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Population Ecology

Evaluating the Ability of Regional Models to Predict Local Avian Abundance

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ABSTRACT Spatial modeling over broad scales can potentially direct conservation efforts to areas with high species-specific abundances. We examined the performance of regional models for predicting bird abundance at spatial scales typically addressed in conservation planning. Specifically, we used point count data on wood thrush (*Hylocichla mustelina*) and blue-winged warbler (*Vermivora cyanoptera*) from 2 time periods (1995–1998 and 2006–2007) to evaluate the ability of regional models derived via Bayesian hierarchical techniques to predict bird abundance. We developed models for each species within Bird Conservation Region (BCR) 23 in the upper midwestern United States at 800-ha, 8,000-ha, and approximately 80,000-ha scales. We obtained count data from the Breeding Bird Survey and land cover data from the National Land Cover Dataset (1992). We evaluated predictions from the best models, as defined by an information-theoretic criterion, using point count data collected within an ecological subregion of BCR 23 at 131 count stations in the 1990s and again in 2006–2007. Competing (Deviance Information Criteria <5) blue-winged warbler models accounted for 67% of the variability and suggested positive associations with forest edge and proportion of forest at the 8,000-ha scale, and negative associations with forest patch area (800 ha) and wetness (800 ha and 80,000 ha). The regional model performed best for blue-winged warbler predicted abundances from point counts conducted in Iowa during 1995–1996 ($r_s = 0.57$; $P = 0.14$), the survey period that most closely aligned with the time period of data used for regional model construction. Wood thrush models exhibited positive correlations with point count data for all survey areas and years combined ($r_s = 0.58$, $P \leq 0.001$). In comparison, blue-winged warbler models performed worse as time increased between the point count surveys and vintage of the model building data ($r_s = 0.03$, $P = 0.92$ for Iowa and $r_s = 0.13$, $P = 0.51$ for all areas, 2006–2007), likely related to the ephemeral nature of their preferred early successional habitat. Species abundance and sensitivity to changing habitat conditions seems to be an important factor in determining the predictive ability of regional models. Hierarchical models can be a useful tool for concentrating efforts at the scale of management units and should be one of many tools used by land managers, but we caution that the utility of such models may decrease over time for species preferring relatively ephemeral habitats if model inputs are not updated accordingly. © 2012 The Wildlife Society.

KEY WORDS Bayesian hierarchical model, blue-winged warbler, Breeding Bird Survey, driftless area, ecoregion, model evaluation, National Land Cover Dataset, Prairie–Hardwood Transition, wood thrush.

Availability and variety of geospatial environmental data have increased dramatically in recent years. One outcome has been proliferation of broad-scale predictive models with much potential to inform avian conservation planning (Forcey et al. 2007, Howell et al. 2008, Sauer et al. 2008*a*). Realizing this potential will require evaluation of model predictions over multiple spatial and temporal scales. Such evaluations are needed to determine appropriate uses for model output, as well as their limitations, in a management context.

One increasingly popular form of predictive modeling involves the use of Bayesian hierarchical techniques. Bayesian approaches are particularly suited to complex survey designs typical of ecological studies, in part because of their inherently hierarchical structure (Link et al. 2002, Ntzoufras 2009). Hierarchical models have been used to summarize avian population change over multiple geographic scales while accommodating various nuisance variables related to survey quality and observer effects (Link et al. 2002). Using Markov chain Monte Carlo methods, the prior distribution is combined with the model likelihood via Bayes' theorem to form the posterior distribution of the model parameters (Ntzoufras 2009). Through this process, the general

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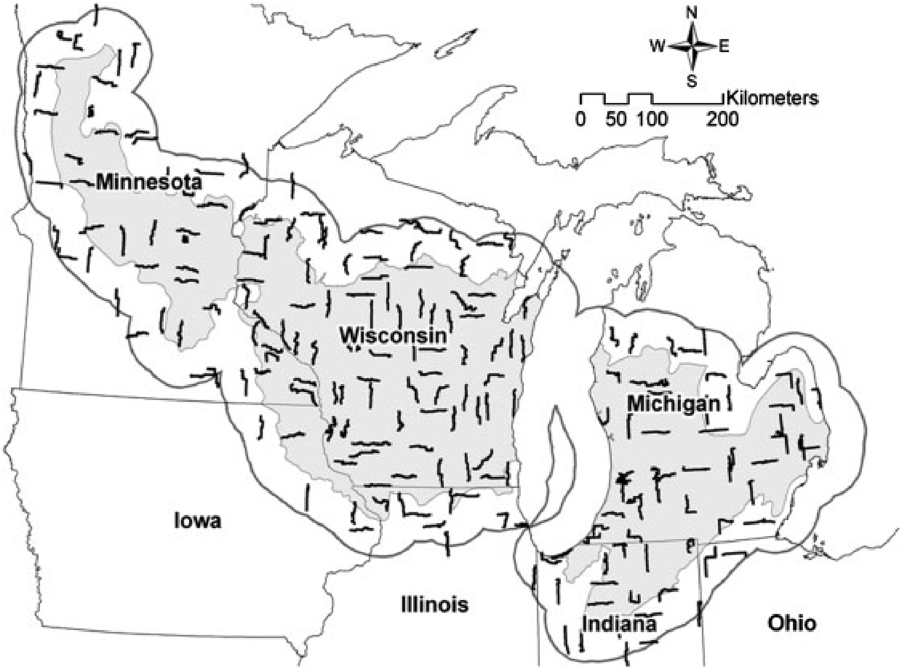

Figure 1. Breeding Bird Survey (BBS) routes ($n = 117$; black lines) in Bird Conservation Region 23 (gray shaded area) and 50-km buffer of additional routes (gray outlined area) included in the individual species regional Bayesian models, 1995–1998 and 2006–2007.

Bayesian hierarchical trend approach of Link and Sauer (2002) has been extended to accommodate the potential effects of autocorrelation and environmental covariates for producing spatially explicit predictions of avian occurrence and abundance (Thogmartin et al. 2004*b*, 2006, 2007; Forcey et al. 2007, 2008).

Using independent data in model evaluation is key in determining their validity in providing the basis for conservation decisions. In most evaluations of species–habitat distribution models, the models are assessed using presence–absence data (e.g., Elith et al. 2006, Tsoar et al. 2007, Jimenez-Valverde et al. 2008). Compared to abundance, presence–absence data are less labor intensive and less prone to observer bias and measurement error, but also potentially less informative for species that are rare or have low detection probabilities (Joseph et al. 2006).

We examined the ability of broad-scale hierarchical Bayesian models to predict the relative abundance of bird species in the upper Midwest using field data collected at finer scales. We focused on the wood thrush (*Hylocichla mustelina*), a mature forest-interior species, and the blue-winged warbler (*Vermivora cyanoptera*), a shrub-forest species associated with forest transition zones, both considered species of conservation concern throughout much of their range (Rich et al. 2004). Our objectives were: 1) develop models from region-wide Breeding Bird Survey (BBS) data, 2) evaluate model performance across multiple spatial scales, and 3) evaluate these models using independent data from a portion of the region.

STUDY AREA

The study area included portions of Minnesota, Iowa, Wisconsin, Illinois, Indiana, and Michigan within the Prairie–Hardwood Transition corresponding to North American Bird Conservation Initiative Bird Conservation Region 23 (Fig. 1, United States North American Bird Conservation Initiative Committee [U.S. NABCI] 2000). Most of this area was glaciated during the Pleistocene epoch except for portions of southwestern Wisconsin (McNab and Avers 1994, Johnson et al. 2002). Bird Conservation Region 23 (BCR 23) covered approximately 230,000 km^2 and historically contained hardwood forest, tall-grass prairie, and oak (*Quercus* spp.) savanna (Nuzzo 1985, U.S. NABCI 2000). In 2006, BCR 23 primarily consisted of row crop agriculture (36%), deciduous forest (21%), and grasslands (27%, Thogmartin et al. 2006). Regional elevation ranged between 175 m and 500 m with local relief not exceeding 200 m and mean annual temperatures ranged from 4° C to 11° C with annual precipitation of approximately 650 mm to 930 mm (McNab and Avers 1994).

We used data collected within a subregion of BCR 23 (i.e., Driftless Area; Fig. 2) to evaluate regional bird models. The Driftless Area covered 42,000 km^2 in northeastern Iowa, southeastern Minnesota, southwestern Wisconsin, and a small portion of northwest Illinois (Fig. 2), and was characterized by highly dissected upland plateaus, abundant rock outcroppings, and deeply cut valleys (Prior 1991, McNab and Avers 1994). We chose this subregion based on readily available data gathered in the context of a larger study (LeBrun 2008).

METHODS

Regional Hierarchical Model

We used an existing hierarchical Bayesian model for the wood thrush (Thogmartin and Knutson 2007) and

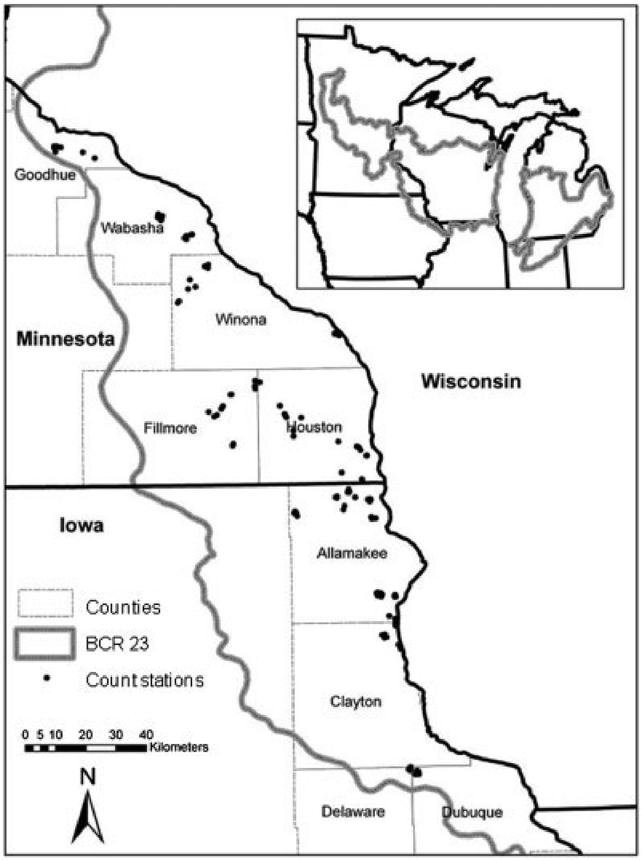

Figure 2. Count stations in the Bird Conservation Region 23 (BCR 23) Driftless Area of the upper-midwestern United States surveyed in the 1990s and in 2006–2007 to evaluate wood thrush and blue-winged warbler regional models.

developed a new model for the blue-winged warbler. Model development essentially followed Thogmartin et al. (2004*b*) and Thogmartin and Knutson (2007). Our hierarchical Bayesian modeling approach used 1981–2001 count data from the North American Breeding Bird Survey (NABBS) and 1992 National Land Cover Data (NLCD) for model construction.

We know of no comprehensive estimate of land cover change for the Prairie–Hardwood Transition over the modeled 20-year period. However, Fry et al. (2009) analyzed land cover change in this region using the 1992 and 2001 NLCD and found only minor shifts (<6%) among categories. Therefore, we assumed that the midpoint of the 20-year bird counts would correspond to the 1992 land cover data for our models (Thogmartin et al. 2004*a*, Thogmartin and Knutson 2007).

We used bird counts collected on 117 routes within BCR 23 for the response variable in the blue-winged warbler models. Within these routes, we used 2,071 counts conducted by 239 observers between 1981 and 2001. For the wood thrush, Thogmartin and Knutson (2007) created models using 1,840 counts conducted on 140 routes by 310 observers, over this same 20-year time frame.

To identify relationships between environmental covariates and avian abundance, we used a Bayesian hierarchical model and iterative simulation (Markov chain Monte Carlo). We modeled bird counts as an overdispersed Poisson regression using a loglinear function of explanatory covariates (Thogmartin et al. 2006, Thogmartin and Knutson 2007). For each model, we iterated the Markov chain in the program WinBUGS 1.4.3 (Spiegelhalter et al. 2003) an additional 10,000 iterations past convergence, which occurred at 15,000 iterations, to assure that the posterior distribution was more heavily influenced by the data rather than by the diffuse prior distribution (Link et al. 2002). To calculate the Gelman–Rubin diagnostic, we ran 3 chains for each model (Lunn et al. 2000, Link et al. 2002). The Gelman–Rubin diagnostic identified whether the multiple chains converged by comparing the within-chain variance to the between-chain variance (Brooks and Gelman 1998).

We chose environmental covariates a priori for each model based on a literature review (Table 1), and calculated variables at 3 logarithmically related scales: 800 ha, 8,000 ha, and 80,000 ha (corresponding to buffers of 0.1 km, 1 km, and 10 km around each BBS route; Thogmartin et al. 2004*b*). This range of scales theoretically corresponds to

Table 1. Environmental and nonhabitat covariates included in global models for the wood thrush (WOTH) and blue-winged warbler (BWWA) in 800 ha, 8,000 ha, and 80,000 ha surrounding bird survey routes in Bird Conservation Region 23 (Prairie–Hardwood Transition).

Class	Variable	Species[a]
Land cover composition	Deciduous forest (%)	WOTH, BWWA
	Pine forest (%)	WOTH
	Wooded wetland (%)	WOTH
Land cover configuration	Forest patch area residuals (%) (residuals from a regression of forest patch area against percent forest)	BWWA
	Forest edge residuals (%) (residuals from a regression of forest edge against percent forest)	BWWA
Physiognomic	Mean static wetness index (scales between 1 [dry] to 19 [moist]) or ln (catchment area/tangent of the slope angle)	WOTH, BWWA
Potential human disturbance	Mean human density (mean county-level human population density)	BWWA
	Mean road density	BWWA
Non-habitat	Route effect (random effect)	WOTH, BWWA
	Year effect (random effect)	WOTH, BWWA
	Temporal trend effect (random effect)	WOTH, BWWA
	Observer effect (random effect)	WOTH, BWWA
	Novice observer effect (fixed effect)	WOTH, BWWA

[a] Variables for the wood thrush were derived by Thogmartin and Knutson (2007).

areas associated with ecological processes affecting breeding bird habitat (Thogmartin et al. 2004*b*).

We derived land-cover variables from the 30-m resolution 1992 NLCD (Vogelmann et al. 2001). The 1992 NLCD is most accurate for row cropland and deciduous forest (i.e., mapping accuracy >55%) and least accurate for rarer land covers such as emergent herbaceous wetland and small grain agriculture (i.e., mapping accuracy <38%; Stehman et al. 2003, Thogmartin et al. 2004*a*). Two of the environmental variables, forest edge and forest patch area, were correlated with percent forested area ($r > 0.64$). We therefore used residuals from regressions of forest patch area and forest edge against percent forest as model covariates (Legendre and Legendre 1998, Lichstein et al. 2002).

In addition to environmental covariates, we examined 5 nonhabitat variables for each species: year, route, observer, novice observer, and temporal trend effects (Table 1). The year random effect accounted for temporal variation in bird abundance, whereas the route random effect accounted for spatial autocorrelation among the routes with a conditional autoregressive prior on the route variance (Thogmartin et al. 2004*b*). We also included 2 observer effects: 1 accounting for inexperienced first time observers (novice observer fixed effect) and the other for differences in surveying abilities among observers (observer random effect). Lastly, we accounted for the remaining temporal variation not captured by any of the other effects in the fixed temporal trend effect (Thogmartin et al. 2004*b*).

We entered the 5 nonhabitat variables and the environmental covariates (Table 1) into each proposed bird model, and considered all combinations of covariates to derive the best models from all 3 scales. We identified the best models using an information-theoretic approach and the deviance information criterion (DIC; Spiegelhalter et al. 2002) where competing models were the set of models with the smallest DIC values. The final models included only the best performing models from all 3 scales (800 ha, 8,000 ha, approx. 80,000 ha) with a ΔDIC of <5 units from the best model (Burnham and Anderson 2002).

We mapped predicted abundances from the final models at each scale (800 ha, 8,000 ha, approx. 80,000 ha) with the ArcGIS Spatial Analyst raster calculator (ArcGIS 9.2 and 9.3, Environmental Systems Research, Inc., Redlands, CA; Thogmartin and Knutson 2007). We then averaged the 3 maps for each species using the model weights (Congdon 2007, Blakesley et al. 2010) to produce a final map of predicted abundance. Predicted abundances were thus mapped as the 20-year expected mean count for a putative BBS route centered on a given raster cell (0.09 ha) and based on variables measured in 800-ha, 8,000-ha, and 80,000-ha focal areas, controlling for temporal and observer differences. Mapping these predictions creates visual representations of high-to-low predicted relative abundances, which land managers can use to make management decisions.

Model Evaluation

We assessed the model fit by comparing simulated values from the posterior predictive distribution of a replicated set of data to the observed data. Because this is a within-model assessment of fit and does not allow evaluation against independent data, we used 4 sets of independently gathered count data to evaluate model predictions. The first of these included randomly chosen BBS data collected in BCR 23 during the period 1981–2001 but not used in model construction ($n = 415$ route counts). We regressed these observed counts against the predicted blue-winged warbler counts; model predictions for the wood thrush were previously evaluated for BCR 23 using a similar approach (Thogmartin and Knutson 2007). We derived the other 3 evaluation data sets from point counts collected in the western half of the Driftless Area (Fig. 2).

Two of the Driftless Area data sets were collected at a subset of count stations ($n = 131$; Fig. 2) in 1995–1996 by Norris (1999) and in 1997–1998 by Niemi et al. (1998) on public and private lands. We resurveyed 58 stations in northeastern Iowa in 2006 and 2007, along with 73 stations in southeastern Minnesota, using methods similar to those employed in the earlier surveys (LeBrun 2008). We conducted unlimited distance 10-minute counts (Howe et al. 1997) twice at each station between 30 May and mid-July, commencing at sunrise, and continuing until 1000 hour. Different individuals conducted the first and second survey at each station in the same year. All stations were >250 m apart and >50 m from the nearest forest edge. We only included birds detected within 100 m of a count station in statistical analyses (Howe et al. 1997).

To ameliorate temporal and spatial differences between point count data and BBS data, we grouped count stations for both data sets by centering 1.5-km buffers on each station and designating those with overlapping buffers as a single site. Temporal variation was reflected in the difference between our 10-minute point counts, and the 3-minute counts conducted 50 times along a BBS route. Spatially, a point count covered an area around the point equivalent to the listening radius associated with the species; each BBS route was comprised of 50 of those counts. By aggregating point counts to some larger collection of points, the difference in both space and time is lessened. We used 1.5 km for our buffer because potential errors within the National Land Cover Dataset may increase the variability in habitat classifications at a scale smaller than 10 km^2 (Thogmartin et al. 2006). Sites ($n = 28$) consisted of 2–9 point count stations.

We used the maximum number of individuals detected on a single survey, as the relative abundance for each focal species at each station in each year (Barker and Sauer 1995, Johnson 2008, Murray et al. 2008). We then averaged these values across stations at a site and across years to obtain a mean observed abundance per site for each focal species in each of the 3 sets of point count data. To quantify mean predicted abundance for each site, we averaged the predictions for each 30-m × 30-m raster cell within a site. Because of differences in the temporal and spatial scale of the observed and predicted abundances, we standardized both data sets by subtracting the overall mean of each set and dividing by the standard deviation (Murray et al. 2008). Thus, standardized

Table 2. Subset of models considered best fitted (i.e., <5 DIC[a] from the best model) to the 1981–2001 Breeding Bird Survey counts ($n = 117$) for the blue-winged warbler in the Prairie–Hardwood Transition region of the United States. The null model includes observer, year, and spatial correlation without environmental covariates.

Best subset model	Explanatory variable	Scale (ha)	DIC	ΔDIC[b]	*wi*[c]
1	Forest, forest edge residuals, forest patch area residuals, wetness index	8,000	1,520.56	0.000	0.152
2	Forest, forest edge residuals, road density, wetness index	8,000	1,522.12	1.560	0.070
3	Forest, forest edge residuals, wetness index	8,000	1,522.42	1.860	0.060
4	Forest, wetness index	80,000	1,522.73	2.170	0.051
5	Forest	8,000	1,523.10	2.540	0.043
6	Forest, forest edge residuals	80,000	1,523.34	2.780	0.038
7	Forest, wetness index	8,000	1,523.39	2.830	0.037
8	Forest, forest edge residuals, wetness index	80,000	1,523.39	2.830	0.037
9	Forest, forest patch area residuals, wetness index	800	1,523.63	3.070	0.033
10	Forest, forest patch area residuals, road density, wetness index	800	1,523.66	3.100	0.032
11	Forest, forest edge residuals, forest patch area residuals, road density, wetness index	8,000	1,524.17	3.610	0.025
12	Forest, human population density	80,000	1,524.67	4.110	0.019
13	Wetness index	800	1,524.81	4.250	0.018
14	Forest	80,000	1,524.81	4.250	0.018
15	Forest, wetness index	800	1,524.86	4.300	0.018
16	Null		1,525.22	4.660	0.015

[a] Deviance Information Criterion.

[b] Difference between the best model and the model of interest.

[c] Model weight.

abundances represented the number of standard deviations from the mean of the respective data sets.

We conducted Spearman rank-correlation tests to measure correspondence between relative observed and predicted abundances for each species. Because different observers collected the count data in each state, we conducted separate analyses on each state individually and then using the pooled data from Iowa and Minnesota in each of the 2 decades. To assess the influence of outliers on our Spearman rank results, we identified influential points using Cook's Distance, removed the most influential points, reanalyzed the data, and plotted our results with and without outliers (PROC REG; SAS Institute 2009).

RESULTS

We identified 6 environmental covariates that predicted blue-winged warbler abundance, compared to 4 environmental covariates for the wood thrush (Table 1). Null models (models including only nonhabitat covariates) for the blue-winged warbler and the wood thrush had model weights of <2% and 4%, respectively, indicating support for the inclusion of environmental covariates within the best subset models. For the blue-winged warbler, 15 models were within the best subset of models (<5 units DIC from the best model) and therefore appropriate for varying degrees of inference (Table 2). Thogmartin and Knutson (2007) identified 10 candidate models within their best subset for the wood thrush.

We predicted that blue-winged warbler abundance would be greatest in forests with high edge-to-patch ratios, high road densities, and low human population densities (Gill et al. 2001). Edge, patch area, and road densities were most influential at intermediate scales, whereas human population was included in only 1 competing model (Table 2). Blue-winged warblers were positively associated with forest edge and proportion of forest, both at the intermediate scale, but negatively associated with forest patch area (at the finest scale) and wetness (at both fine and coarse scales). Results from model averaging indicated that blue-winged warblers associated with areas of dry forest with a high proportion of edge (Table 3). The best model explained 38% of the variance in counts despite the low predicted abundance for this species (Fig. 3). Overall, the predicted relative abundance for the blue-winged warbler was greatest in the eastern half of the Driftless Area and in southern and eastern Michigan while exhibiting an east to west gradient through the Prairie–Hardwood Transition region (Fig. 4).

We observed the wood thrush more often than the blue-winged warbler during both the BBS surveys and point counts. Spearman rank correlation values between predicted

Table 3. Explanatory variables included in the final competing models for the blue-winged warbler in the Prairie–Hardwood Transition Region of the United States. We report median (fiftieth percentile of the simulations) with lower (LCI) and upper (UCI) credible intervals.

Explanatory variables	Model scale (ha)	Median	95% LCI	95% UCI
Forest edge residuals (%)	8,000	0.7716	0.3569	1.2180
Forest patch area residuals (%)	800	−0.7549	−1.2510	−0.3187
	8,000	−0.0590	−0.4731	0.3598
Forest (%)	800	0.3217	−0.1203	0.7686
	8,000	0.8233	0.3939	1.2920
	80,000	0.3620	−0.1271	0.8784
Mean static wetness index	800	−0.5550	−0.9987	−0.1210
	8,000	−0.3323	−0.7437	0.0760
	80,000	−0.5850	−1.0270	−0.1349

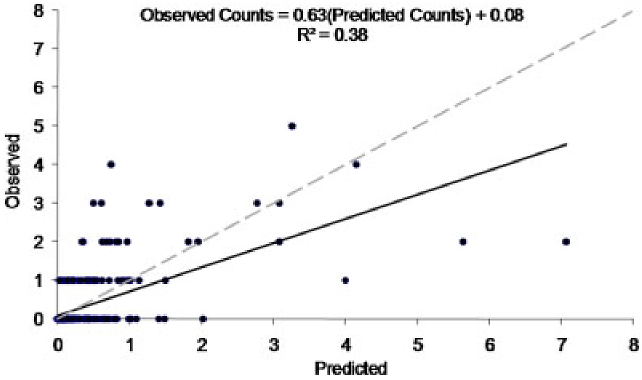

Figure 3. Regression of observed Breeding Bird Survey counts ($n = 415$), withheld during the construction of the blue-winged warbler hierarchical model in Bird Conservation Region 23 during 1981–2001, on predicted counts. The dashed, gray line is the line of 1:1 correspondence and the solid black line represents the trend line.

BBS abundances and observed point count abundances were positive, though the strength of the correlations varied over time and space (Table 4). Overall, the wood thrush exhibited greater Spearman rank correlations for the Iowa-only and the combined Minnesota and Iowa point count data, whereas the blue-winged warbler's greatest Spearman rank correlation was for the Iowa-only point count data. Wood thrush correlation was greatest for the point count data collected in Iowa from 2006 to 2007 (Spearman correlation = 71%); combined data for the 2 time periods exhibited a Spearman rank correlation of 58% (Table 4; Fig. 5C, D). Spearman rank correlations for the blue-winged warbler were not significant; correlation was greatest for the point count data collected in Iowa from 1995 to 1996 (57%), 27% for the combined early, and 13% for the combined late periods (Table 4; Fig. 5A, B).

When assessing the effect of outliers on our Spearman-rank results, we found varying degrees of influence on predicted versus observed correlations for the 2 species. After removing outliers for the blue-winged warbler, Spearman rank correlation increased from 27% to 36% for the early Iowa period (Fig. 5A); however, these results were not significant and were highly variable. Generally, we found little change when we removed outliers for the wood thrush. Plots of the predicted BBS versus observed point count abundance for the blue-winged warbler exhibited evidence of both under- and over-prediction (Fig. 6C, D). In comparison, the wood thrush plots exhibited primarily over-predictions for the Minnesota data (Fig. 7C, D).

DISCUSSION

In general, we found the wood thrush regional models to be better predictors of regional abundance across the Prairie–Hardwood Transition (BCR 23) than the models created for the blue-winged warbler. Our models for the blue-winged warbler support research-indicating associations with

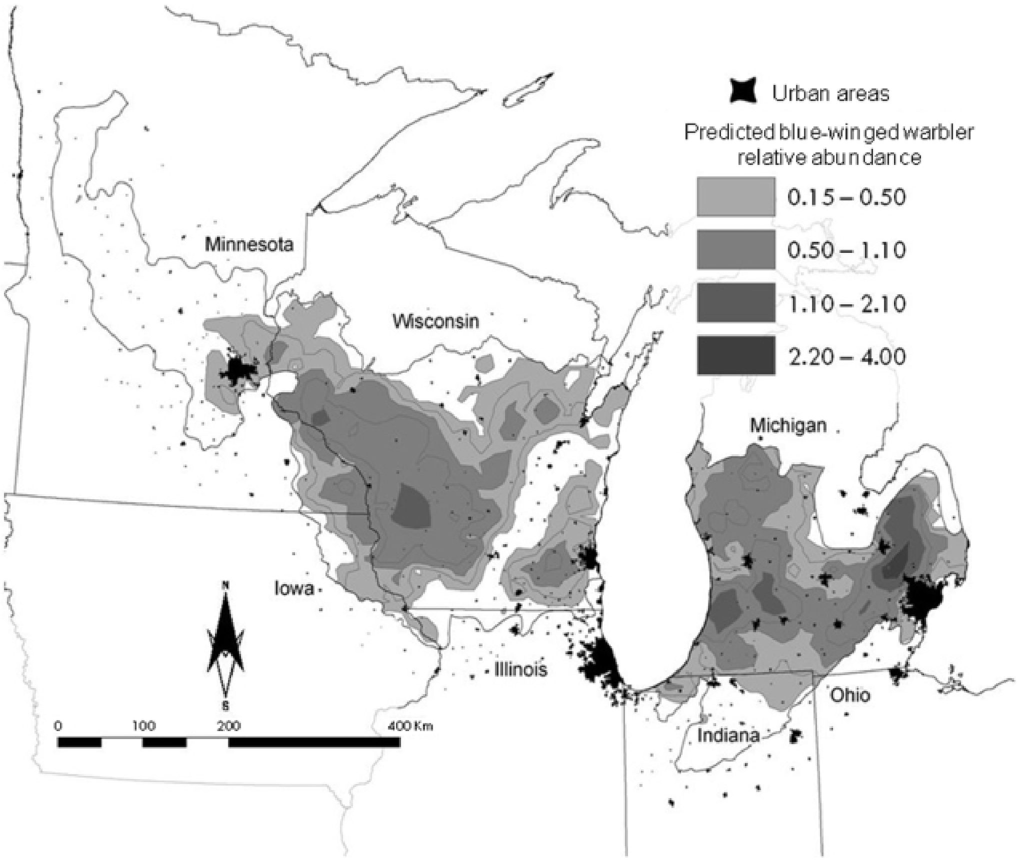

Figure 4. Predicted relative abundance of the blue-winged warbler in Bird Conservation Region 23. Relative abundance corresponds to the 20-year expected mean count during the period of 1981–2001.

Table 4. Results of Spearman rank correlation tests (r_s) comparing predicted (derived from 1981–2001 Breeding Bird Survey data) and observed (collected at point count stations in 2006–2007) abundances for the blue-winged warbler and wood thrush in the Driftless Area of the midwestern United States.

Species data[a]	No. of sites[b]	r_s[c]	*P*
Blue-winged warbler			
IA 1995–1996	8	0.57	0.14
IA 1995–1996 and MN 1997–1998	23 (21)	0.27 (0.36)	0.21
MN 2007	15	0.24	0.39
MN 1997–1998	15	0.20	0.48
IA 2006–2007 and MN 2007	28	0.13	0.51
IA 2006–2007	13	0.03	0.92
Wood thrush			
IA 2006–2007	13	0.71	0.0068
IA 1995–1996 and MN 1997–1998	23	0.58	0.0035
IA 2006–2007 and MN 2007	28	0.58	0.0012
IA 1995–1996	8	0.20	0.63
MN 1997–1998	15	0.08	0.77
MN 2007	15	0.08	0.78

[a] IA, Iowa; MN, Minnesota.
[b] Parentheses indicate the number of sites when outliers are removed.
[c] Parentheses indicate results with outliers removed.

successional habitat (Confer and Knapp 1981, Gill et al. 2001). The predicted abundance for the blue-winged warbler primarily had positive associations for forest cover and edge at the intermediate scales and negative associations for lower elevation and wetter areas at fine and broad scales. In contrast to predicted abundance of the blue-winged warbler, Thogmartin and Knutson (2007) found that wood thrush had a weak positive association with wooded wetlands at intermediate and coarse scales and exhibited a positive association with the proportion of the landscape in deciduous forest at all scales, similar to habitat associations reported elsewhere (Roth et al. 1996, Donovan and Flather 2002). Within the Prairie–Hardwood Transition region, blue-winged warbler models suggested avoidance of low elevation wetter areas. However, published research suggests this pattern varies across the eastern United States with paired males more likely to occur in dry, higher elevations (Gill et al. 2001). Similar to our findings, Thogmartin and Knutson's (2007) wood thrush models also indicated a mixed response for the wetness index. Overall, blue-winged warblers were most abundant in dry upland forests with a high ratio of forest edge, whereas wood thrush were more abundant in forested landscapes with large patches that were in close proximity to one another (Thogmartin and Knutson 2007).

In evaluating our models using data collected from a portion of the Prairie–Hardwood Transition region, we found positive relationships between model predictions and point count data for both focal species. The rank correlations

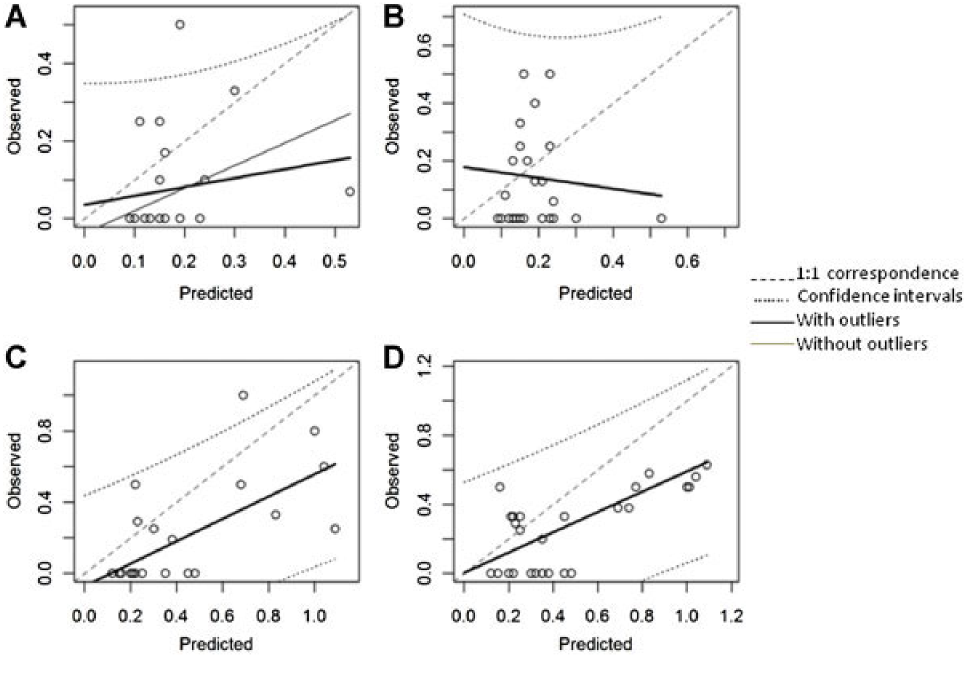

Figure 5. Observed abundances of the blue-winged warbler and the wood thrush based on survey data collected in Minnesota and Iowa fitted against predicted relative abundances from models of Breeding Bird Survey data. Panels represent observed versus predicted for (A) blue-winged warbler 1990s data, (B) blue-winged warbler 2000s data, (C) wood thrush 1990s data, and (D) wood thrush 2000s data.

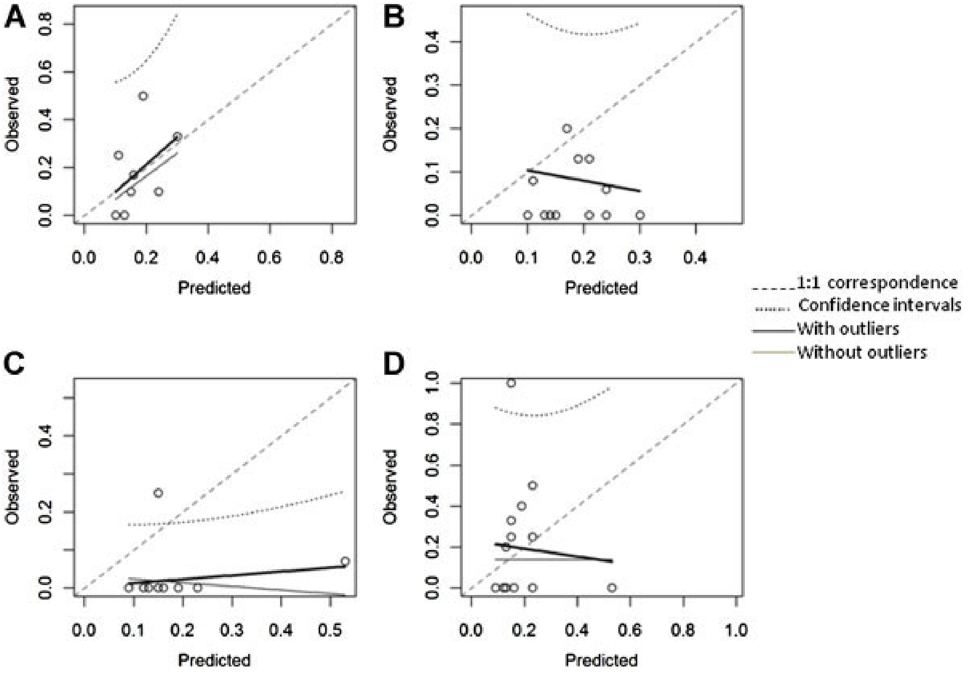

Figure 6. Observed abundances of independent data collected for the blue-winged warbler fitted against predicted relative abundances from models of Breeding Bird Survey data for Bird Conservation Region 23. Panels represent observed versus predicted for (A) Iowa 1995–1996 data, (B) Iowa 2006–2007 data, (C) Minnesota 1997–1998 data, and (D) Minnesota 2007 data.

indicated that our models produced reasonable predictions of count data over extended time frames for the wood thrush, but not for the blue-winged warbler, at spatial scales of 800 ha, 8,000 ha, and 80,000 ha. Consistency among model predictions tended to increase for the wood thrush with repeated surveys and wider coverage. In contrast, the blue-winged warbler exhibited slight increases in model consistency using the combined 1990s data for Minnesota and Iowa.

One possible reason for the lack of consistency in the blue-winged warbler predictions is the potential interaction with the brown-headed cowbird (*Molothrus ater*). Blue-winged

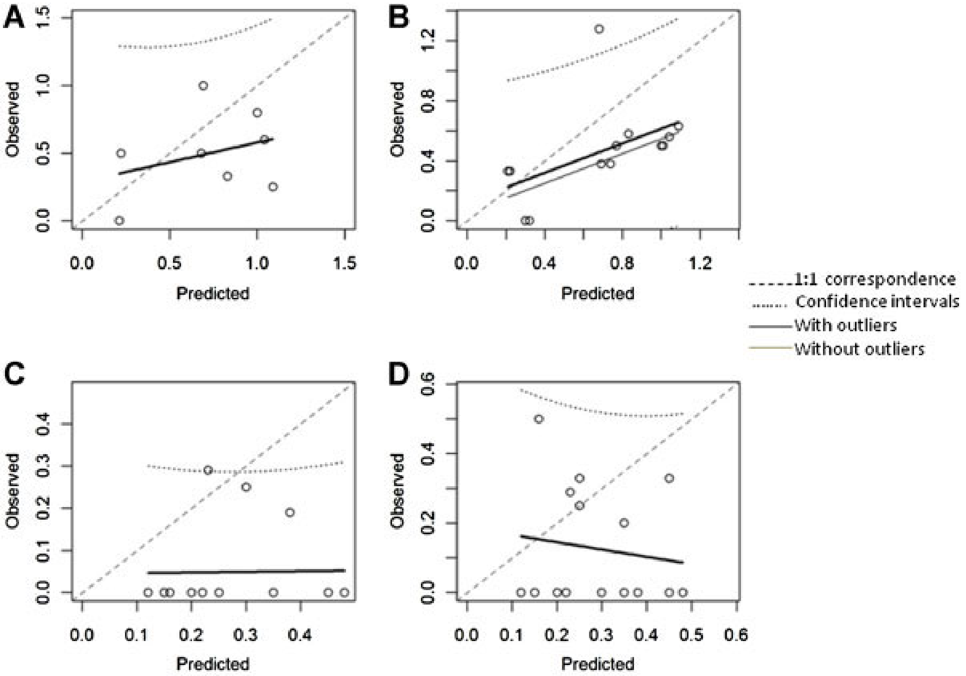

Figure 7. Observed abundances of independent data collected for the wood thrush fitted against predicted relative abundances from models of Breeding Bird Survey data for Bird Conservation Region 23. Panels represent observed versus predicted for (A) Iowa 1995–1996 data, (B) Iowa 2006–2007 data, (C) Minnesota 1997–1998 data, and (D) Minnesota 2007 data.

warblers are commonly parasitized by cowbirds in heavily fragmented habitats (Gill et al. 2001). Research conducted by Elliott (1999) revealed not only cowbird nest parasitism, but also cowbird infanticide of blue-winged warbler nestlings. At the regional scale, brown-headed cowbirds have declined in abundance (Sauer et al. 2008*a*). In the Driftless Area, however, brown-headed cowbird populations have been largely stable or increasing in abundance over the last decade (W. Thogmartin, United States Geological Survey, unpublished data). Our results may be an indication that the dynamic relationship between these species affects abundance at local scales in at least some parts of the region.

We believe that another key contributor to model discrepancies for blue-winged warbler predictions resulted from relatively low abundance in the Minnesota and Iowa sections of the Driftless Area (Keller and Scallan 1999, Lawler and O'Connor 2004). The western half of the Driftless Area is on the edge of the blue-winged warbler's breeding range. In contrast, the range of the wood thrush extends well past the Driftless Area to the Missouri River (Roth et al. 1996, Sauer et al. 2008*b*). Several studies have found that detection of rare species increased with additional counts (Link et al. 1994, Vaughan and Ormerod 2005). Our blue-winged warbler models may have performed better if we evaluated them with additional counts across the extent of its range (Vaughan and Ormerod 2005, Murray et al. 2008).

The greatest difficulty in using avian point counts for evaluating the performance of regional models and maps derives from spatial and temporal differences between the data used for model construction and the independent data used to test model performance. We compared the spatial resolution of 10-minute point counts to 150-minute route counts (3-min counts at 50 stops on a BBS route), and the temporal resolution of point counts conducted over 2 years versus a 20-year mean abundance. Both of these differences in data resolution make comparisons difficult. To deal with these spatial and temporal differences in data resolution others have suggested increasing the number of point counts (Vaughan and Ormerod 2005), or increase the number of survey replicates (Dettmers et al. 1999, Murray et al. 2008). Doing this may not only have decreased the differences in our data resolution, but also may have likely increased the predictive ability of the models (Murray et al. 2008).

Another factor affecting model assessment involves tradeoffs between environmental features measured at broad scales that parameterize the models and fine-scale resources that characterize habitat (Miller et al. 2004, Miller and Hobbs 2007, Gallant 2009). For example, LeBrun (2008) quantified fine-scale blue-winged warbler habitat features that could not be detected through remote sensing and included these in models of habitat suitability, improving their predictive ability. Such habitat features were not represented in our regional-scale models and this could be problematic for a species that occurs in ephemeral habitat, such as the blue-winged warbler. Conversely, models for a species occurring in mature forests, such as the wood thrush, may not be as sensitive to fine-scale changes that influence habitat use.

Temporal rather than spatial dissonance likely affects model performance in other ways. We used land cover data dated from 1992 to create the models and maps, and then tested them with count data collected as much as 15 years later. In a comparison of unpublished digitized forest cover data from a study by LeBrun (2008), forest cover had not significantly changed ($P = 0.33$) between the early 1990s and mid 2000s within the Driftless Area of Iowa. However, successional changes likely occurred in the interim. For instance, LeBrun (2008) documented a decline in oaks and a decrease in canopy openings over this period. The wood thrush is known to be associated with mature deciduous forest, whereas the blue-winged warbler is more commonly found in early successional, shrubby areas along forest edges (Gill et al. 2001). Loss of transitional habitat along edges due to an increase in agricultural intensity or successional changes may be influencing model performance for the blue-winged warbler more than the wood thrush. This may suggest that species whose habitat is more varied or under greater rates of change may need updating of model inputs (i.e., land cover) more frequently.

A final caveat is that we only tested model performance in an area approximately an eighth of the entire model region. Testing only a portion of the area modeled may result in missing variation occurring over broader scales to which the model is attuned (Royle and Nichols 2003, Vaughan and Ormerod 2003, Barry and Elith 2006, Franklin et al. 2009). However, understanding the degree to which these regional models scale to finer resolutions is important for constraining management recommendations resulting from regional exercises in conservation planning.

MANAGEMENT IMPLICATIONS

Considerable effort is occurring in the development of regional models and maps for conservation planning (Thogmartin et al. 2004*b*, 2006, 2007; Chan et al. 2006; National Ecological Assessment Team 2006; Forcey et al. 2007, 2008). We found that models from broad-scale avian surveys are not necessarily well suited for assessment by avian point counts collected over a small spatial and time-limited extent. We also surmise that species abundance and species sensitivity to changing habitat conditions might be influential factors affecting the predictive ability of regional models. Therefore, managers should consider the ecology of a species sensitive to relatively rapid changes in habitat conditions and update model inputs (i.e., land cover) accordingly. We suggest that predictive models should be one of many tools land managers use to inform conservation actions. When using these predictive models, we recommend that managers be cognizant of the species ecological requirements and especially cautious when planning conservation actions for rare species to guard against the expiration of mapped predictions.

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