-winged blackbird abundance by 2.9%. The percentage of wetland in the landscape was even more influential for yellow-headed blackbirds with a 1 standard deviation increase in the finest (2.7%), intermediate (3.4%), and coarsest scales (7.2%) increasing abundance by 12%, 11%, and 82.5% respectively.

Conversely, common grackles were not associated with precipitation or the amount of wetland habitat but were strongly associated with warmer spring temperatures (Table 2). A 1 standard deviation increase in spring temperature (2.1° C) increased common grackle abundance by 3.3%. Forest edge density was negatively associated with abundance for yellow-headed blackbirds at the finest and intermediate scales and common grackles at the coarsest scale. A 1 standard deviation increase in the percentage of forest at the finest (11.6%) and intermediate scales (11.5%) decreased yellow-headed blackbird abundance by 7.7% and 6.7%, respectively. Similarly a 1 standard deviation increase in the percentage of forest at the coarsest scale (10.9%) decreased common grackle abundance by 6.5%. The majority of parameter estimates for each species were equivocal and consistent across spatial scales, suggesting little scale dependence in habitat associations (Table 2). Spatial patterns in blackbird abundance were also strongly mediated by the spatial structure of the data, as represented by the strong effects of the conditional autoregressive term in our models (Table 2).

Model uncertainty was high for all 3 species, with the most supported models exhibiting DIC weights of 0.059, 0.197, and 0.093 for red-winged blackbirds, yellow-headed blackbirds, and common grackles respectively (Table S1). For each species, there were at least 14 models within 4 ΔDIC units of the best model, each of which contained weather and landscape variables (Table S1). For red-winged blackbirds and common grackles, little pattern was evident among the best-supported models with regards to the spatial scale at which the models were developed. However, for yellow-headed blackbirds, the top 6 models were all developed at the 100,000-ha scale and collectively contained 0.657 of the total model weight (Table S1).

Geographical patterns in relative abundance varied among species. Red-winged blackbirds were predicted to be abundant across BCR11, with high predicted relative abundance in northwest Minnesota and lower elsewhere

Table 2. Posterior distributions of explanatory variable associations in the best subset of models for explaining blackbird abundance in the United States region of Bird Conservation Region 11, 1980–2000. We present means, 95% credibility intervals (lower [LCL] and upper credibility limits [UCL]); strong effects are those variables whose 95% credibility interval does not overlap 0.

Species	Variable[a]	Mean[b]	95% LCL	95% UCL
Red-winged blackbird	Spring temperature	−0.003	−0.029	0.023
	Yearly precipitation	0.009	−0.003	0.021
	Previous year spring temperature	0.001	−0.005	0.007
	*Previous year precipitation	0.026	0.006	0.046
	Herbaceous planted (%) 1,000	0.006	−0.002	0.014
	Herbaceous planted (%) 10,000	0.006	−0.002	0.014
	Herbaceous planted (%) 100,000	0.006	−0.004	0.016
	Herbaceous upland (%) 1,000	−0.006	−0.018	0.006
	Herbaceous upland (%) 10,000	−0.007	−0.017	0.003
	Herbaceous upland (%) 100,000	−0.006	−0.018	0.006
	Wetland interspersion juxtaposition index 1,000	0.006	−0.014	0.026
	Wetland interspersion juxtaposition index 10,000	−0.002	−0.024	0.020
	Wetland interspersion juxtaposition index 100,000	−0.022	−0.046	0.002
	*Wetland area (%) 1,000	0.029	0.005	0.053
	Wetland area (%) 10,000	0.026	0.000	0.052
	Wetland area (%) 100,000	0.009	−0.023	0.041
	Contagion 1,000	0.005	−0.003	0.013
	Contagion 10,000	0.002	−0.004	0.008
	Contagion 100,000	0.002	−0.004	0.008
	*Patch richness density 1,000	0.028	0.004	0.052
	*Patch richness density 10,000	−0.025	−0.049	−0.001
	Patch richness density 100,000	−0.002	−0.018	0.014
	Simpson's diversity index 1,000	−0.003	−0.011	0.005
	Simpson's diversity index 10,000	0.000	−0.010	0.010
	Simpson's diversity index 100,000	0.002	−0.008	0.012
	*Spatial conditional autoregressive	4.602	4.480	4.724
Yellow-headed blackbird	Spring temperature	0.003	−0.013	0.019
	Yearly temperature	−0.010	−0.082	0.062
	*Yearly precipitation	0.086	0.002	0.170
	Previous year spring temperature	0.004	−0.010	0.018
	*Previous year precipitation	0.076	0.026	0.126
	Developed area (%) 1,000	−0.042	−0.088	0.004
	Developed area (%) 10,000	−0.006	−0.038	0.026
	Developed area (%) 100,000	−0.052	−0.462	0.358
	*Forest edge density 1,000	−0.080	−0.144	−0.016
	*Forest edge density 10,000	−0.069	−0.117	−0.021
	Forest edge density 100,000	−0.298	−0.746	0.150
	Wetland interspersion juxtaposition index 1,000	0.007	−0.041	0.055
	Wetland interspersion juxtaposition index 10,000	0.029	−0.017	0.075
	Wetland interspersion juxtaposition index 100,000	−0.338	−0.702	0.026
	*Wetland area (%) 1,000	0.114	0.048	0.180
	*Wetland area (%) 10,000	0.108	0.056	0.160
	*Wetland area (%) 100,000	0.602	0.192	1.012
	Wetland largest patch 100,000	0.029	−0.007	0.065
	Patch richness density 100,000	−0.029	−0.081	0.023
	Contagion 100,000	−0.076	−0.156	0.004
	*Spatial conditional autoregressive	1.320	1.052	1.588
Common grackle	*Spring temperature	0.032	0.012	0.052
	Yearly precipitation	0.002	−0.004	0.008
	Previous year precipitation	−0.005	−0.027	0.017
	Previous year spring temperature	0.030	0.000	0.060
	Developed area (%) 1,000	0.084	−0.002	0.170
	Developed area (%) 10,000	0.115	−0.001	0.231
	Developed area (%) 100,000	−0.013	−0.099	0.073
	Forest edge density 1,000	−0.051	−0.111	0.009
	Forest edge density 10,000	−0.072	−0.144	0.000
	*Forest edge density 100,000	−0.067	−0.121	−0.013
	Wetland area (%) 1,000	0.015	−0.025	0.055
	Wetland area (%) 10,000	0.000	−0.040	0.040
	Wetland area (%) 100,000	−0.020	−0.052	0.012
	Patch richness density 1,000	−0.011	−0.033	0.011
	Patch richness density 10,000	−0.003	−0.043	0.037
	Patch richness density 100,000	0.003	−0.009	0.015
	Contagion 1,000	0.014	−0.006	0.034
	Contagion 10,000	0.002	−0.030	0.034

(*Continued*)

Table 2. (*Continued*)

Species	Variable[a]	Mean[b]	95% LCL	95% UCL
	Contagion 100,000	0.004	−0.006	0.014
	Simpson's diversity index 1,000	−0.019	−0.041	0.003
	Simpson's diversity index 10,000	−0.017	−0.055	0.021
	Simpson's diversity index 100,000	−0.014	−0.034	0.006
	*Spatial conditional autoregressive	3.567	3.415	3.719

[a] A starred (*) variable had strong effects (95% credibility intervals do not overlap 0) for predicting blackbird abundance. Numbers after variables indicate scale in hectares.

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

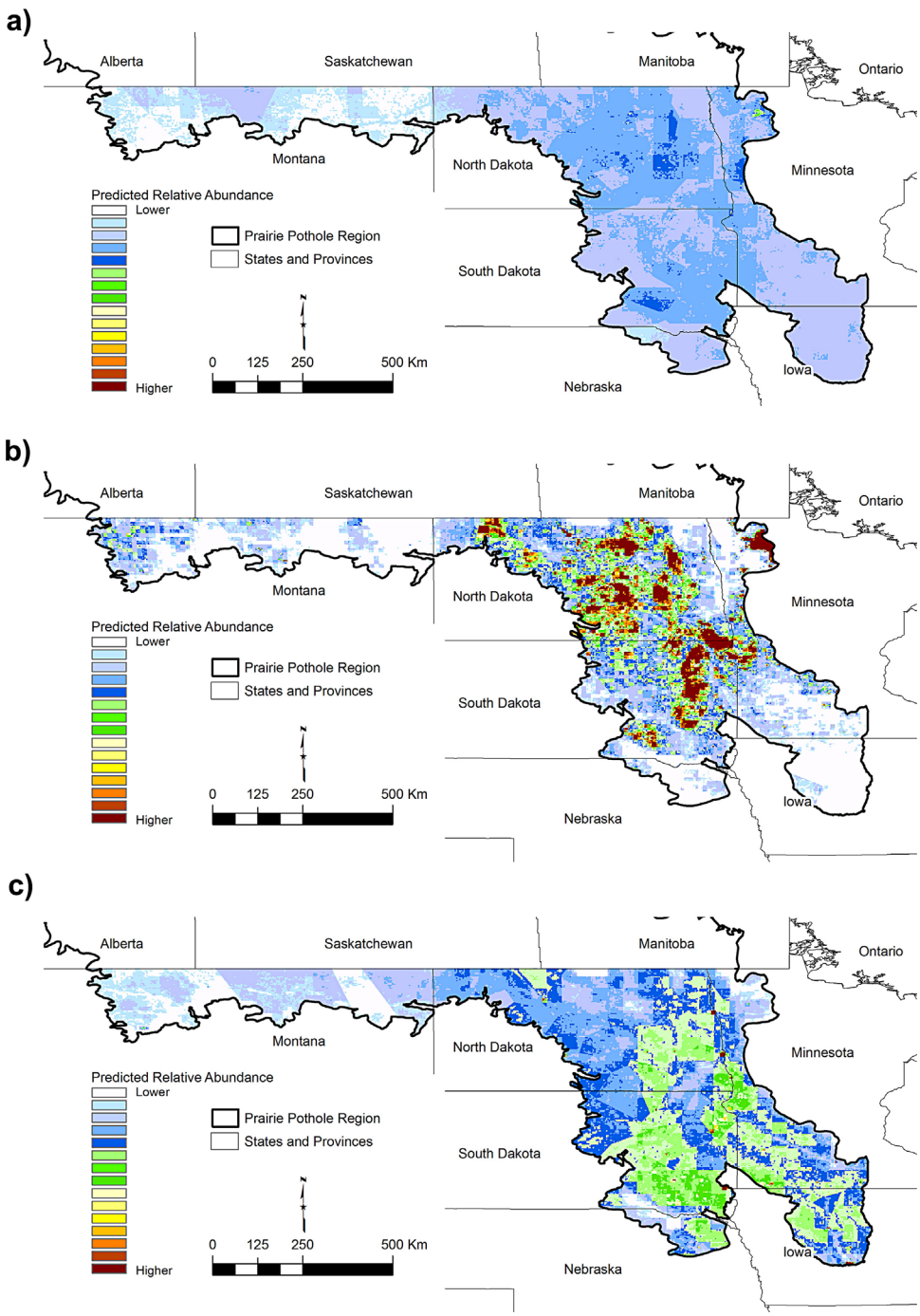

Figure 2. Predicted relative abundance for red-winged blackbird (a), yellow-headed blackbird (b), and common grackle (c) in the United States region of Bird Conservation Region 11, the Prairie Potholes based on survey data from 1980 to 2000. Different color shades should only be treated as a difference in predicted relative abundance within a species.

(Fig. 2). Yellow-headed blackbirds were predicted to exhibit locally high numbers throughout North Dakota and eastern South Dakota and lower relative abundances elsewhere, with very little area predicted to have intermediate densities (Fig. 2). Common grackles were predicted to be most abundant in western Minnesota and southeastern South Dakota, with lower densities throughout the northern portion of the study area (Fig. 2).

In general, model evaluation indicated models predicting blackbird abundance had moderate fit ($R^2 = 0.23$–0.49, $P < 0.001$). Red-winged blackbirds and common grackles were accurately predicted but with poor precision at intermediate levels of predicted abundance, whereas yellow-headed blackbirds were precisely predicted but biased high relative to observed counts (Fig. 3).

DISCUSSION

Hierarchical modeling elucidated relationships between blackbird relative abundance and large-scale landscape and weather variables at all 3 spatial extents, although the level of influence varied among species, scales, and variable types (landscape vs. weather). Overall, no particular spatial extent had a predominant effect on bird relative abundance, although models at the coarsest scale did garner a large amount of the overall model weights for yellow-headed blackbird. However, even for this species there were multiple models from each spatial scale receiving some support (ΔDIC <4). Much of the model selection uncertainty we observed was due to models with the same variables at different scales occurring in the best subset, indicating a weak influence of spatial scale on our focal species. Although spatial scale at which covariates were measured has been shown to be important in other studies (Pribil and Picman 1997, Saab 1999, Holland et al. 2004), it may be unimportant for most blackbirds in BCR11 because the scales used in the analyses do not correspond to the scales that influence blackbirds or because of other limitations (see below).

Landscape Effects

We included wetland area as a variable in all a priori candidate models because all 3 blackbird species use wetland areas to some extent in BCR11. Our hypotheses regarding positive relationships with wetland area were largely confirmed with red-winged blackbirds and yellow-headed blackbirds, showing a positive relationship with this variable at 1 or more scales. Although red-winged blackbirds were positively associated with this variable, the strength of this variable was weak compared to yellow-headed blackbirds. We attribute this to the red-winged blackbird's ability to occupy upland and agricultural habitat in addition to wetland areas (Yasukawa and Searcy 1995). Another explanation is that some dominant wetland vegetation such as cattail (*Typha* spp.) is not distinctly identified in the NLCD. Cattail density is an important influence on the presence of blackbirds and other wetland-dwelling birds in the prairie landscape (Twedt and Crawford 1995, Yasukawa and Searcy 1995, Linz et al. 1996), but this vegetation was not classified as a separate land use type and therefore could not be modeled. Red-winged blackbirds have also been shown to greatly benefit from the presence of land set aside by the Conservation Reserve Program (CRP; Johnson and Igl 1995). Although cattail density and CRP likely have some

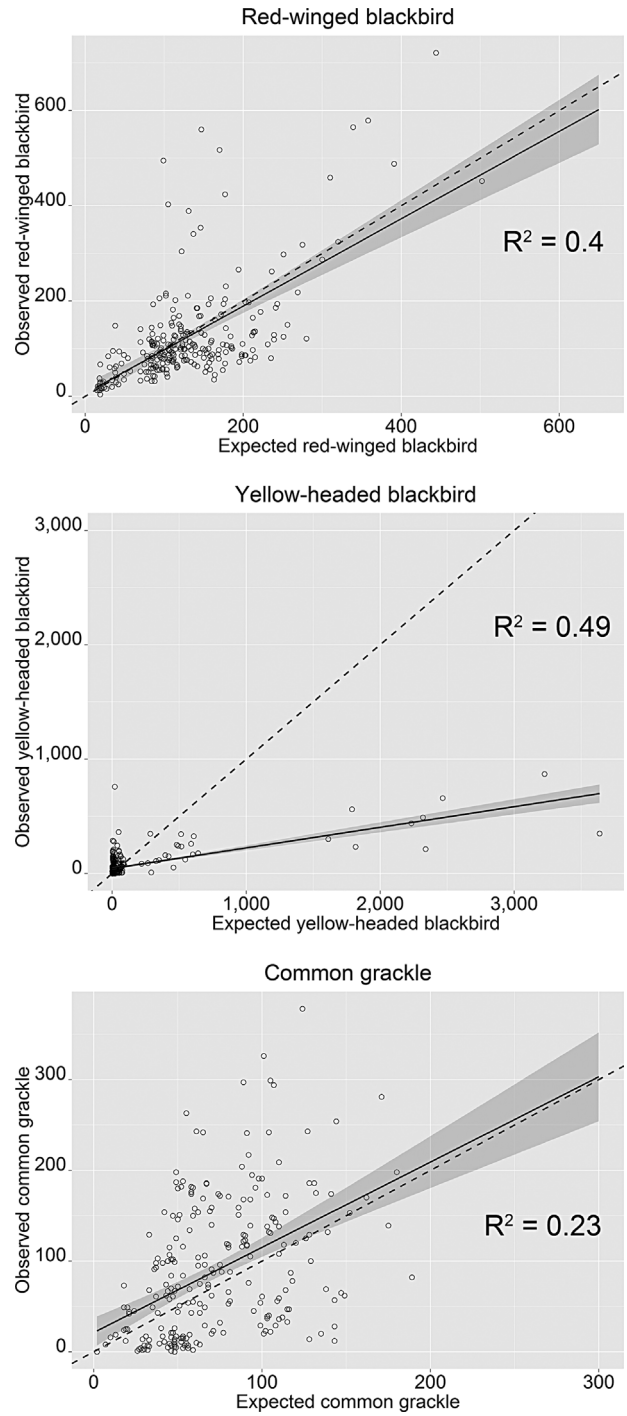

Figure 3. Simple linear regression plots used to evaluate the validity of spatial models for predicting bird relative abundance in the United States region of Bird Conservation Region 11, 1980–2000. The solid line represents the regression line, the dotted line represents a 1–1 correspondence line, and the shaded areas represent the 95% confidence interval on the regression line. The units on both the x and y axes represent the number of birds per Breeding Bird Survey route.

effect on blackbirds in BCR11, the lack of spatial data on these variables limited our ability to reveal these relationships.

Counts of yellow-headed blackbirds showed strong positive relationships with wetland area, indicating the importance of this habitat during the breeding season (Twedt and Crawford 1995). Although Fairbairn and Dinsmore (2001) found percentage of marsh to be an important predictor of common grackle density, we did not find a similar result in our study. The negative relationship with wetland area and common grackle relative abundance can be explained by this species' preference for woody vegetation rather than strictly wetland habitat (Peer and Bollinger 1997). Another potential reason could be interpretation errors that can occur when images are classified into discrete land use types. Uncommon land use types and small ephemeral wetlands are especially prone to being incorrectly classified or completely overlooked when digitizing Thematic Mapper data (Thogmartin et al. 2004*a*, Gallant 2009). Successfully classifying smaller continuous areas of habitat is often dependent on the output resolution. In Canada, where land use data resolution is 100 m, Forcey et al. (2007) found little influence of landscape variables on bird abundance, whereas many strong relationships occurred in our study in the United States with 30-m resolution land use data. We attribute this finding to differences in land use data resolution and classifications between the United States and Canada and not to ecological differences between countries. Despite having access to 30-m land use data, we attempted to minimize classification errors by reclassifying the NLCD 1992 into broader land use categories similar to the Anderson level 1 classification system (Anderson et al. 1976).

Our a priori hypothesis of a negative relationship between both developed area and forest edge density and yellow-headed blackbird relative abundance was confirmed only at the finest scale for forest edge density and not at any scale for the amount of developed area, although parameter estimates for each variable were negative. Naugle et al. (1999) did not find any strong associations between yellow-headed blackbirds and woody vegetation, which partially supports our inconsistent findings with respect to forest edge density. Yellow-headed blackbirds generally prefer large continuous areas of habitat with little interspersion of other cover types during the breeding season (Twedt and Crawford 1995). Twedt and Crawford (1995) also supports our finding of a negative relationship between relative abundance and forest edge density for yellow-headed blackbird; however, the influence of the amount of wetland area appears to overwhelm the negative influence of habitat fragmentation in this case. Forest edge density was negatively associated with common grackle relative abundance, which was unexpected for this species given that it is frequently associated with woody vegetation for nesting (Peer and Bollinger 1997). Conflicting results from our study are likely due to the land use data, which represent only larger continuous areas of forest and overlooks small patches of trees that surround wetlands.

There was little evidence of an association between red-winged blackbird abundance and herbaceous planted vegetation, which was unexpected because strong associations between red-winged blackbirds and crop production have been previously reported (Clark et al. 1986). Murkin et al. (1997) found positive relationships between the number of vegetation interfaces in wetlands and bird abundance; however, we found little support for wetland juxtaposition being an important predictor of red-winged blackbird relative abundance. However, we did find evidence that patch richness density was positively associated with relative abundance at the smallest spatial scale, although it was negatively associated with red-winged blackbird relative abundance at the intermediate scale. This discrepancy shows an unclear relationship among scales for patch richness density.

Weather Effects and Implications for Climate Change

Weather variables were also important predictors of bird relative abundance, and all candidate models for each species in the best subset included at least 1 weather variable. Red-winged blackbirds and yellow-headed blackbirds were positively associated with precipitation variables and common grackles were positively associated with warmer temperatures. The lack of a relationship between precipitation variables and common grackle abundance is likely because they are less wetland dependent (Peer and Bollinger 1997) than red-winged blackbirds and yellow-headed blackbirds (Twedt and Crawford 1995, Yasukawa and Searcy 1995) or potentially because of issues with the weather data interpolations. Interpolations of weather data are imperfect and may limit our ability to find specific temperature and precipitation relationships with blackbirds. Areas of imperfection would be largest in areas with few weather stations and at small scales. Because our interpolations are based on a large sample of weather stations ($n = 245$), we suggest that large-scale errors over BCR11 are unlikely and that micro variation in weather variables at small scales is not relevant for landscape-scale models.

The importance of weather in our study concurs with other studies including Venier et al. (2004), who found that adding weather variables to models with landscape covariates improved fit for forest songbirds and Cotgreave (1995) also noted strong relationships between temperature and precipitation variables and bird abundance patterns. Cerulean warblers and 5 grassland bird species were also shown to be associated with weather variables, though the strength of the associations varied among species (Thogmartin et al. 2004*b*, 2006). Weather associations found in our study may have been more pronounced because of additional information present in multi-year time series data as opposed to a mean of >10 years of data used in several of the previously mentioned studies. Conflating time series weather data with static land use data still precludes an evaluation of how bird populations respond to land use change over time. This issue might be more pronounced in BCR11 because of the addition of CRP land in this area from 1980 to 2000; however, changes in land use over time would be accommodated in our model by the random

effect associated with years. Despite the absence of time series land use data, we were able to show effects of land use on blackbirds in BCR11. Those effects were, in some cases, greater than weather influences. This finding is likely due to land use, which directly dictates foraging and nesting suitability during the breeding season more than weather variables.

The positive association of previous-year precipitation with abundance of red-winged blackbirds and yellow-headed blackbirds was expected given the strong effects of wetland area on these species. Annual precipitation directly influences wetland availability (Johnson et al. 2010), which is also a strongly influential covariate for predicting abundance of these species. These results suggest the presence of interactive effects of weather and landscape variables in BCR11 and underscores the importance of understanding weather change and its influence on temporal land use changes. The majority of models predicting future climate conditions in BCR11 suggest an increased mean temperature of nearly 4° C but only small shifts in mean annual precipitation (−5% to +10%; Johnson et al. 2010). This suggests that red-winged blackbirds and yellow-headed blackbirds will largely be unaffected by a changing climate, but that common grackles could be more strongly affected. Conversely, the hydrologic cycle is expected to have increased variation between wet and dry years, leading to an increased frequency of drought and floods (Ojima et al. 2002, Johnson et al. 2004). These large precipitation swings would have ramifications for red-winged blackbirds and yellow-headed blackbirds because of their dependence on wetland availability. Our models could be used in conjunction with climate models to forecast the magnitude of these potential consequences.

Model Evaluation

Results from calibration and discrimination model evaluation show that models generally predicted the withheld data fair to moderately well ($R^2 = 0.23$–0.49). Generally, models under-predicted bird abundance when observed abundance was high. Low to intermediate abundance within each species was generally accurately predicted or over-predicted. Models grossly over-predicted abundances for yellow-headed blackbirds for 9 counts on route 18 in north-central North Dakota. This route is surrounded by a disproportionate amount of wetland area at the finest and intermediate scales compared to other routes in BCR11. Given the strength of association of these variables with yellow-headed blackbirds (Table 2), the model over-predicted abundance of this species on this NABBS route. However, the observed numbers on this route were in the upper range of abundances recorded for this species during the NABBS (>500 birds). This suggests that although estimated raw numbers of birds may be unreliable for certain species, the models still predicted patterns in abundance well. Despite a lower R^2 value for common grackle, mapping model predictions may still be useful as long as the results from model evaluation are considered when interpreting the maps.

We suggest that over- or under-prediction of observed abundance is not fatal to valid inferences for 2 reasons, First, managers will concentrate decision-making on the patterns in the relative predictions rather than the magnitude of the prediction at any single location; in this regard, the models predicted higher expected counts where observed numbers were also higher and vice-versa. Second, the model evaluation exercise identified how the models perform under a range of input values; this knowledge can be applied when interpreting the outputs or when being used as a predictive tool. Relative abundance maps for blackbirds in BCR11 should be interpreted with this consideration and should not be used to evaluate absolute abundance. Before any blackbird management decisions are made, abundance maps should be supplemented with ancillary field data to validate presence and relative abundance of the species of interest (LeBrun et al. 2012).

MANAGEMENT IMPLICATIONS

Increased agricultural production fosters wetland loss and increases the chances of human-blackbird conflicts due to crop depredation. Application of hierarchical spatial count models to blackbird conservation and management can serve 2 purposes: 1) models provide information on how blackbirds are associated with weather and landscape patterns at different spatial scales, and 2) maps of predicted relative abundance indicate locations where management efforts should be focused so that they are optimally effective. Although weather is not a factor that can be managed, it is possible to manage landscape patterns to aid in the management of blackbirds in BCR11. Understanding the influences of weather on blackbirds may allow researchers to assess the magnitude of climatic influences on future patterns of distribution and abundance and adjust management planning accordingly. For example, managers interested in reducing blackbird damage to crops may wish to focus their efforts on areas with high levels of precipitation, as our results suggest that such areas may harbor greater numbers of red-winged blackbirds and yellow-headed blackbirds. An understanding of regional variability in weather and climate could greatly aid in the management of species that respond in a consistent and predictable manner to climate and weather patterns.

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