



Research Papers

Modeling and Mapping Golden-winged Warbler Abundance to Improve Regional Conservation Strategies

Modélisation et cartographie de l'abondance en tant qu'outils de perfectionnement des stratégies régionales de conservation chez la Paruline à ailes dorées

*Wayne E. Thogmartin*¹

ABSTRACT. Conservation planning requires identifying pertinent habitat factors and locating geographic locations where land management may improve habitat conditions for high priority species. I derived habitat models and mapped predicted abundance for the Golden-winged Warbler (*Vermivora chrysoptera*), a species of high conservation concern, using bird counts, environmental variables, and hierarchical models applied at multiple spatial scales. My aim was to understand habitat associations at multiple spatial scales and create a predictive abundance map for purposes of conservation planning for the Golden-winged Warbler. My models indicated a substantial influence of landscape conditions, including strong positive associations with total forest composition within the landscape. However, many of the associations I observed were counter to reported associations at finer spatial extents; for instance, I found Golden-winged Warblers negatively associated with several measures of edge habitat. No single spatial scale dominated, indicating that this species is responding to factors at multiple spatial scales. I found Golden-winged Warbler abundance was negatively related with Blue-winged Warbler (*Vermivora cyanoptera*) abundance. I also observed a north-south spatial trend suggestive of a regional climate effect that was not previously noted for this species. The map of predicted abundance indicated a large area of concentrated abundance in west-central Wisconsin, with smaller areas of high abundance along the northern periphery of the Prairie Hardwood Transition. This map of predicted abundance compared favorably with independent evaluation data sets and can thus be used to inform regional planning efforts devoted to conserving this species.

RÉSUMÉ. La conservation requiert l'identification des paramètres d'habitat pertinents et l'identification de lieux géographiques où l'aménagement du territoire peut bonifier l'habitat des espèces hautement prioritaires. J'ai développé des modèles d'utilisation de l'habitat et j'ai cartographié l'abondance prévue de la Paruline à ailes dorées (*Vermivora chrysoptera*), espèce dont le statut de conservation est considéré comme hautement préoccupant, en utilisant des dénombrements d'oiseaux, des variables environnementales et des modèles hiérarchiques appliqués à de multiples échelles spatiales. Mon but était de comprendre les associations entre cette espèce et son habitat à plusieurs échelles et de créer une carte d'abondance prévue afin de planifier la conservation de la Paruline à ailes dorées. Mes modèles indiquent que le contexte du paysage a une influence substantielle, incluant de fortes relations positives avec le couvert forestier total. Cependant, plusieurs des associations que j'ai observées allaient à l'encontre de celles qui sont rapportées à des résolutions spatiales plus fines; par exemple, j'ai trouvé que les Parulines à ailes dorées étaient reliées négativement à plusieurs variables caractérisant l'habitat de lisière. Aucune échelle spatiale ne dominait, indiquant que cette espèce répond à des facteurs qui agissent à plusieurs échelles spatiales. J'ai observé une relation négative entre l'abondance de la Paruline à ailes dorées et celle de la Paruline à ailes bleues (*Vermivora cyanoptera*). J'ai aussi observé un gradient nord-sud qui suggère

¹USGS Upper Midwest Environmental Sciences Center



Sponsored by the Society of
Canadian Ornithologists and
Bird Studies Canada

Parrainée par la Société des
ornithologistes du Canada et
Études d'oiseaux Canada



BIRD STUDIES
ÉTUDES D'OISEAUX CANADA

un effet climatique régional qui n'avait pas encore été rapporté chez cette espèce. La carte d'abondance prévue indique une grande concentration dans le centre-ouest du Wisconsin, ainsi que d'autres zones de forte abondance le long de la périphérie nord de la zone de transition entre la prairie et la forêt feuillue. Cette carte d'abondance prévue se compare favorablement à des jeux de données indépendants et peut donc être utilisée dans le cadre des initiatives régionales visant à conserver cette espèce.

Key Words: conservation design; hierarchical spatial count models; midwestern United States; regional conservation planning; species distributional modeling

INTRODUCTION

Conserving regional to hemispheric populations of species is an immense task, requiring a broad-scale perspective in species management. Conservation biogeography is one facet of this broad-scale species management, charged with addressing ecological patterns and processes over large extents of space and time. Conservation biogeography has been defined as “the application of biogeographical principles, theories, and analyses, being those concerned with the distributional dynamics of taxa individually and collectively, to problems concerning the conservation of biodiversity” (Whittaker et al. 2005:3). In North America, the U.S. Fish and Wildlife Service has formally adopted principles of conservation biogeography, titled Strategic Habitat Conservation, as a primary means of conducting conservation activity (NEAT 2006). Strategic Habitat Conservation is an adaptive management framework involving biological planning, conservation design, conservation delivery, and evaluation of conservation effectiveness (NEAT 2006, Thogmartin et al. 2009). Entry into this adaptive management framework can come at any stage of the process. Here I describe elements of the conservation design aspect of Strategic Habitat Conservation for a species garnering much attention by the U.S. Fish and Wildlife Service and other conservation entities in North America, the Golden-Winged Warbler (*Vermivora chrysoptera*).

The Golden-winged Warbler has been identified by Partners in Flight as one of 28 landbirds in North America requiring immediate action to ensure persistence of the species (Rich et al. 2004). The U.S. Fish and Wildlife Service identified the species as a regional and national resource conservation priority (U.S. Fish and Wildlife Service 2002, Buehler et al. 2006) because of substantial declines

in abundance in the United States portion of its breeding range (annual average decline: -2.9% year⁻¹; Sauer et al. 2008). In the last decade, Golden-winged Warblers have declined by $>3\%$ annually in the core of their breeding range, the north-central states of Minnesota, Wisconsin, and Michigan. The Golden-winged Warbler is an early successional forest species. Causes for the decline are generally attributed to habitat lost as a result of maturation of fields and other early-successional land cover into older seral stage forest and the loss of wetland and other habitat to human development (Confer 1992). Young aspen forest (*Populus* spp.) is particularly favored by this warbler but this habitat is decreasing in area; for instance, in central Wisconsin, aspen exhibited a 36% decrease in area between the 1983 and 1996 Forest Inventories (Schmidt 1997) as forest disturbance, i.e., logging and fire, essential for this species was reduced (Cleland et al. 2001). Although the exact nature of the relationship between the Golden-winged Warbler and their conspecific the Blue-winged Warbler (*Vermivora cyanoptera*) is unknown, it appears that Golden-winged Warblers are being replaced by Blue-winged Warblers in large areas of sympatry, including the southern portions of Minnesota, Wisconsin, and Michigan (Vallender et al. 2007, 2009). To conserve this species will require focusing critical resources in areas of their greatest impact (Possingham and Wilson 2005, Buehler et al. 2007, Thogmartin et al. 2009).

Despite the priority status of this species, there is little information for where to devote scarce regional management resources. To overcome this paucity of information, I derived habitat models and mapped predicted abundances for the Golden-winged Warbler in the upper midwestern United States using time series of bird counts, environmental variables, and hierarchical models

applied at multiple spatial scales. My purpose was to understand habitat associations for this species at multiple spatial scales and from this information create a predictive map of abundance for purposes of regional conservation planning (Thogmartin et al. 2009). In doing so, I tested whether field-level understanding about the habitat associations of this species translated to coarser spatial extents.

METHODS

Study area

I modeled Golden-winged Warbler abundance for the population breeding in Bird Conservation Region 23, the Prairie Hardwood Transition. This region was historically dominated by prairies in the south and west and beech-maple forest in the north and east, separated by an oak savanna (McNab and Avers 1994, U.S. NABCI Committee 2000). The Prairie Hardwood Transition occupies 230,111 km², stretching from central Minnesota through central and southern Wisconsin and Michigan, including small sections of northeastern Iowa, and northern Illinois and Indiana. Lake Michigan bisects the region. The predominant land uses and land cover classes in this region are row crop agriculture (36%), agricultural grassland (27%), and deciduous forest (21%), of which Aspen/Birch (*Betula* spp.) comprised approximately half that amount. Much of the region is a rolling plain of loess-mantled ridges over sandstone and carbonate bedrock and pre-Illinoian ground moraine, contributing to a diversity of topographic relief and vegetation types (McNab and Avers 1994). There is a gradient in climate, primarily increasing precipitation, from northwest to southeast, with climatic differences most pronounced east of Lake Michigan.

The North American Landbird Conservation Plan (Rich et al. 2004) estimated approximately 10% of the global population (~210,000) of this species occurs in this region in the breeding season (T. Will, U.S. Fish and Wildlife Service, *personal communication*). The core of the species range (~159,000 birds) exists in Bird Conservation Region 12, the Boreal Hardwood region, immediately north of the Prairie Hardwood Transition.

Modeling approach

I used counts from 1840 routes collected between 1981 and 2001 by the North American Breeding Bird Survey (BBS) as the response in my models (Thogmartin et al. 2004a). Each BBS route contains 50 survey locations (stops) spaced approximately 800 m apart at which an observer counts all birds seen or heard in a 3-min period within a 400 m radius of the stop. I used the sum of counts from the 50 stops in a year's route survey as an index of abundance along the route for that year. The 1840 counts I used for model building were produced by 310 observers over 140 routes; an additional randomly selected 396 counts were held back for model evaluation. Over a 20-year period observers changed; not all routes were run each year and no route was run more than once per year.

I employed a hierarchical modeling approach to map predicted abundances of Golden-winged Warblers at a regional scale. I used a multilevel Bayesian model (Gelman et al. 1995, Link et al. 2002) to derive unbiased estimates of associations between environmental covariates and bird abundance. The approach was statistically hierarchical because multiple parameters in the model, i.e., the observer, year, and spatial dependence effects described below, were related or connected by the structure of the problem, i.e., a joint probability model for these inter-related parameters reflected the dependence among them (Gelman et al. 1995). In this case, bird counts were similar to each other to varying degrees because of temporal and spatial correlation and correlated observational error (Link and Sauer 2002, Thogmartin et al. 2004a), each of which created a level of correlated structure between survey counts. In combination with the other random effects, the nesting of observers within routes over time constituted the statistical hierarchy organizing the data.

I used Moran's *I* to preliminarily assess spatial correlation between annual route counts (Cliff and Ord 1981). I expected routes nearer to one another to be positively correlated in their counts of Golden-winged Warblers. Because similarity of counts over space was observed, I used the methodology introduced by Thogmartin et al. (2004a) to derive associations between bird abundance and environmental variables while controlling for the potential effects of spatial relatedness between counts. Thus, counts were modeled as a loglinear

function of explanatory variables describing habitat, spatial relatedness, and individual random effects of observer and year. The model is written as:

$$Z(s_i) = \mu(s_i) + \sum_{k=1}^n c_{ik}(Z(s_k) - \mu(s_k)) + \omega(s_i) + \eta_1(s_i) + \gamma(s_i) + \varepsilon(s_i) \quad (1)$$

where s_i are spatial coordinates for location i , $\mu(s_i)$ is the large-scale, nonspatial trend surface described by environmental covariates, and c_{ik} are the spatial dependence parameters, $i, k=1, \dots, n$. The error terms (ε_i) are assumed independent with zero mean and constant variance (σ^2); treated as a random effect, this allows for the variance to exceed the mean, accounting for potential overdispersion (McCarthy 2007).

Spatial dependence between survey counts was incorporated as a first-order conditional autoregression based upon an irregular lattice describing the spatial neighborhood of routes (Thogmartin et al. 2004a). Dependence in the spatial correlation parameter was symmetric and pair-wise between neighboring survey locations. In this formulation, an appropriate set of environmental covariates to explain the spatial structure in counts would obviate the need for this spatial correlation term, i.e., the sum of c_{ik} would be negligible. I also considered a competing model with a spatially uncorrelated random effect associated with route and a Northing term treated as a fixed effect to accommodate a first-order north-south trending in abundance.

Observer effects η (novice) and ω (observer variability) were accommodated in the model to minimize bias in the parameter estimates (Link and Sauer 2002). Novice observers were those in their first year of BBS data collection. A year effect γ and a fixed effect associated with trend were included to reveal a temporally-unbiased estimate of counts relative to environmental characteristics. The result was, in effect, an overdispersed mixed-effects Poisson regression, with diffuse or noninformative priors and hyper-priors assigned to each parameter (Appendix 1).

The initial environmental variables considered in the models were identified a priori from published habitat associations of the species (Table 1; Confer 1992 and references therein). A species expert, Tom Will (U.S. Fish and Wildlife Service, Region 3 Migratory Birds) reviewed an a priori global model. Land cover composition was derived from the National Land Cover Dataset 1992 (Vogelmann et al. 2001) and the Forest Resources of the United

States Forest Cover Type Dataset 1997 (Zhu and Evans 1994). Forest stand-size and age were not available for the region of interest and thus were not considered. Forest configuration was described as bypatchy forests, where forest cover was <40%, transitional forests, where forest cover was 40% to 60%, and perforated forests, where forest cover was >60% forest with high structural connectivity of forest patches (Riitters et al. 2000). A mapped index to Blue-winged Warbler abundance, obtained through simple interpolation of Breeding Bird Survey route counts, was obtained from the Breeding Bird Survey (J. R. Sauer, *personal communication*). In areas of sympatry, Golden-winged Warblers and Blue-winged Warblers partition the habitat along a moisture gradient, with Golden-winged Warblers favoring moister forest conditions (Confer et al. 2010); a covariate characterizing this gradient is the topographic convergence index. The topographic convergence index, derived from 30-m digital elevation models of the region, was calculated as the $\ln(\text{Catchment Area}/\text{tangent of the slope angle})$; Beven and Kirkby 1979). Each variable was evaluated at three spatial extents, derived from logarithmically related buffers around BBS routes. These buffers were 0.1, 1, and 10 km, and corresponded to 800 (fine), 8000 (intermediate), and ~80,000 ha (coarse), respectively. These buffers correspond to a spectrum of scales between Johnson's (1980) third- and second-orders of selection (Meyer 2007).

I considered environmental variables associated with forest cover composition and configuration because field-level studies indicated Golden-winged Warblers are associated with aspen and other early seral stage forest conditions. Remotely sensed information on seral stage was not widely available in mapped form for the Prairie Hardwood Transition, so I modeled species-habitat relations under the assumption that the full spectrum of seral stage was available at each of the scales I considered. Under such an assumption, I would expect to see at the finest scale much greater variability in the association of this species to forest cover composition because the full spectrum of seral stages may not be evident in every sample. Conversely, the relation to forest cover composition at coarser scales might be more precise. To test this hypothesis, I compared the width of the 95% credible intervals around the parameter estimates for each of the three forest covariates I examined: aspen forest, deciduous forest, and total forest composition. I found the credible intervals for the

Table 1. Environmental variables included in initial (global) models of habitat associations for the Golden-winged Warbler (*Vermivora chrysoptera*) in Bird Conservation Region 23, the Prairie Hardwood Transition.

Environmental suite	Variable
Land cover composition	Aspen forest (<i>Populus</i> spp.) composition (%)
	Deciduous forest composition (%)
	Total forest composition (%)
Land cover configuration	Patchy forest composition (%) [†]
	Perforated forest composition (%) [†]
	Transitional forest composition (%) [†]
	Shrub/grass/forest edge (km/km ²) [‡]
Terrain heterogeneity and physiognomy	Topographic convergence index (scales between 1 [dry] to 19 [moist]) [‡]
Interspecific competition	Blue-winged Warbler (<i>Vermivora cyanoptera</i>) abundance [§]
Spatial correlation	Universal transverse mercator northing
	Normal conditional autoregression [¶]

[†] Mean composition of constituent forest fragmentation types for 81 km² areas. Patchy forests were areas where forest composition was <40%; transitional forests were 40% to 60% forest; and perforated forests were >60% forest with high connectivity of forest patches (Riitters et al. 2000).

[‡] Also known as the static wetness, this index is measured as $\ln(\text{Catchment Area}/\text{tangent of the slope angle})$.

[§] As indexed by an inverse-distance-weighted interpolation of Breeding Bird Survey data (J. Sauer, unpublished data).

[|] First-order trend.

[¶] Second-order (small area) correlation.

association to habitat cover widened considerably with refinement in scale for total forest composition (88% wider for the fine-scale result vs. the intermediate scale), but not for aspen (1.5% wider for the intermediate scale vs. the coarse scale), providing equivocal support for this hypothesis (W. E. Thogmartin, unpublished data).

I fitted models with WinBUGS (Spiegelhalter et al. 2003), a statistical package for conducting Bayesian inference with Markov chain Monte Carlo methods (Gibbs Sampling; Link and Sauer 2002). For each model I ran the Markov chain until convergence

occurred (15,000 iterations) followed by an additional 6000 iterations past convergence. This chain creation was conducted five times to create replicate chains for the Gelman-Rubin diagnostic (Brooks and Gelman 1998, Spiegelhalter et al. 2003), comparing within-chain and between-chain variability. To reduce problems of autocorrelation in the model chains I sampled every tenth iteration. Code similar to the model I implemented is available in Thogmartin et al. (2004a).

I followed an information-theoretic approach to model building (Burnham and Anderson 2002),

using the Deviance Information Criterion (DIC), a Bayesian analogue to Aikike's Information Criterion, to rank models (Spiegelhalter et al. 2002). I constrained inference and model averaging to only those models within 2 DIC units of the best model, which Burnham and Anderson (2002) suggest is the model set with substantial support. As a reference, I also calculated a null model which contained observer and year (nuisance) effects, but which did not contain environmental covariates.

I mapped the final statistical model in the geographic information systems ArcGIS 9.2 (Environmental Systems Research, Inc., Redlands, California, USA) by combining grid layers based upon their model-averaged slope coefficients. Kubel and Yahner (2007) suggested Golden-Winged Warblers were detected out to a distance of 85 m from a point count; I used this distance to determine a reasonable mapping resolution, resolving the final map to 113.5 ha ($\pi \times 85^2 \text{ m} \times 50$ stops).

Model adequacy

I evaluated model adequacy using a goodness of fit procedure described by Gelman et al. (1995); in this procedure, parameter sets derived from the original data are compared to parameter sets derived from a replicate data set. For each of the 30,000 sets of parameters (5×6000 iterations) sampled by simulation, a replicate data set was generated following model specifications. The Gelman-Rubin diagnostic compares this replicate data set with the true data set. I also used Breeding Bird Survey data held back from model creation to preliminarily assess the validity of the models and maps I developed. The root mean square prediction error (RMSPE) was calculated as a measure of model fit against the withheld (independent) data. The RMSPE is the square root of the differences between the observed counts, i.e., withheld BBS counts, and expected counts (model predictions) divided by the sample size; smaller values of this metric indicate better model performance relative to the independent data.

RESULTS

A total of 660 Golden-winged Warblers counted from 1981 to 2001 were included in the model, yielding a mean count of 0.36 birds per survey and

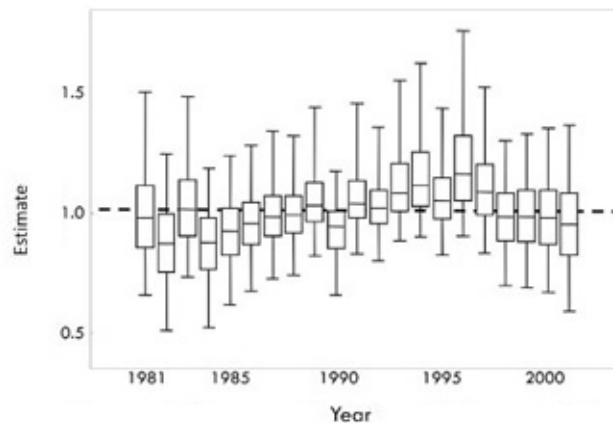
a variance equal to 1.87. The proportion of annual counts recording Golden-winged Warblers was 13.6%. For those survey locations that did count Golden-winged Warblers, the mean count was 2.64 birds/survey ($\sigma^2 = 7.73$). Golden-winged Warbler abundance was generally stationary between 1981 and 2001 (Fig. 1). However, there appeared to be a general increase in median abundance between 1984 and 1989, followed by a perturbation in 1990 and a subsequent increase until 1996. Thereafter, the population exhibited increasing variability in abundance.

The standard deviations of the random effects indicated that the preponderance of between-count variance was attributable to observer variability ($\sigma_{\text{observer}} = 1.54$, $\sigma_{\text{route}} = 0.13$, $\sigma_{\text{year}} = 0.15$, $\sigma_{\text{error}} = 0.54$). Only 14 of the 310 observers possessed credibility intervals failing to overlap 0; that is, 5.4% of the observers exhibited a substantive difference from the majority of observers in how they counted Golden-winged Warblers. However, because I expect 5% of any randomly acquired sample to behave in this fashion, I conclude that there were no substantive differences in detectability associated with observer ability.

The best model for the Golden-winged Warbler possessed a model weight of 74% (Table 2). Golden-winged Warbler abundance was strongly, positively associated with total forest composition, especially deciduous forests dominated by aspen (Table 3, Fig. 2). Golden-winged Warbler abundance was negatively associated with habitat edge density and patchy, perforated, and transitional forests at intermediate and coarse spatial scales. There was a strong negative association with Blue-winged Warbler abundance at the intermediate spatial scale. Some a priori variables chosen because of previously reported positive associations with species abundance had negative associations at the scales I examined, including the variables I included as surrogates to the edge habitat favored by this species (Table 3, Fig. 2).

The spatial-relatedness term (conditional autoregression) was dropped because of insufficient discriminability (Moran's $I < 0.2$), though a regional north-south trend in abundance was characterized by a northing term. The random effects associated with route contributed 4.7% to the mean expected count (mean = 0.015 [0.005, 0.050]); this was (noncorrelated spatial) variance in the counts occurring as a consequence of variables I did not consider.

Fig. 1. Posterior estimates of annual relative Golden-winged Warbler (*Vermivora chrysoptera*) abundance after incorporating effects of year and trend. The boxplots represent interquartile ranges and the solid black line bisecting each box is the annual median estimate of abundance; the arms of each box extend to cover the 95% credible interval.



Golden-winged Warblers in the Prairie Hardwood Transition had their greatest predicted abundance in west-central Wisconsin (Fig. 3). Other predicted high abundance areas occurred along the northern periphery of the study area, south of the species core in Bird Conservation Region 22, the Boreal Hardwood.

Model adequacy

The posterior predictive model check indicated the tail-area probability for the model was 0.396, providing little evidence of lack of fit. Observations from the withheld BBS data indicated slightly higher counts for the Golden-winged Warbler than I predicted (RMSPE = 0.34), but this was expected given that I did not remove the random effects associated with observer and year, resulting in a 'regression to the mean' (Harrell 2001). The mean of the observations compared to the mean of the expectation was moderately correlated ($r = 0.48$). Ninety-five percent of withheld BBS counts for Golden-winged Warbler were within one bird of the expectation.

DISCUSSION

The Golden-winged Warbler is a species of considerable conservation concern because of small, declining populations and competitive interactions with the Blue-winged Warbler (Knutson et al. 2001, U.S. Fish and Wildlife Service 2002, Rich et al. 2004, Buehler et al. 2006, COSEWIC 2006). The Golden-winged and Blue-winged Warblers are so closely related as to be nearly genetically identical and hybrids are common (Confer 1992). The Golden-winged Warbler model confirmed a strongly negative landscape-level association with Blue-winged Warbler abundance first identified at a forest stand level (Confer 1992).

I also identified strong regional associations with aspen. However, I failed to support reported positive associations between various measures of forest edge identified at the field level; instead I observed negative associations between the species and various measures of edge. Further, purported associations with mesic forest conditions in Wisconsin north of this region (Roth and Lutz 2004; A. Roth, *personal communication*) were also not observed at the scales I studied. These results are surprising as habitat descriptions for the species emphasize their association with shrubs, forest edges, and mesic forest-shrub conditions (Ficken and Ficken 1968, Will 1986, Roth and Lutz 2004).

Table 2. Parameter estimates for the best subset of models fitted to 1981–2001 Breeding Bird Survey route counts for the Golden-winged Warbler (*Vermivora chrysoptera*) in the Prairie Hardwood Transition of the upper midwestern U.S. The Null model, included for comparison, is a model with observer and year random effects, but without environmental covariates.

Best subset model	Explanatory variables	Scale (ha)	Parameters [†]	DIC [‡]	ΔDIC [§]	$w_i^ $	Evidence ratio [¶]
1	Shrub/grass/forest edge, (Total, Patchy, Perforated, and Aspen Forest, <i>Populus</i> spp.), Blue-winged Warbler (<i>V. cyanoptera</i>) abundance, Northing	80,000	171.8	1,411.5	0.00	0.79	1.00
2	Shrub/grass/forest Edge, (Total, Transitional, Aspen, and Deciduous forest), Blue-winged Warbler abundance, Northing	8,000	174.2	1,414.1	2.61	0.21	3.69
Null			182.8	1,423.7	12.23	0.002	452.60

[†] Parameters is the effective number of parameters (pD) and is given by the posterior mean of the deviance minus the deviance of the posterior means.

[‡] DIC is Deviance Information Criterion. See text for details.

[§] ΔDIC is the difference between the best model and the model of interest.

^{||} w_i is the model weight, as described in the text (the remaining set of models constituted <6% of the total model weight).

[¶] Evidence ratio is the model weight for the best model divided by the weight for the model of interest.

There are a number of potential reasons for these contradictory findings. It is possible that the land cover maps I used do not accurately represent the relatively ephemeral shrub and transitional habitat characteristic of Golden-winged Warbler habitat at local scales (Thogmartin et al. 2004b); this may be particularly true given that I used 20 years of BBS data, but the land cover maps were static, generated in the early 1990's (Vogelmann et al. 2001). Also, these land cover maps did not distinguish young forests from older forests, or mesic forests from dry forests. Another explanation may be that the species may display different habitat associations at fine (stand – level) vs. coarse spatial scales (Wiens et al. 1987, Thogmartin 2007).

I believe the more likely reason this species exhibits negative relations to various edge metrics is that the area I studied has relatively little forest (mean <30% and median <20%; Fig. 1) occurring in a relatively

high state of edge density (35–45 km/km²). What we are probably observing is one end of the spectrum of responses exhibited by this species, balanced against the more frequently reported observations, albeit at a finer scale, of the species occurring in edge environs in more forested systems. I submit that in low-forest, high-edge landscapes akin to the situation in the Prairie Hardwood Transition, Golden-winged Warblers achieve greater density in more forested situations, whereas in high-forest, low-edge landscapes, they will achieve their greatest density in those areas where forest is less abundant and most fragmented by early successional patches. To test the former in a post-hoc fashion, I amended the best-fit models with two additional terms, Proportion of Forest Cover in interaction with Proportion of Patchy Forest Cover and Proportion of Perforated Forest Cover, and repeated the model fitting with the methods described previously. Both interactions

Table 3. Median and lower (LCL) and upper (UCL) confidence limits of the posterior distribution of explanatory variable slopes for an average model derived from the Kullback-Leibler best subset of models for the Golden-winged Warbler (*Vermivora chrysoptera*) in the Prairie Hardwood Transition of the upper midwestern United States.

Explanatory Variable	Scale (ha)	Median	95% LCL	95% UCL
Shrub/Grass/Forest Edge (km/km ²)	8000	-0.63	-0.63	-0.62
Shrub/Grass/Forest Edge (km/km ²)	80,000	-0.68	-0.69	-0.68
Total Forest Composition (%)	8000	0.79	0.78	0.80
Total Forest Composition (%)	80,000	1.33	1.32	1.33
Patchy Forest Composition (%)	80,000	-0.40	-0.41	-0.40
Perforated Forest Composition (%)	80,000	-0.20	-0.20	-0.19
Transitional Forest Composition (%)	8000	-0.52	-0.52	-0.51
Aspen Forest (<i>Populus</i> spp.) Composition (%)	8000	0.25	0.25	0.26
Aspen Forest Composition (%)	80,000	0.22	0.21	0.22
Deciduous Forest Composition (%)	8000	0.45	0.44	0.46
Blue-winged Warbler (<i>Vermivora cyanoptera</i>) Abundance		-0.33	-0.33	-0.33
Northing [†]		1.10	1.09	1.11
Intercept		-4.07	-4.07	-4.06

[†] Highly correlated with maximum temperature in November, $r = -0.96$.

were negative and statistically credible (from the coarsest-scale model, $\beta_{\text{Forest} \times \text{Patchy}} = -0.47$ [-0.88, -0.07], $\beta_{\text{Forest} \times \text{Perforated}} = -0.34$ [-0.65, -0.02]); as forest increased in the landscape, Golden-winged Warblers were more abundant as edge forest declined (Fig. 4). Neither model, however, was closer than 4.5 DIC to the best fit model previously reported ($w < 0.08$, evidence ratios > 9.5), possibly because of the limited regional availability of forest. A more explicit test of this hypothesis would require a multiregional examination, encompassing a wider range in forest cover than is available in the Prairie Hardwood Transition. At this time, evidence points to this species preferring edges embedded within a larger forested landscape (Klaus and Buehler 2001, Hanowski 2002). This cross-scale result emphasizes

the need for properly characterizing the context in which species-habitat studies are conducted, as these cross-scale contradictions have the potential for leading to much confusion if not handled deftly (Thogmartin 2007).

A role for climate?

The northing term in the final model represented a broad spatial trend possibly associated with climate. Venier et al. (2004) suggested that because climate and land cover are often highly correlated in forested systems, climate may not improve species-habitat models that already incorporate land cover. Latitude nearly perfectly correlates in the Prairie Hardwood

Fig. 2. Mean contribution of environmental covariates to the expected Golden-winged Warbler (*Vermivora chrysoptera*) count ($y = e^{\beta x}$, where y is the expected count and x is the value of the standardized variable), as derived from an average model for the Prairie Hardwood Transition of the upper midwestern United States. Coarse refers to the variable at the 80,000 ha scale; intermediate refers to the variable at the 8000 ha scale. Note the differing y-axes.

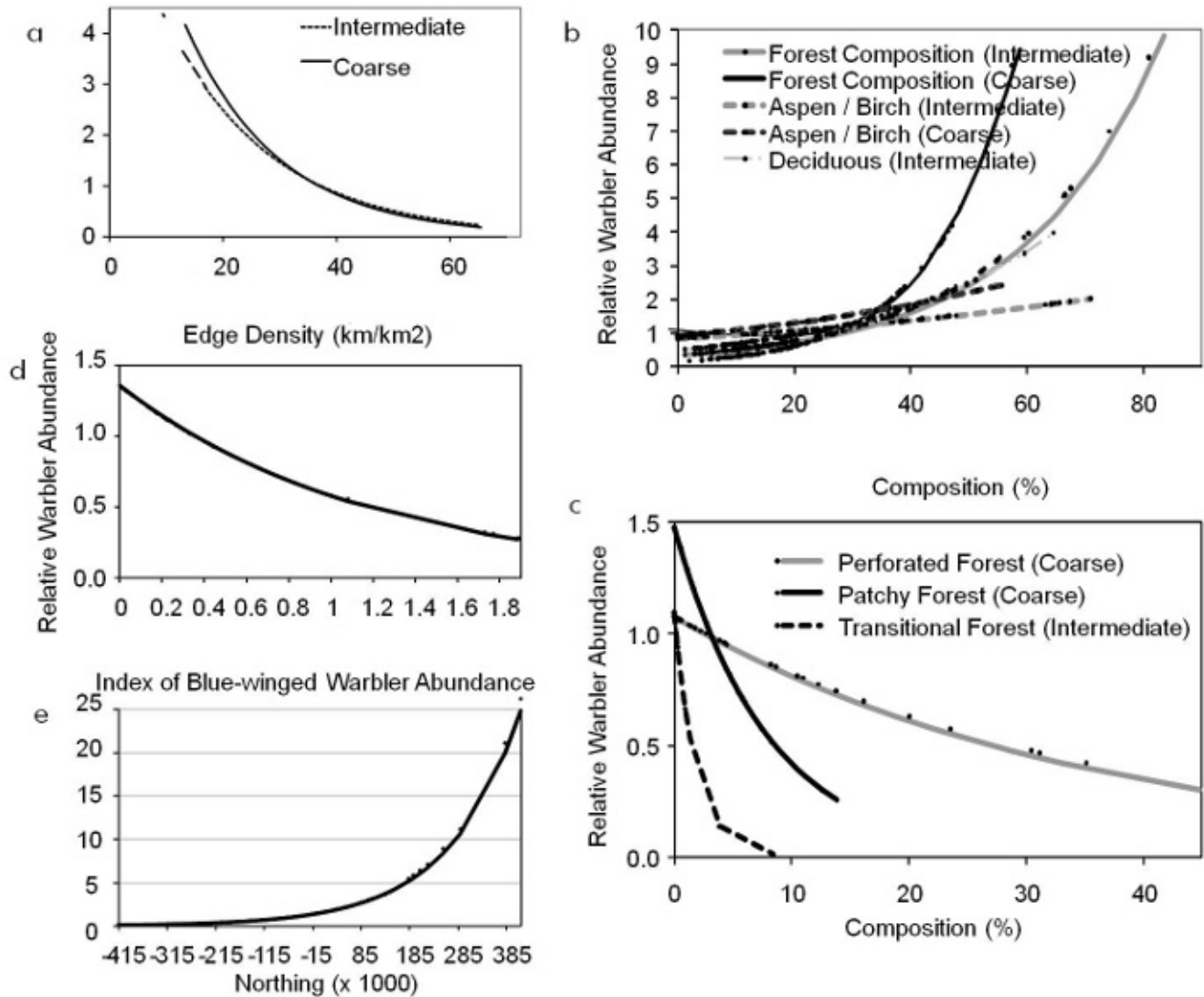


Fig. 3. Map of predicted relative abundance (birds \times 100 predicted per survey) for the Golden-winged Warbler (*Vermivora chrysoptera*) in the Prairie Hardwood Transition of the upper midwestern United States. The primary peak of predicted abundance for Golden-winged Warblers occurs in west-central Wisconsin (inset).

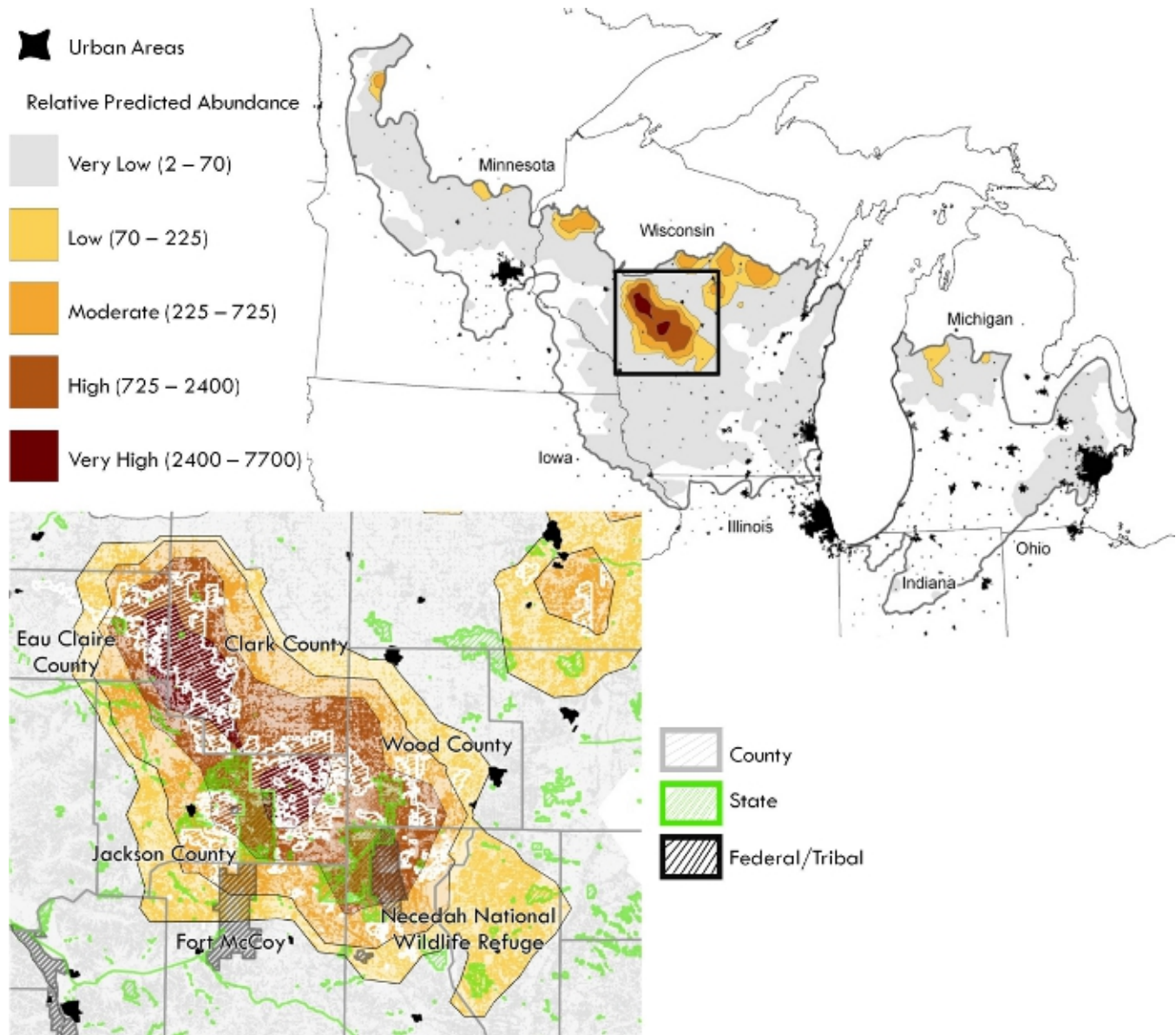
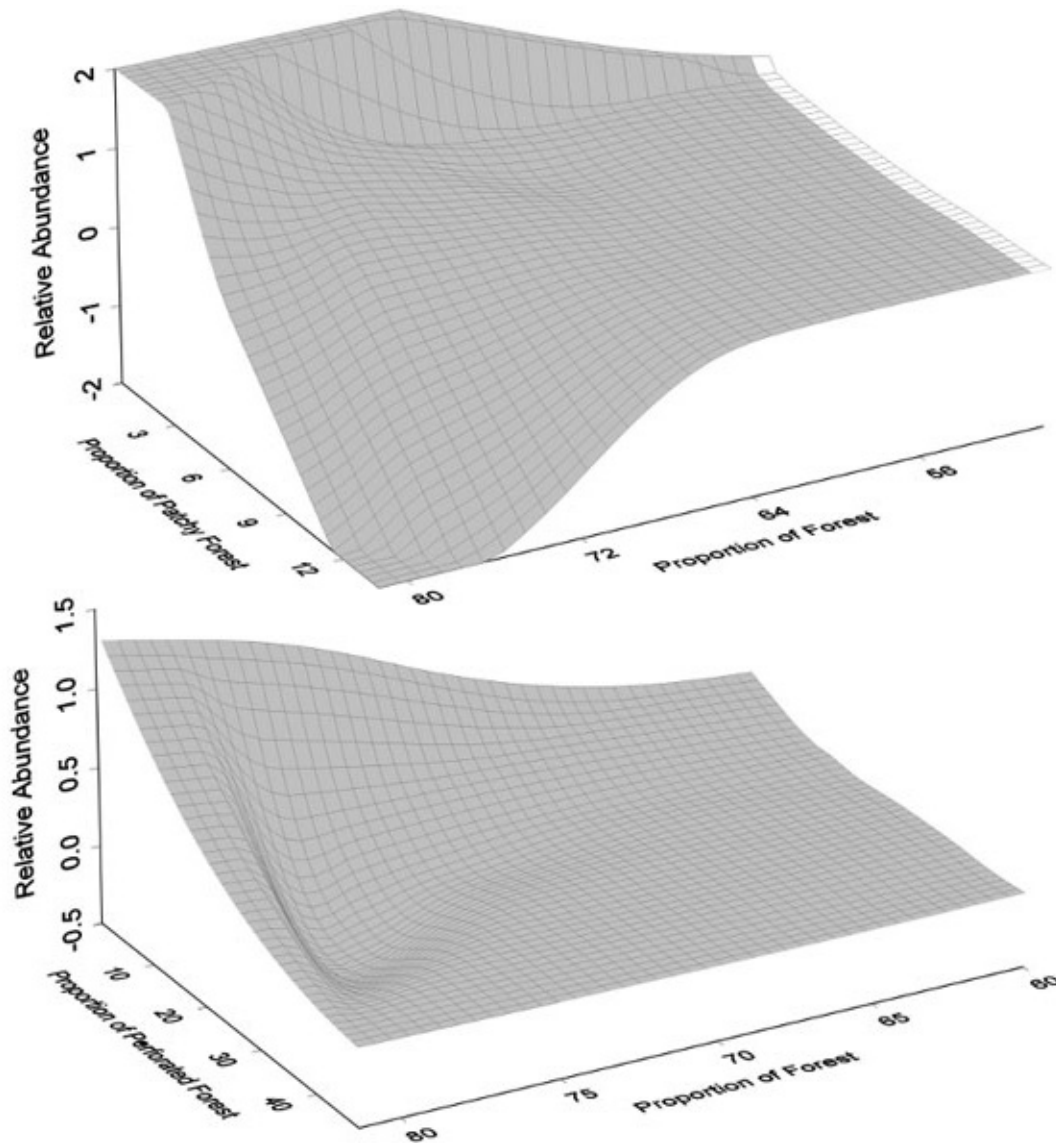


Fig. 4. The interaction of forest cover and two measures of edge forest conditions (patchy and perforated forest) indicate Golden-winged Warblers (*Vermivora chrysoptera*) increase in abundance as the proportion of forest increases and the amount of edge forest decreases.



Transition with climatic factors such as summer precipitation and temperature (r 's ≈ 0.95 , unpublished data). Given the inclusion of land cover variables in the model, it seems reasonable to hypothesize some influence of climate on the abundance of this species over and above the influences of land cover. Moths and their larvae are among the most favored food items of Golden-

winged Warblers (Confer 1992), and there is evidence suggesting that moths are responding to global warming (Fleming and Candau 1998). Thus, this gradient in warbler abundance, should it reflect an underlying gradient in food abundance, may at some point reveal itself asynchronous with the habitat because of changing climate (Visser et al. 1998, Visser and Holleman 2001, Price 2004).

Conclusions

Less than 20% of the predicted population of Golden-winged Warblers in the Prairie Hardwood Transition occurs on land managed by federal (4.4%), tribal (5.2%), or state (9.5%) land management agencies (Thogmartin and Rohweder 2009). Thus, the majority of the species occurs outside of direct governmental jurisdiction. Efforts to manage this species will be most successful if the focus of conservation is on habitat in private ownership or levels of governmental jurisdiction finer than the state. For instance, Necedah National Fish and Wildlife Refuge might use the map I created to focus their private lands program on habitat to the northwest of their refuge (Fig. 3), areas which are presently highly forested. To do so would require a close partnership with Wisconsin county forest programs, owner of much of the land associated with this hotspot, and adjacent private landowners.

No single spatial scale dominated any model, indicating that this species is responding to factors at multiple spatial scales. However, the best models resolved themselves at the coarser scales (8000 and 80,000 ha); the finest scale (800 ha) was excluded. This suggests that conservation for this species might best occur over landscapes ranging in size from 8000 to 80,000 ha, similar to the size of townships and counties. Given the positive response to forest composition and negative response to edge density, conservation of contiguous tracts of forests in the northern portions of the Prairie Hardwood Transition, especially in Wisconsin, will most benefit the species as further declines in composition and consequent increases in edge density appear contraindicated for this species.

Responses to this article can be read online at:
<http://www.ace-eco.org/vol5/iss2/art12/responses/>

Acknowledgments:

I thank the many individuals involved in the collection of Breeding Bird Survey data, which made this analysis possible. I thank T. C. Will for providing important feedback regarding development of the a priori models, D. McKenney and P. Papadopol of the Canadian Forest Service for interpolations of mean climate conditions, T. J. Fox,

J. C. Nelson, and J. J. Rohweder for geographic information systems support, and A. M. Roth, S. Barker Swarthout, T. C. Will, J. R. Sauer, and two anonymous reviewers for their inspection of an earlier version of this manuscript. Further details regarding the models described here, as well as for other species, are available at http://www.umesc.usgs.gov/terrestrial/migratory_birds/bird_conservation.html.

LITERATURE CITED

Beven K. J., and M. J. Kirkby. 1979. A physically based variable contributing area model of basin hydrology. *Hydrologic Science Bulletin* **24**:43-69.

Brooks, S., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* **7**:434-455.

Buehler, D. A., J. L. Confer, R. A. Canterbury, T. C. Will, W. C. Hunter, R. Dettmers, and D. Demarest. 2006. *Status assessment and conservation plan for the Golden-winged Warbler, Vermivora chrysoptera, in the United States.* Fish and Wildlife Service Biological Technical Publication FWS/BTP-R6XXX-2006. U.S. Department of the Interior, Washington, D.C., USA.

Buehler, D. A., A. M. Roth, R. Vallender, T. C. Will, J. L. Confer, R. A. Canterbury, S. Barker Swarthout, K. V. Rosenberg, and L. P. Bulluck. 2007. Status and conservation priorities of Golden-winged Warblers (*Vermivora chrysoptera*) in North America. *The Auk* **124**:1439-1445.

Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference: a practical information theoretic approach.* Second edition. Springer-Verlag, New York, New York, USA.

Cleland, D. T., L. A. Leefers, and D. I. Dickmann. 2001. Ecology and management of aspen: a Lake States perspective. Pages 81-100 in W. D. Shepperd, D. Binkley, D. L. Bartos, T. J. Stohlgren, and L. G. Eskew, editors. *Sustaining aspen in western landscapes.* Proceedings RMRS-P-18. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Cliff, A. D., and J. K. Ord. 1981. *Spatial processes*. Pion, London, UK.

Committee on the Status of Endangered Wildlife in Canada (COSEWIC). 2006. *Canadian species at risk, May 2006*. COSEWIC, Ottawa, Ontario, Canada.

Confer, J. L. 1992. Golden-winged Warbler (*Vermivora chrysoptera*). In A. Poole and F. Gill, editors. *The birds of North America*, Number 20. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D. C., USA. [online] URL: <http://bna.birds.cornell.edu/bna/species/020/articles/introduction>.

Confer, J. L., K. W. Barnes, and E. C. Alvey. 2010. Golden- and Blue-winged Warblers: distribution, nesting success, and genetic differences in two habitats. *The Wilson Journal of Ornithology* **122**:273-278.

Ficken, M. S., and R. W. Ficken. 1968. Ecology of Blue-winged Warblers, Golden-winged Warblers, and some other *Vermivora*. *American Midland Naturalist* **79**:311-319.

Fleming, R. A., and J.-N. Candau. 1998. Influences of climatic change on some ecological processes of an insect outbreak system in Canada's boreal forests and the implications for biodiversity. *Environmental Monitoring and Assessment* **49**:235-249.

Gelman, A., J. B. Carlin, H. S. Stern, and D. R. Rubin. 1995. *Bayesian data analysis*. Chapman and Hall, New York, New York, USA.

Hanowski, J. 2002. Habitats and landscapes used by breeding Golden-winged Warblers in western Great Lakes forests. *The Loon* **74**:127-133.

Harrell, F. E., Jr. 2001. *Regression modeling strategies, with applications to linear models, logistic regression, and survival analysis*. Springer-Verlag, New York, New York, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource performance. *Ecology* **61**:65-71.

Klaus, N. A., and D. A. Buehler. 2001. Golden-winged Warbler breeding habitat characteristics and nest success in clearcuts in the southern Appalachian mountains. *Wilson Bulletin* **113**:297-301.

Knutson, M. G., G. Butcher, J. Fitzgerald, and J. Shieldcastle. 2001. *Partners in Flight Bird Conservation Plan for The Upper Great Lakes Plain* (Physiographic Area 16). U.S. Geological Survey Upper Midwest Environmental Sciences Center in cooperation with Partners in Flight, La Crosse, Wisconsin, USA.

Kubel, J. E., and R. H. Yahner. 2007. Detection probability of Golden-winged Warblers during point counts with and without playback recordings. *Journal of Field Ornithology* **78**:195-205.

Link, W. A., E. Cam, J. D. Nichols, and E. Cooch. 2002. Of BUGS and birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. *Journal of Wildlife Management* **66**:277-291.

Link, W. A., and J. R. Sauer. 2002. A hierarchical analysis of population change with application to Cerulean Warblers. *Ecology* **83**:2832-2840.

McCarthy, M. A. 2007. *Bayesian methods for ecology*. Cambridge University, Cambridge, UK.

McNab, W. H., and P. E. Avers. 1994. *Ecological subregions of the United States*. U.S. Department of Agriculture Forest Service, Ecosystem Management Team, WO-WSA-5, Washington, D. C., USA.

Meyer, C. B. 2007. Does scale matter in predicting species distributions? Case study with the marbled murrelet. *Ecological Applications* **17**:1474-1483.

National Ecological Assessment Team (NEAT). 2006. *Strategic habitat conservation: a report from the National Ecological Assessment Team*, June 29, 2006. U.S. Fish and Wildlife Service, Washington, D.C., and U.S. Geological Survey, Reston, Virginia, USA. [online] URL: http://training.fws.gov/EC/resources/shc/shc_finalrpt.pdf.

Possingham, H. P., and K. A. Wilson. 2005. Biodiversity: turning up the heat on hotspots. *Nature* **436**:919-920.

Price, J. 2004. Climate change and Wisconsin's nongame birds. *Passenger Pigeon* **66**:51-59.

Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. Bradstreet, G. S. Butcher, D. Demarest, E. H. Dunn, W. C. Hunter, D. Inigo-

- Elias, J. A. Kennedy, A. Martell, A. Panjabi, D. N. Pashley, K. V. Rosenberg, C. Rustay, S. Wendt, and T. Will.** 2004. *Partners in Flight North American landbird conservation plan*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Riitters, K., J. Wickham, R. O'Neill, B. Jones, and E. Smith.** 2000. Global-scale patterns of forest fragmentation. *Conservation Ecology* 4(2): 3. [online] URL: <http://www.consecol.org/vol4/iss2/art3/>.
- Roth, A. M., and S. Lutz.** 2004. Relationship between territorial male Golden-Winged Warblers in managed aspen stands in northern Wisconsin, USA. *Forest Science* 50:153-161.
- Sauer, J. R., J. E. Hines, and J. Fallon.** 2008. *The North American breeding bird survey, results and analysis 1966 - 2007*. Version 5.15.2008. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA.
- Schmidt, T. L.** 1997. *Wisconsin forest statistics, 1996*. U.S. Department of Agriculture Forest Service North Central Experiment Station, Research Bulletin NC-183, Rhinelander, Wisconsin, USA.
- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. van der Linde.** 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society B* 64:583-639.
- Spiegelhalter, D. J., A. Thomas, and N. G. Best.** 2003. *WinBUGS Version 1.4 user manual*. Medical Research Council Biostatistics Unit, Cambridge, UK.
- Thogmartin, W. E.** 2007. Effects at the landscape scale may constrain habitat relations at finer scales. *Avian Conservation and Ecology - Écologie et conservation des oiseaux* 2(2): 6. [online] URL: <http://www.ace-eco.org/vol2/iss2/art6/>.
- Thogmartin, W. E., J. A. Fitzgerald, and M. T. Jones.** 2009. Conservation design: Where do we go from here? Pages 426-436 in T. D. Rich, C. Arizmendi, D. Demarest, and C. Thompson, editors. *Tundra to tropics: connecting birds, habitats and people*. Proceedings of the 4th International Partners in Flight Conference, 13-16 February 2008. McAllen, Texas, USA.
- Thogmartin, W. E., A. L. Gallant, M. G. Knutson, T. J. Fox, and M. J. Suárez.** 2004b. A cautionary tale regarding the 1992 National Land Cover Data. *The Wildlife Society Bulletin* 32:970-978.
- Thogmartin, W. E., and J. J. Rohweder.** 2009. Conservation opportunity assessment for rare birds in the midwestern United States: a private lands imperative. Pages 419-425 in T. D. Rich, C. Arizmendi, D. Demarest, and C. Thompson, editors. *Tundra to tropics: connecting birds, habitats and people*. Proceedings of the 4th International Partners in Flight Conference, 13-16 February 2008. McAllen, Texas, USA.
- Thogmartin, W. E., J. R. Sauer, and M. G. Knutson.** 2004a. A hierarchical spatial model of avian abundance with application to Cerulean Warblers. *Ecological Applications* 14:1766-1779.
- Thomas, A., N. Best, R. Arnold, and D. Spiegelhalter.** 2002. *GeoBugs User Manual, Version 1.1 Beta*. Medical Research Council Biostatistics Unit, Cambridge, UK.
- U.S. Fish and Wildlife Service.** 2002. *Birds of conservation concern*. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, Virginia, USA.
- U.S. North American Bird Conservation Initiative (NABCI) Committee.** 2000. *North American Bird Conservation Initiative: bird conservation region descriptions*. U.S. Fish and Wildlife Service, Division of Bird Habitat Conservation, Arlington, Virginia, USA.
- Vallender, R., R. J. Robertson, V. L. Friesen, and I. J. Lovette.** 2007. Complex hybridization dynamics between golden-winged and blue-winged warblers (*Vermivora chrysoptera* and *Vermivora pinus*) revealed by AFLP, microsatellite, intron and mtDNA markers. *Molecular Ecology* 16:2017-2029.
- Vallender, R., S. L. Van Wilgenburg, L. P. Bulluck, A. Roth, R. Canterbury, J. Larkin, R. Fowlds, and I. J. Lovette.** 2009. Extensive rangewide mitochondrial introgression indicates substantial cryptic hybridization in the Golden-winged Warbler (*Vermivora chrysoptera*). *Avian Conservation and Ecology - Écologie et conservation des oiseaux* 4(2): 4. [online] URL: <http://www.ace-eco.org/vol4/iss2/art4/>.

Venier, L. A., J. Pearce, J. E. McKee, D. W. McKenney, and G. J. Niemi. 2004. Climate and satellite-derived land cover for predicting breeding bird distribution in the Great Lakes Basin. *Journal of Biogeography* **31**:315-331.

Visser, M. E., and L. J. M. Holleman. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London B* **268**:289-294.

Visser, M. E., A. J. van Noordwijk, J. M. Tinbergen, and C. M. Lessels. 1998. Warmer springs lead to mistimed reproduction in Great Tits (*Parus major*). *Proceedings of the Royal Society of London B* **265**:1867-1870.

Vogelmann, J. E., S. M. Howard, L. Yang, C. R. Larson, B. K. Wylie, and N. Van Driel. 2001. Completion of the 1990s National Land Cover Data set for the conterminous United States from Landsat Thematic Mapper data and ancillary data sources. *Photogrammetric Engineering and Remote Sensing* **67**:650-652.

Whittaker, R. J., M. B. Arauko, P. Jepson, R. J. Ladle, J. E. M. Watson, and K. J. Willis. 2005. Conservation biogeography: assessment and prospect. *Diversity and Distributions* **11**:3-23.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effect of spatial scale. *Oikos* **48**:132-147.

Will, T. C. 1986. *The behavioral ecology of species replacement: Blue-winged and Golden-winged Warblers in Michigan*. Dissertation, University of Michigan, Ann Arbor, Michigan, USA.

Zhu, Z., and D. L. Evans. 1994. U.S. forest types and predicted percent forest cover from AVHRR Data. *Photogrammetric Engineering and Remote Sensing* **60**:525-531.

APPENDIX 1. Priors and effect type for the main model effects of the hierarchical spatial count model.

Variable	Definition	Effect type	Prior distribution (expected value, precision [†])
μ	Environmental factors	Fixed	Normal (0.0, 0.000001) [‡]
Z	Spatial relatedness	Random	Flat (for the Conditional Autoregression-related intercept) [§] $\tau_{\text{Space}} \sim \text{Gamma} (0.5, 0.0005)$
ω	Observer-experience effect	Random	Normal (0.0, τ_{Observer}) $\tau_{\text{Observer}} \sim \text{Gamma} (0.001, 0.001)$
η	Novice-observer effect	Fixed	Normal (0.0, 0.000001)
γ	Year effect	Random	Normal (0.0, τ_{Year}) $\tau_{\text{Year}} \sim \text{Gamma} (0.001, 0.001)$
ε	Error	Random	Normal (0.0, τ_{Noise}) $\tau_{\text{Noise}} \sim \text{Gamma} (0.001, 0.001)$

[†] Precision rather than variance is described, with precision simply 1/variance.

[‡] Essentially a flat or noninformative prior distribution.

[§] See Thomas et al. (2002) for details regarding flat prior relating to the conditional autoregression implemented in WinBUGS.
