

Modeling and Mapping Abundance of American Woodcock Across the Midwestern and Northeastern United States

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ABSTRACT We used an over-dispersed Poisson regression with fixed and random effects, fitted by Markov chain Monte Carlo methods, to model population spatial patterns of relative abundance of American woodcock (*Scolopax minor*) across its breeding range in the United States. We predicted North American woodcock Singing Ground Survey counts with a log-linear function of explanatory variables describing habitat, year effects, and observer effects. The model also included a conditional autoregressive term representing potential correlation between adjacent route counts. Categories of explanatory habitat variables in the model included land-cover composition, climate, terrain heterogeneity, and human influence. Woodcock counts were higher in landscapes with more forest, especially aspen (*Populus tremuloides*) and birch (*Betula* spp.) forest, and in locations with a high degree of interspersed forest, shrubs, and grasslands. Woodcock counts were lower in landscapes with a high degree of human development. The most noteworthy practical application of this spatial modeling approach was the ability to map predicted relative abundance. Based on a map of predicted relative abundance derived from the posterior parameter estimates, we identified major concentrations of woodcock abundance in east-central Minnesota, USA, the intersection of Vermont, USA, New York, USA, and Ontario, Canada, the upper peninsula of Michigan, USA, and St. Lawrence County, New York. The functional relations we elucidated for the American woodcock provide a basis for the development of management programs and the model and map may serve to focus management and monitoring on areas and habitat features important to American woodcock. (JOURNAL OF WILDLIFE MANAGEMENT 71(2):376–382; 2007)

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The realization of conservation goals for many North American birds requires strategies for managing species within human-dominated landscapes (Jones and Bock 2002, Thogmartin et al. 2004b). Kiester et al. (1996:1333) suggested, “Biodiversity is largely a matter of real estate. And as with other real estate, location is everything.” Unfortunately for many species, researchers do not adequately understand their distribution and patterns of abundance in human-dominated landscapes. Predictive mapping of species abundance over broad areas would facilitate attainment of conservation goals by focusing management and monitoring efforts on areas and habitat features important for their continued persistence (Thogmartin et al. 2004b).

American woodcock (*Scolopax minor*) populations have exhibited consistent declines in the eastern and central United States since at least the late 1960s (Straw et al. 1994). These declines have been attributed in part to loss of old field and early successional habitats through urban and agricultural development (Dwyer et al. 1983, Sauer and Bortner 1991, Straw et al. 1994); the draining of wetlands and bottomland hardwood forest are also believed to have contributed to the decline. These declines and threats to

habitat prompted the United States Shorebird Conservation Plan (Brown et al. 2001) to list the woodcock as a Species of High Conservation Concern. The International Association of Fish and Wildlife Agencies also created a Woodcock Task Force in 2002 to develop the Woodcock Conservation Plan to reverse these observed declines.

Fine-scaled studies of woodcock habitat use suggest the species is positively associated with early successional mesic forests and wetlands, and is negatively associated with agricultural and urbanized lands (Kinsley et al. 1980, Gutzwiller et al. 1983, Hudgins et al. 1985, Keppie and Whiting 1994, Klute et al. 2002). With this information in mind, our objectives were 1) to relate remotely sensed variables of these habitat descriptors against regional annual counts derived from the North American woodcock Singing Ground Survey (SGS) to create models of predicted abundance and 2) to use parameters from these models to map predicted abundance and associated measures of uncertainty.

STUDY AREA

We studied woodcock in their primary breeding range in the United States, which comprised 18 states in the northeast and north-central United States stretching from Minnesota to Maine and as far south as Illinois, Indiana, and Virginia. We did not study patterns in woodcock abundance in Canada because of disparities in land-cover data, nor did we

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study patterns in areas outside of the northeastern and midwestern United States because of a lack of survey data.

METHODS

We used SGS route counts as the response in our models. This survey consisted of 10 stops spaced along 5.4-km routes situated on randomly selected secondary roads. Observers counted the number of woodcock heard calling (peenting) at each stop, and the number of woodcock counted per route is an index of woodcock in a geographic area. The dates of surveys coincide with peaks in courtship behavior of local woodcock.

The SGS counts provided estimates of annual relative abundance of breeding woodcock to the extent that detection probability was constant or controlled by the survey design (Tautin et al. 1983, Sauer and Bortner 1991). This assumption of constant detection probability is a largely untested assumption. In reality, a host of factors likely influenced detection of woodcock, including woodcock vocalization rates as they relate to weather and time of day and increasing urbanization along the survey routes during the period of study. The survey design controls for some of these factors (e.g., weather) better than it controls for others (e.g., urbanization).

We used counts from 1,148 routes collected between 1981 and 2003 in model building and evaluation (this period roughly coincides with the date for which the environmental data were relevant, i.e., approx. 1991). For various reasons counts were not available from all routes in all years and, thus, the total number of counts ($n = 9,142$) used in model building is substantially less than the total number conceivable. Furthermore, we withheld 3,213 counts for model evaluation.

A unique aspect of the SGS protocol is the cessation of running routes in areas in which woodcock are considered absent. Routes for which observers do not hear woodcock for 2 consecutive years enter a constant zero status and are not run for the subsequent 5 years. If observers hear woodcock on a constant zero route after the 5-year period, the route reverts to normal status and is included each year thereafter. Data from constant zero routes are included in this analysis only for the years in which observers actually surveyed them (Sauer and Bortner 1991). The effect of this would be to under-represent areas of absence (i.e., structural zeroes) and raise the relative mean abundance for the region. One reviewer (J. A. Royle, United States Geological Survey, personal communication) suggested the bias that may result from failing to include constant zero routes was likely minimal.

We adopted a Bayesian framework for inference and prediction, implemented with Markov chain Monte Carlo (MCMC) methods (Gibbs Sampling; Link et al. 2002). The MCMC is a simulation-based approach to resolving mathematically intractable calculations such as the hierarchical spatial count model that we describe here. The general methods by which predicted abundance was modeled and mapped were outlined in Thogmartin et al. (2004b, 2006) with Breeding Bird Survey counts as the

response; briefly, the Thogmartin et al. (2004b, 2006) model was a spatial extension of the Link and Sauer (2002) hierarchical Bayesian trend count models, incorporating potential spatial autocorrelation between survey counts and remotely sensed environmental covariates. Here we similarly extend the model of Sauer et al. (unpublished) for trend estimation in woodcock SGS counts to accommodate spatial effects. The model had the form

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

where Z is the mean of the Poisson distribution of the predicted counts at location s_i for route i , $\mu(s_i)$ is the large-scale trend surface that depends on covariates (independent environmental variables), c_{ik} are the spatial dependence parameters, $i, k = 1, \dots, n$ where the dependence is symmetric and pair-wise dependence occurs only between neighboring survey locations (as determined by tessellation; Thogmartin et al. 2004b), and $\varepsilon(s_i)$ are the error terms that are independent with zero mean and constant variance τ^2 . Random observer and year effects are ω (observer experience), and γ (yr). Ostensibly, as the large-scale trend surface as determined by environmental covariates increases in importance in explaining patterns in the counts, the necessity for spatial dependence between route counts declines. We assigned diffuse or noninformative priors and hyper-priors to each parameter to represent an initial null expectation of the variables and their precision on bird counts (Appendix).

Environmental covariates derived from a review of the literature (Keppie and Whiting 1994, Straw et al. 1994) included forest, shrub, and grass composition, an aggregation index describing the clumping of forest, shrub and grass land covers, topographic convergence index, and the date of the start of the growing season. We derived human land-cover composition from an aggregated cover type defined as low-, medium-, or high-density residential areas, transportation, commercial, or industrial areas, and urban grass. We derived land-cover composition 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 to us for our region of interest and, thus, we did not consider them. We re-sampled the landscape composition of grass (i.e., coarsened in resolution) to include only those grass patches ≥ 1.2 ha, as fields (especially openings in forest) of this size may be important roosting and calling grounds (Sepik and Derleth 1993). The topographic convergence index, also known as static wetness potential, is the $\ln[\text{catchment area}/\tan(\text{slope angle})]$, where slope angle is in degrees (Moore et al. 1991) and is an index to mesic and xeric conditions resulting from terrain physiognomy. We hypothesized that moist soil conditions might prove favorable to earthworm (Family Lumbricidae) availability and, thus, to woodcock abundance. We used the 30-year mean day of the year marking the start of the

growing season as an index to the average last day in spring for frost, which has been associated with the northern limit of earthworms, an important food source for woodcock (Keppie and Whiting 1994). We considered another long-term climate mean, 30-year mean winter precipitation, which has been associated with the northern boundary to woodcock occurrence (Keppie and Whiting 1994); however, we discarded this variable early in the modeling as it was correlated ($r > 0.5$) with the start of the growing season but did not describe the apparent latitudinal long-range trend in abundance as well as the day of the year marking the start of the growing season. D. McKenney (Canadian Forestry Service, personal communication) provided mean climate conditions for woodcock routes. We considered models with both aspen (*Populus tremuloides*) and birch (*Betula* spp.) and forest composition together as they were not substantially correlated ($r = 0.16$). We also considered models with woodcock abundance as a curvilinear response to forest composition, as we believed that woodcock may be reduced in abundance in landscapes where forest composition was too great to allow for sufficient open areas for breeding.

A previous study of woodcock at a landscape level considered individual stops on 96 routes in Pennsylvania (Klute et al. 2002). In comparison, we considered 1,184 route-level counts. The aggregation of stop counts to the route has important implications for the minimum resolution of the analysis, namely that the counts were known only for some subjective area associated with the route and not for individual stops (stops were not georeferenced). Thus, because the data could only be minimally resolved to some area about the route, we assessed each environmental variable at 3 buffer distances around the routes. Those buffers translated to scales of approximately 350 (100-m buffer around routes), 4,000 (1,000-m buffer), and 106,000 ha (10,000-m buffer). We expected this range of spatial extents to encompass the population responses of woodcock to landscape factors, realizing that the data resolution precluded inferences about individual biological response (e.g., survival and fecundity) to local environmental factors.

We fit and predicted models with WinBUGS 1.4.1 (Spiegelhalter et al. 2003), a statistical package for conducting Bayesian inference with MCMC. For each model, we ran the Markov chain until convergence occurred (15,000 iterations) and an additional 3,000 iterations past convergence. We used the Gelman–Rubin diagnostic to evaluate model fit between 3 replicate chains (Brooks and Gelman 1998, Spiegelhalter et al. 2003), comparing within-chain and between-chain variability. We guarded against multicollinearity in the environmental variables by inspecting the multi-chain iteration histories and the Gelman–Rubin diagnostic plots of the slope parameters.

We employed an information-theoretic perspective to our modeling by comparing the Deviance Information Criterion (DIC) between models. DIC is an information criterion analogous to Akaike’s Information Criterion, with the most parsimonious model possessing the smallest DIC (Spiegelhalter et al. 2002). We calculated model weights akin to the

method suggested by Burnham and Anderson (2002) for Akaike’s Information Criterion weights:

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

where Δ_i is the difference between the DIC from model i (of R models) and the DIC possessed by the most parsimonious model (the model possessing the minimum DIC). An all-possible-models approach was not sensible. Akin to Thogmartin et al. (2004b), we selected backwards from global models, constructed at each of the 3 spatial scales; each global model comprised all of the environmental covariates at a specific scale. We dropped those environmental variables whose 95% credibility intervals for the model parameters contained zero. We continued selection in this manner until all remaining variables had credibility intervals that excluded zero. We then used the best model within each of the 3 scales to average the environmental variables across spatial scales (Burnham and Anderson 2002).

We mapped the statistical models by combining Geographic Information Systems (ArcGIS 9.0) grid layers of model variables based upon their model-averaged slope coefficients. We derived grid layers from regular lattices with cell sizes coincident with the scales of study (350 ha, 4,000 ha, and 106,000 ha), with the environmental covariates summarized for each cell within the lattice; this led to lattices of 1.37 million cells, 118,174 cells, and 4,586 cells, respectively. Because of computational difficulties associated with mapping environmental covariates at the finest extent of this lattice (350 ha), we based final maps on covariates derived for the coarsest extent (106,000 ha), regardless of the resolution identified during the model selection process (the wt [slope coeff.] were specific to the appropriate model, however). We standardized the environmental grid layers before their layering in the ArcGIS Spatial Analyst map calculator to reflect standardization of the environmental covariates prior to modeling, which was done to increase the efficiency of the iteration process (Gilks and Roberts 1996) and to identify standardized model parameters.

We evaluated the models in 2 ways. Gelman et al. (1995) described a goodness-of-fit procedure using a posterior predictive check whereby parameter sets derived from the original data are compared to parameter sets derived for a replicate data set. As in Link and Sauer (2002) and Thogmartin et al. (2004b), for each of the 9,000 sets of parameters (3 chains \times 3,000 iterations) sampled by simulation, we generated a replicate data set following model specifications. The Gelman et al. (1995) diagnostic compared this replicate data set with the true data set; the model was suspect if the posterior probability was close to zero or one. This method may be described as an internal evaluation. We also assessed the model against independent (or external) data by regressing observed data against imputed (expected) values derived from the final mapped model. The observed

Table 1. Parameter estimates for the best subset of models fitted to 1981–2001 American woodcock Singing Ground Survey route counts from 18 states in the midwestern and northeastern United States.

Best subset model	Fixed explanatory variables ^a	Scale (ha)	Parameters ^b	DIC ^c	ΔDIC ^d	w_i ^e	Evidence ratio ^f
1	Forest + shrub + aspen – human land use – aggregation index – growing season + TCI ^g	350	2,771.9	33,551.2	0	0.58	1.00
2	Forest + shrub + aspen – grass – human land use – aggregation index – growing season	4,000	2,789.1	33,552.3	1.1	0.34	1.73
3	Forest – forest ² + shrub + aspen – grass – human land use – aggregation index – growing season	4,000	2,797.5	33,556.8	5.6	0.04	16.44
4	Forest + shrub + aspen – grass – human land use – aggregation index – growing season + TCI	4,000	2,790.1	33,556.9	5.7	0.03	17.29
5	Forest + shrub + aspen – grass – human land use – aggregation index – growing season	106,000	2,768.0	33,560.5	9.3	0.01	104.58
6	Forest + shrub + aspen + human land use – growing season	350	2,798.7	33,560.8	9.6	0.005	121.51
Null	Includes only random effects associated with observer, year, and route	NA	2,887.4	33,670.9	119.7	0	9.83 E + 25

^a See Table 2 for variable definitions.

^b Parameters is the effective no. of parameters and is given by the posterior mean of the deviance minus the deviance of the posterior means (Spiegelhalter et al. 2003).

^c DIC is Deviance Information Criterion.

^d ΔDIC is the difference between the best model and the model of interest.

^e w_i is the model wt.

^f Evidence ratio is the model wt for the best model divided by the wt for the model of interest.

^g Topographic convergence index.

data were data randomly withheld from the modeling process ($n = 2,158$) and data collected from 2002 and 2003 ($n = 1,055$). This imputation was consistent with the data and priors, and was conditional on the values of the model parameters. We did not model woodcock on their breeding grounds in Canada because of differences in land-cover data, but a further test of this model might be to modify it to land-cover data for Canada and evaluate it against woodcock SGS counts collected there.

RESULTS

The mean woodcock count for 9,142 surveys was 3.39 (SD = 4.00) and reflected high premodeling overdispersion. Zeroes comprised 27% of the counts, the median count was 2, and the maximum count was 47.

The most plausible model of woodcock abundance was resolved at the finest spatial extent (350 ha). Composition of the landscape in forest, shrub, and aspen and birch, and the topographic convergence index were positively associated with abundance whereas composition of the landscape in human land use, the aggregation index, and the date when the growing season commenced were negatively associated with abundance (Table 1). As forest, shrub, and grass aggregated in the landscape, woodcock abundance declined; as these land covers intermixed, abundance increased. Woodcock abundance increased as the topographic convergence index increased or as mesic conditions developed in the landscape, though this variable was the weakest in magnitude relative to the other environmental covariates. The date when the growing season began is correlated with latitude, which reflects a decline in abundance from south to north in the context of the other parameters. Thus, this climate parameter appears to dampen the increasing abundance in woodcock south to north. From a univariate perspective, landscapes with forest composition of >80% had a mean abundance of 3.15

birds per survey with 95% confidence limits (2.97, 3.33) versus 3.44 birds per survey with 95% confidence limits (3.35, 3.53) for landscapes with <80% forest composition; furthermore, while non-credibly different from zero, the coefficient for the squared term for the proportion of the landscape in forest was in the expected direction.

The within-scale averaged models of woodcock abundance indicated a substantial association with environmental variables at each of the 3 scales of study (Table 2). The model parameters fluctuated in relative strength across the scales but, in general, the date when the growing season began was the variable with the greatest influence on abundance, followed by the aggregation index and human land-use composition (each of which was negatively associated with abundance). Confidence intervals on the averaged slope coefficients suggested that contributions could not be distinguished from zero for the proportion of the landscape in shrub at any of the 3 scales, proportion of the landscape in grass at the finest scale, and topographic convergence index at the intermediate scale.

Estimates of the variability in the random effects are one means of communicating the importance of these parameters in the model. The posterior densities of the standard deviations of the random effects were greatest for the route ($\bar{x} = 1.93$, 95% CI [1.79, 2.08]), and substantially less for observer (0.65, [0.60, 0.70]) and year (0.10, [0.07, 0.16]). The variability associated with year, however, was minimal compared to that of the model residual variability (ϵ , Poisson overdispersion) unaccounted for by the other random effects and the environmental covariates (0.29, [0.27, 0.31]). The proportion of the variability in the random effects that was due to spatial clustering (i.e., correlation between routes) after we accounted for the effects of the environmental covariates was 0.87 [1.93/(1.93 + 0.29)], indicating a strong

Table 2. Parameter estimates and standard deviation averaged within each of 3 scales for hierarchical, spatial count models describing mean American woodcock abundance across the upper midwestern and northeastern United States, 1981–2001.

Variable ^a	Finest scale (350 ha)	SD	Medium scale (4,000 ha)	SD	Coarsest scale (106,000 ha)	SD
Intercept	0.019	0.097	0.070	0.113	0.057	0.154
Start of season ^b	-0.367	0.166	-0.330	0.122	-0.329	0.159
Aggregation index ^c	-0.289	0.044	-0.359	0.054	-0.263	0.069
Proportion human ^d	-0.215	0.045	-0.255	0.044	-0.152	0.051
Proportion grass	-0.010	0.048	-0.206	0.054	-0.141	0.067
Proportion aspen	0.094	0.037	0.123	0.048	0.201	0.075
TCI ^e	0.099	0.043	0.002	0.053	NA	NA
Proportion shrub ^f	0.174	0.110	0.170	0.113	0.124	0.140
Proportion forest	0.183	0.049	0.148	0.046	0.087	0.048
Proportion forest ^{2 f}	NA	NA	-0.007	0.051	NA	NA

^a The coeff. for each variable with the highest absolute magnitude is identified in bold.

^b Start of season is an index to date of last frost, an important variable relating to earthworm availability.

^c Aggregation index is a measure of the extent to which forest, shrub, and grass are clumped in the landscape. Higher values of this variable indicate that shrub, grass, and forest are not intermixed to a great extent.

^d Human land cover is an aggregated cover type defined as low-, medium-, and high-density residential areas, transportation, commercial, and industrial areas, and urban grass.

^e TCI is the topographic convergence index, which estimates flow accumulation and is measured as the upslope contributing area for water runoff divided by the tangent of the slope in degrees. Higher values of this variable describe drier, higher areas, whereas lower values describe moister, lower areas.

^f We did not deem proportion of the landscape in shrub and the squared proportion of forest credible predictors of woodcock abundance and, thus, we did not include them in preparing the map.

residual effect of spatial correlation not accounted for by the environmental covariates.

Predicted relative abundance of woodcock peaked in east-central Minnesota (east of Mille Lacs Lake) and at the intersection of Vermont, USA, New York, USA, and Ontario, Canada (Burlington–Plattsburgh–St. Paul-de l'île-aux-Noix area; Fig. 1). We predicted smaller areas of peak density for the upper peninsula of Michigan, USA, and St. Lawrence County, New York. Predictive precision was a function of the mean count (Fig. 2), not survey density as might be expected.

The Gelman et al. (1995) posterior predictive diagnostic showed good model fit for all candidate models. Data withheld from model construction and data from the years 2002 and 2003 suggested good correspondence ($r^2s \geq 0.73$) relative to the observed counts (Fig. 3).

DISCUSSION

We found the environmental covariates incorporated in the models largely concurred with our a priori expectations

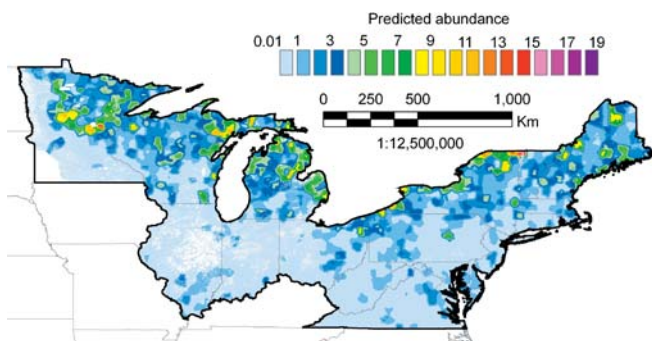


Figure 1. American woodcock abundance (birds/route) predicted for the upper midwestern and northeastern United States circa 1991, as determined by a hierarchical Bayesian spatial count model of Singing Ground Survey counts from 1981–2001.

drawn from fine-scaled studies of woodcock habitat associations (Kinsley et al. 1980, Gutzwiller et al. 1983, Hudgins et al. 1985), though the relative strength of the relations was a novel result. The climate parameter, the date when the growing season commenced, was the most important influence on woodcock abundance, followed closely by the extent to which forest, shrub, and grass land cover were aggregated. The former is not amenable to management, but the latter is, as are the other environmental covariates in the model. However, management of habitat characters may need to be cognizant of overarching limitations placed on woodcock by climate. The potential expansion in the breeding distribution of woodcock to the north and west in recent decades (Smith and Barclay 1978, Marshall 1982, Keppie et al. 1984) may be as much a response to changes in climate as it is to changing forest management practices, if this relationship with the start of the growing season is correct.

We found shrub land cover was equivocal in its relation to woodcock abundance, as the variance in the parameter estimate made it difficult to distinguish from zero despite its magnitude. It is possible that this uncertain result may be a

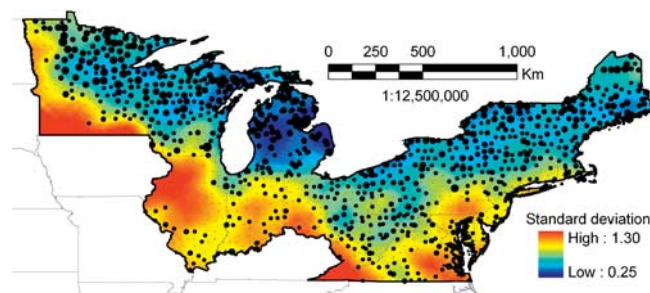


Figure 2. Posterior standard deviation of expected route-count predictions from the final model of American woodcock abundance, circa 1991, for the upper midwestern and northeastern United States. Dot size corresponds to the relative mean expectation for the period 1981–2001.

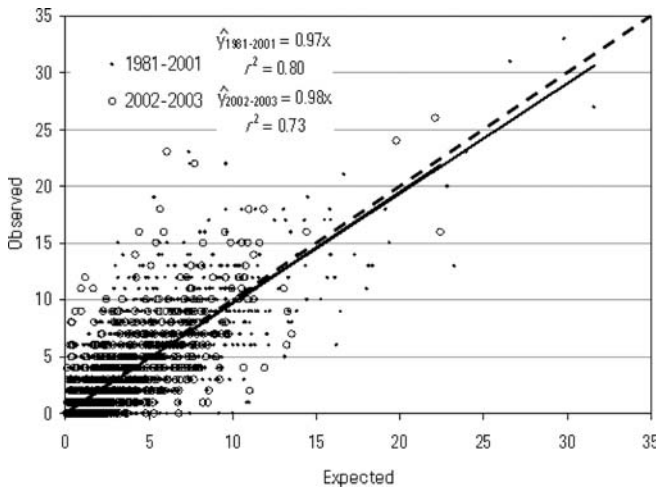


Figure 3. Observed American woodcock Singing Ground Survey counts from the upper midwestern and northeastern United States compared to expected (predicted) counts (birds/route) from the best model of woodcock abundance. Observed counts were data withheld from model building (collected between 1981 and 2001) and data collected for 2002 and 2003. The bold dashed line is the line of one-to-one correspondence between observed and predicted counts. We fitted observed versus expected counts with individual linear least-squares regressions, but they substantially overlap one another.

function of how shrub land cover was mapped in the eastern United States, as Thogmartin et al. (2004a) found discrepancies in the mapping of rare land covers, including shrub, in the upper midwestern United States. We also found with the data we studied that the relationship of woodcock to forest suggested a curvilinear relationship as forest composition increased in the landscape but variability in this relationship at the highest proportions of forest cover precluded definitive determination of this relationship.

Klute et al. (2002) studied potential correlation between stop-level occurrences of woodcock and reported that the scale most appropriate in their study was approximately 1,385 ha ($\pi \times 2,100^2$, as 2,100 m was the most parsimonious clique size from their study). We found for route-level counts that the best-performing model was scaled at 350 ha, but that important contributions were provided at the intermediate scale (4,000 ha), a scale an order of magnitude greater. Parameter estimates for some of the environmental covariates changed from one scale to another, but the changes in parameter magnitude were relatively small compared to the observed variability. One potentially important result, however, was that 3 of the 4 environmental covariates positively associated with woodcock abundance had their highest magnitude at the finest scale, whereas 3 of the 4 variables negatively associated with abundance had their greatest magnitude at the intermediate scale. Factors operating at the finer scales might be appropriate first targets for management, given that this scale is within the reach of local units of government and nongovernmental conservation organizations.

Any mapping exercise based on association analyses must be viewed as limited in its ability to define causal factors associated with variation in abundance. For example, the

strong association of date of initiation of growing season with woodcock abundance likely does not reflect a causal relationship with this variable, but instead may be a surrogate for a biologically important feature (e.g., earthworm availability) that is not presently well-represented by our remotely sensed predictors of woodcock abundance. We encourage additional modeling exercises with better predictor information. For instance, annual rather than mean climate conditions, forest stand age and structure, soil characteristics, and increased thematic and spatial resolution of land cover would provide further insight into patterns of abundance. Further, we suggest that it would be useful for woodcock biologists to think in terms of model sets that incorporate alternative predictions of how habitat and environmental features influence woodcock populations. For instance, we could not evaluate the effects of forest structure in our study, yet manipulating structure via timber harvest is one of the primary means managers may use to manage woodcock habitat. Model sets incorporating these relevant factors can then be used for prediction of the effects of habitat management, and additional monitoring can then be used to evaluate the relative value of the alternative models. This adaptive management approach should further enhance our understanding of factors influencing woodcock management.

MANAGEMENT IMPLICATIONS

The Woodcock Conservation Plan (WCP) is identifying population deficits by differencing present period estimates of abundance from estimates obtained for the 1970–1975 period (Kelley 2005). The WCP multiplies this population deficit by 50 ha to identify the amount of habitat (the habitat deficit) that must be created to meet the population goal of the plan. Assuming the map we developed proves accurate under field scrutiny, researchers could use the map of predicted abundance to study woodcock over habitat sustaining varying levels of abundance. This would allow the development of means that would secure populations in areas of high abundance and increase populations in areas of low or medium abundance. Managers can also use this map to focus monitoring on habitat where woodcock are predicted to occur in high abundance to identify and counter threats facing woodcock on their primary breeding grounds.

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Appendix. Priors and effect type for the main model effects for the model $Z(s_i) = \mu(s_i) + \sum_{k=1}^n \epsilon_{ik}[Z(s_k) - \mu(s_k)] + \omega_k(s) + \gamma_k(s) + \epsilon(s_k)$.

Variable	Definition	Effect type	Prior distribution (exp value, precision ^a)
μ	Environmental factors	Fixed	Normal (0.0, 1.0E-6) ^b
Z	Spatial relatedness	Random	Flat (for the CAR-related intercept) ^c $\tau_{\text{Space}} \sim \text{Gamma}(0.5, 0.0005)$
ω	Observer-experience effect	Random	Normal (0.0, τ_{Observer}) $\tau_{\text{Observer}} \sim \text{Gamma}(0.0001, 0.001)$
y	Yr 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}) $\tau_{\text{Noise}} \sim \text{Gamma}(0.001, 0.001)$

^a Precision rather than variance is described, with precision simply 1/variance.

^b Essentially a flat or noninformative prior distribution.

^c See Thomas et al. (2002) for details regarding flat prior relating to the conditional autoregression implemented in WinBUGS. CAR = conditional autoregressive.