



Population Ecology

Using Multi-Species Occupancy Models in Structured Decision Making on Managed Lands

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ABSTRACT Land managers must balance the needs of a variety of species when manipulating habitats. Structured decision making provides a systematic means of defining choices and choosing among alternative management options; implementation of a structured decision requires quantitative approaches to predicting consequences of management on the relevant species. Multi-species occupancy models provide a convenient framework for making structured decisions when the management objective is focused on a collection of species. These models use replicate survey data that are often collected on managed lands. Occupancy can be modeled for each species as a function of habitat and other environmental features, and Bayesian methods allow for estimation and prediction of collective responses of groups of species to alternative scenarios of habitat management. We provide an example of this approach using data from breeding bird surveys conducted in 2008 at the Patuxent Research Refuge in Laurel, Maryland, evaluating the effects of eliminating meadow and wetland habitats on scrub-successional and woodland-breeding bird species using summed total occupancy of species as an objective function. Removal of meadows and wetlands decreased value of an objective function based on scrub-successional species by 23.3% (95% CI: 20.3–26.5), but caused only a 2% (0.5, 3.5) increase in value of an objective function based on woodland species, documenting differential effects of elimination of meadows and wetlands on these groups of breeding birds. This approach provides a useful quantitative tool for managers interested in structured decision making. © 2012 The Wildlife Society.

KEY WORDS breeding birds, managed lands, multi-species occupancy model, objective function, scrub-successional species, structured decision making, woodland species.

Administrators of managed lands are often faced with management choices that influence wildlife populations. These choices usually involve manipulation of habitats, either specifically to enhance the value of the area for wildlife or for other purposes such as timber harvest that influence the presence of wildlife. Decisions about the value of proposed management for a diverse collection of target species are complicated by the need to predict consequences of the management for the collection of species, and habitat manipulations that enhance habitat for some species may limit habitat for other species. On the Patuxent Research Refuge in Maryland, United States, for example, priority bird species have widely differing habitat preferences, and refuge managers must balance the needs of these groups when choosing among alternative management options.

Structured decision making provides a convenient framework for making this choice (Lyons et al. 2008). The management options (decision alternatives) are clearly defined, as are the resources likely to be influenced by the decisions. Then, predictions are made about the effects on the resources of each alternative management decision, and based on these predictions, an overall valuation of each alternative is made. The valuation is often made in terms of an objective function, in which the total value of the resources under each management option is calculated as a weighted sum of the predicted status of each managed species for that management option. This provides a quantitative way of choosing the management that has the best cumulative effect on the resources. The planning and technical expertise required to implement structured decision making is considerable, as it brings together conservation planning, monitoring, and statistical analyses into a single framework. Traditional decision support tools provide geographically based displays and summaries of habitats, but additional modeling of biological resources is generally required to incorporate locally collected biological data, integrate it with the habitat information, and provide multi-species summaries (Korschgen et al. 2005).

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Multi-species occupancy models (Royle and Dorazio 2008) provide a convenient framework for estimating metrics and predictions needed for structured decision making. Occupancy models fit well in the structured decision making process because 1) repeated presence-absence sampling can be used to collect data simultaneously on many species with differing detection rates; 2) habitat covariates can model site occupancy for multiple species and be used to predict occupancy under different management options; 3) uncertainty is readily expressed for the predictions; and 4) objective functions that combine the predictions are easily defined in terms of total occupancy among species.

We describe an approach to structured decision making on managed lands that employs multi-species occupancy models to provide a quantitative basis for predicting the consequences of habitat management. We illustrate the approach with data from a replicated point count survey of birds conducted in 2008 on the Patuxent Research Refuge, using objective functions and scenarios of habitat management that reflect actual management concerns.

STUDY AREA

The Patuxent Research Refuge is a National Wildlife Refuge located in Maryland, USA and consists of 51.97 km² of upland forest, grassland and successional habitats, and wetlands. During the 1940s, a permanent grid with vertices at 100.6-m (330 ft) intervals was established in the existing refuge area to assist with biological sampling. The vertices were permanently marked with posts, and as the refuge acquired additional land, the grid was extended, although recent (post 1975) land acquisitions were not permanently marked; these locations were marked with plastic tubes during a bird survey conducted in 1997–1998 (D. Bystrak, U.S. Geological Survey Patuxent Wildlife Research Center, personal communication).

METHODS

Data

We used the refuge grid system as our sampling frame, and conducted point counts at grid vertices. To maintain a reasonable distance (approx. 400 m) between bird samples, we sampled at every fourth grid marker. We conducted point counts at 316 of the 328 selected grid markers, eliminating only a few inaccessible points and points adjacent to a major highway on the west side of the refuge. We used a Global Positioning System (GPS) to locate markers, and flagged them with fluorescent tape to simplify relocations.

Seventeen observers collected data over the period from 31 May to 4 July 2008. All observers were experienced birders and followed a consistent protocol for recording birds. Each observer stood at the center of the point count circle and recorded birds within 100 m within a 5-minute count period. They conducted replicate counts at almost all points; locations were surveyed 1–7 times ($\bar{x} = 2.54$). We counted all birds seen or heard within the point count circle, excluding birds flying over the point. We categorized distance to each

bird in 3 distance bands (0–25 m, 25–50 m, and 50–100 m). Observers also recorded wind and sky conditions.

We used the National Land Cover Data (NLCD) 1992 (Vogelmann et al. 2001) as our initial base layer to describe the land cover classes on the refuge. We chose the NLCD 1992 instead of the NLCD 2001 (Homer et al. 2004) after direct comparisons with aerial photographs of the refuge taken in 2007 (Maryland Department of Natural Resources 2007) indicated that the NLCD 1992 more accurately described the most current state of the refuge. We updated the NLCD 1992 layer by overlaying hand-digitized polygons we created based on the aerial photographs and polygons of meadows and wetlands obtained from refuge staff. We defined the following land cover classes that likely influenced the bird community on the refuge: mixed deciduous forest (deciduous forest mixed with small areas of evergreen forest); evergreen forest (areas dominated by evergreen trees); scrub (scrub–shrub and transitional areas combined); meadows; wetlands (mostly freshwater impoundments); and forested wetlands (mostly deciduous forested wetlands). We categorized remaining habitat as other. Using this modified NLCD data, we calculated the proportion of area of each land cover class within 100 m of the center of each point count location.

Analysis

We used a hierarchical multi-species site occupancy model (Dorazio and Royle 2005, Royle and Dorazio 2008, Russell et al. 2009) to estimate occupancy for a collection of bird species of management interest, to associate occupancy of each species with habitat at the points and to make predictions about effects of habitat management on occupancy. The models provide estimates of probability of occurrence as well as probability of detection for each species (Mackenzie et al. 2006). Multi-species site occupancy models require a sampling design in which a number of sample points are surveyed multiple times within a period in which occupancy status remains constant.

In the multi-species model, each species in the sample has distinct parameters that are related among species using a hierarchical model. The goal of the modeling is to estimate true occupancy of species at sampled points as a function of habitat covariates while controlling for variation in detection among species and associated with observers; hierarchical structure in species-specific detectability and habitat coefficients for occupancy are employed to strengthen inference by modeling species as random effects governed by common underlying distributions. To do this, we make assumptions about the structure and distributions associated with detection and occupancy. The model has components representing the true occupancy state of location j for species i , $z(i,j)$, and observed occupancy state during a sample (k) of the site, $x(i,j,k)$. Both z and x are binary and take values 0 (absent/non-detected) or 1 (present/detected). The $z(i,j)$ are latent variables in the model, as they are only partially observed (i.e., when x is 1, z is known to be 1; if x is 0 the value of z is uncertain), and we model the observations $x(i,j,k)$ conditional on $z(i,j)$. We assume that the $x(i,j,k)$ are Bernoulli random

variables having parameter $p(i,j,k)$ describing detection probability for an occupied point,

$$x(i,j,k) \sim \text{Bernoulli}(p(i,j,k) \times z(i,j)).$$

When $z(i,j) = 0$ the observations are fixed zeros; otherwise, sampling zeros occur with probability $1 - p(i,j,k)$ (Royle and Kery 2007). We model detection probability of species i at sample k , assuming that detection probability is dependent only on species identity and the observer conducting the count, or

$$\text{logit}(p(i,j,k)) = \eta(i) + \sum_{m=1}^M \beta(m) * O_m(j,k),$$

where $\eta(i)$ is a species-specific random effect, $\beta(m)$ are the coefficients relating detection to observer at point j and sample k and $O_m(j,k)$ is an indicator variable that takes on value 1 if observer m conducted the survey at point j at sample k . The species-specific effects $\eta(i)$ are normally distributed with a common mean and variance.

Because the state variables $z(i,j)$ are only partially observed, we define a model to describe the relationship among the variables across space and species. In general, true occupancy is governed by an occurrence parameter,

$$z(i,j) \sim \text{Bernoulli}(\psi(i,j)).$$

To evaluate the habitat effects on species occupancy, we included the term

$$\text{logit}(\psi(i,j)) = \alpha(i,h) \times H(j,h)$$

where $H(j,h)$ is a matrix of sites (j) and habitats (h) and consists of the proportion of habitat h at point j . The $\alpha(i,h)$ are the coefficients that relate habitat h to species i ; each of these species level coefficients are normally distributed with a common mean and variance (which was similarly assumed for the parameters in the detection model). This hierarchical structure on the habitat and species-specific detection coefficients is a distinctive feature of the multi-species model, and permits estimation for all observed species rather than just for a subset of well-sampled species. In implementing the model, we defined a primary habitat (proportion mixed deciduous forest) as an intercept, allowing us to consider forest as a baseline habitat from which the other habitat covariates either increase or decrease occupancy relative to forest.

We performed a Bayesian analysis of the model to estimate occupancy and detection parameters, $\psi(i,j)$ and $p(i)$. Bayesian methods have both the conceptually appealing aspect of providing direct probability statements about parameters and the practical benefit of providing computational approaches for fitting complex hierarchical models (Royle and Dorazio 2008). We fit the model using the software WinBUGS, which uses Markov-chain Monte Carlo (MCMC) methods to estimate the posterior distributions of the parameters of interest (Lunn et al. 2000). We provide model code containing a description of prior distributions for all random variables; we used uninformative prior distributions (annotated model code is presented in

Appendix S1, available online at www.onlinelibrary.wiley.com). The MCMC procedure requires an initial burn-in period for the sequential estimates to converge to a stationary process, after which the sequential estimates can be used to calculate medians and credible intervals associated with the parameters of interest. For inference, we ran 3 chains of length 30,000, discarded the first 20,000 iterations as burn-in, and thinned the remaining results by taking each 10th value from the chains. We verified convergence using the Gelman-Rubin diagnostic (Brooks and Gelman 1998) and evaluated autocorrelations of chain histories for evidence of problems with convergence.

Summary and Prediction Using the Model

We used the model to predict occupancy, by species and for groups of species, under present habitat conditions and under 3 alternative management scenarios. We used point-specific predicted habitat data under each scenario in conjunction with estimated species-specific habitat associations from the model to predict occupancy at a point. We defined point-specific habitat associated with a management strategy ($H^m(j,h)$), and used the $\alpha(i,h)$ to predict $\psi^m(i,j)$ for each species i . From $\psi^m(i,j)$, the total occupancy over all the points in the area for management strategy m and species i is $\sum_j \psi^m(i,j)$, the total summed occupancy for all (or for a group of $i < I$) species is $\sum_i \sum_j \psi^m(i,j)$. We defined this total sum as the objective function, which is a metric that reflects the cumulative occupancy of the target species over all habitats. We note that our objective functions can be interpreted as prediction of the cumulative species richness, summed over the points, as summed (among species) predicted occupancy at a point is equivalent to estimated species richness; its maximum value is thus the number of species times the number of points, $I \times J$.

Objective functions are calculated from model parameters (i.e., they are derived statistics), and the posterior distributions of objective functions can be estimated directly in the Bayesian analysis. As in estimation of model parameters, outcomes from the MCMC iterations are replicates that can be used to make inference about medians and credible intervals of objective functions. We used this approach to estimate credible intervals of several alternative objective functions under different management scenarios, and to directly estimate medians and credible intervals for the differences in the objective functions.

Choice of species that comprise an objective function should be a direct consequence of the goals of management. Objective functions can be based on single species if management is focused solely on that species, on a collection of species, or on a weighted sum of species. Although ultimately a single objective function will govern management decisions, we illustrate the process for the Patuxent refuge by considering 4 alternative objective functions, all based on summed occupancy of groups of species. Three of these functions are defined for groups of species of management concern (e.g., Watts 1999, Maryland Department of Natural Resources 2004): 1) scrub-successional species breed in grasslands, successional, and scrub habitats, and are of

particular management interest because of documented regional population declines (Peterjohn and Sauer 1999, Sauer et al. 2008); we designate an objective function based on scrub-successional species as O_s ; 2) woodland-breeding species are of interest because of regional loss of forest due to increasing urbanization, and we designate their objective function as O_w ; and 3) we considered a combined objective function for scrub-successional and woodland breeding species, and we designate their objective function as O_{sw} . We defined species groups (Appendices 1 and 2) following Peterjohn and Sauer (1993), Hunter et al. (2001), and Poole (2010). In addition to those groups of species, we also defined an objective function based on all species encountered in the survey, designated as O_a .

We considered 4 alternative management scenarios for the Patuxent Wildlife Refuge: 1) maintaining similar amounts of habitats on the refuge; 2) allowing meadows on the refuge to revert to mixed deciduous forest (no meadows scenario); 3) allowing wetlands (primarily impoundments) to revert to mixed deciduous forest (no wetlands scenario); and 4) allowing both meadows and wetlands to revert to mixed deciduous forest (no meadows or wetlands scenario). Options 1 and 4 are based on scenarios from refuge planning documents (H. H. Obrecht, U.S. Fish and Wildlife Service, personal communication). The refuge is approximately 33% deciduous forest, 17% evergreen forest, 14% mixed deciduous forest, 16% woody wetlands (primarily seasonally flooded mixed forest), 5% wetlands, 4% meadows, and 3% scrub or transitional habitat. To model the habitat consequences of the management scenarios, we modified the habitat information associated with each point, replacing the wetland and meadow habitat at each point with mixed deciduous forest.

Lyons et al. (2008) define 3 basic elements that must be defined for structured decision making: 1) objectives; 2) potential actions; and 3) prediction of consequences from each potential action, stated in terms of the objectives. Using the multi-species occupancy model, we estimated summary values for each of the 4 objective functions for the 4 management alternatives, and calculated the change in the objective functions between the alternatives.

Because the objective function is a random variable, we can use it to make statistical statements regarding differences in the value under different management scenarios, providing managers with quantitative measures of the extent and significance of changes in occupancy. We predicted that conversion of either meadows or wetlands to forest was likely to result in increased occupancy by woodland species, whereas removal of meadows or wetlands was likely to result in reduced occupancy of scrub-successional species. Impounded wetlands generally provide scrub or meadow habitat around their margins or in seasonally dry patches, and scrub-successional species were often encountered in or near wetlands.

RESULTS

We conducted 805 counts at the 316 sample points, with replicates of 1 (at 40 points), 2 (138), 3 (88), 4 (32), 5 (13), 6 (3), and 7 (2). We recorded 90 species and 11,285 individual birds during our point counts (Appendix 1). Twenty-four

species were early-successional and 27 were woodland species. Red-eyed vireo (*Vireo olivaceus*), tufted titmouse (*Baeolophus bicolor*), ovenbird (*Seiurus aurocapillus*), wood thrush (*Hylocichla mustelina*), and acadian flycatcher (*Empidonax virescens*) were the most common bird species recorded in terms of total number of occurrences at points (Appendix 1). Seventeen observers participated in the survey, but we pooled 6 observers that conducted <20 surveys into a single group for analysis, leaving 11 observers in the analysis.

Parameter Estimates for Species

The multi-species model provided estimates of predicted occupancy and detectability for each of the 90 species (Fig. 1). We found no evidence of lack of convergence from Gelman-Rubin diagnostics or from visual evaluation of chain histories and autocorrelation functions. Detectability varied greatly among species and observers. We do not present individual parameters for observers, but note that relative magnitudes of coefficients corresponded to a priori expectations about observers. We scaled the species detectability to the level of the mean observer for presentation (Fig. 1C). Several forest species (e.g., ruby-throated hummingbird [*Archilochus colubris*] and worm-eating warbler [*Helmitheros vermivorus*]) had particularly low detection rates (Fig. 1C). Precision of species-specific detection estimates varied greatly, and species with few encounters (Appendix 1) tended to have the widest credible intervals. For example, grasshopper sparrow (*Ammodramus savannarum*) and eastern meadowlark (*Sturnella magna*) have very large credible intervals (Fig. 1C).

We present coefficients relating habitats at a site to logit occupancy for the 51 early-successional or woodland species (Appendix 2). All but 3 of the 51 species showed significant coefficients associated with at least 1 habitat, and these associations followed predictable patterns among species. Scrub-successional species had increased occupancy as proportion of meadows (22 of 24 species had significant positive associations), scrub (15 of 24 species), or wetlands (17 of 24 species) increased (Appendix 2), and intercepts associated with mixed deciduous forest had negative coefficients indicating low occupancy in that habitat (20 of 24 species). No scrub-successional species had significant positive coefficients associated with evergreen habitats, and 6 scrub-successional species (4 negative, 2 positive) had significant associations of occupancy with increases in proportion of woody wetlands (Appendix 1).

Woodland species had larger intercept values indicating higher occupancies in mixed deciduous forest (18 of 27 significant, with 4 negative and 14 positive) and positive associations with increased woody wetlands (12 of 27 significant, with 2 negative and 10 positive). Pine warbler (*Setophaga pinus*) and ovenbird were the only species with significant positive associations of occupancy with proportion of evergreen forest; 4 species had negative associations (Appendix 1). Six woodland species had negative associations with meadows, only (and unexpectedly) northern parula (*Setophaga americana*) showed a positive association with meadows. Five woodland species had negative associations

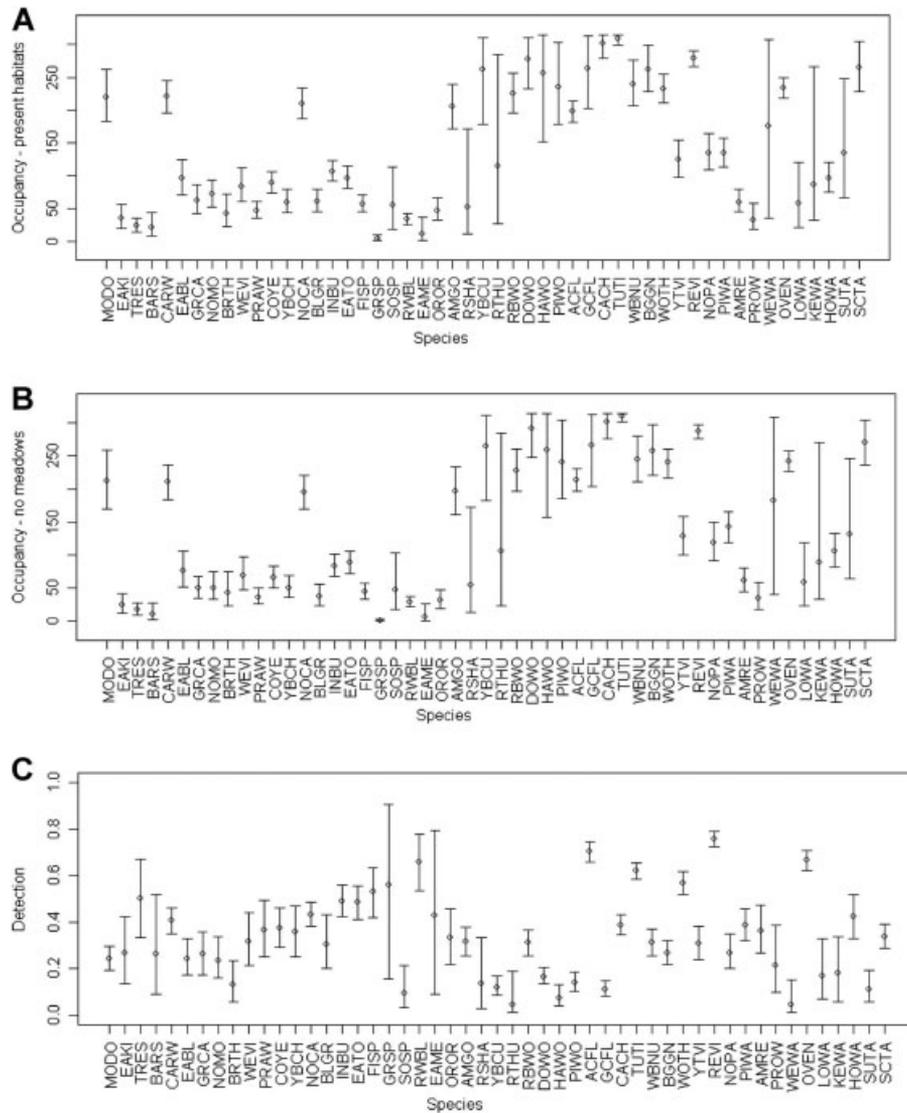


Figure 1. Predicted total occupancies with 95% credible intervals based on point count surveys conducted in 2008 on the Patuxent Research Refuge for 51 early-successional and woodland bird species under (A) present habitats and (B) the no meadow scenario. Detection probabilities associated with each species with 95% credible intervals (C) are also presented. Species are referenced as MODO: Mourning dove (*Zenaidra macroura*); EAKI: Eastern kingbird (*Tyrannus tyrannus*); TRES: Tree swallow (*Tachycineta bicolor*); BARS: Barn swallow (*Hirundo rustica*); CARW: Carolina wren (*Thryothorus ludovicianus*); EABL: Eastern bluebird (*Sialia sialis*); GRCA: Gray catbird (*Dumetella carolinensis*); NOMO: Northern mockingbird (*Mimus polyglottos*); BRTH: Brown thrasher (*Toxostoma rufum*); WEVI: White-eyed vireo (*Vireo griseus*); PRAW: Prairie warbler (*Setophaga discolor*); COYE: Common yellowthroat (*Geothlypis trichas*); YBCH: Yellow-breasted chat (*Icteria virens*); NOCA: Northern cardinal (*Cardinalis cardinalis*); BLGR: Blue grosbeak (*Passerina caerulea*); INBU: Indigo bunting (*Passerina cyanea*); EATO: Eastern towhee (*Pipilo erythrophthalmus*); FISP: Field sparrow (*Spizella pusilla*); GRSP: Grasshopper sparrow (*Ammodramus savaannarum*); SOSP: Song sparrow (*Melospiza melodia*); RWBL: Red-winged blackbird (*Agelaius phoeniceus*); EAME: Eastern meadowlark (*Sturnella magna*); OROR: Orchard oriole (*Icterus spurius*); AMGO: American goldfinch (*Spinus tristis*); RSHA: Red-shouldered hawk (*Buteo lineatus*); YBCU: Yellow-billed cuckoo (*Coccyzus americanus*); RTHU: Ruby-throated hummingbird (*Archilochus colubris*); RBWO: Red-bellied woodpecker (*Melanerpes carolinus*); DOWO: Downy woodpecker (*Picoides pubescens*); NOCA: Northern cardinal (*Cardinalis cardinalis*); PIWO: Pileated woodpecker (*Dryocopus pileatus*); ACFL: Acadian flycatcher (*Empidonax vireescens*); GCFI: Great crested flycatcher (*Myiarchus crinitus*); CACH: Carolina chickadee (*Poecile carolinensis*); TUTI: Tufted titmouse (*Baeolophus bicolor*); WBNU: White-breasted nuthatch (*Sitta carolinensis*); BGGN: Blue-gray gnatcatcher (*Poliptila caerulea*); WOTH: Wood thrush (*Hylocichla mustelina*); YTVI: Yellow-throated vireo (*Vireo flavifrons*); REVI: Red-eyed vireo (*Vireo olivaceus*); NOPA: Northern parula (*Setophaga americana*); PIWA: Pine warbler (*Setophaga pinus*); AMRE: American redstart (*Setophaga ruticilla*); PROW: Prothonotary warbler (*Protonotaria citrea*); WEGA: Worm-eating warbler (*Helminthos vermivorus*); OVEN: Ovenbird (*Seiurus aurocapillus*); LOWA: Louisiana waterthrush (*Parkesia motacilla*); KEWA: Kentucky warbler (*Geothlypis formosa*); HOWA: Hooded warbler (*Setophaga citrina*); SUTA: Summer tanager (*Piranga rubra*); SCTA: Scarlet tanager (*Piranga olivacea*).

with wetlands, but prothonotary warbler (*Protonotaria citrea*) and yellow-throated vireo (*Vireo flavifrons*) had positive associations with proportion of wetlands. Five woodland species had negative associations with scrub, but summer tanager (*Piranga rubra*) had a positive association with proportion of scrub (Appendix 2).

Summary of Predictions and Objective Functions

As expected from the a priori categorizations, species-specific total occupancy of scrub-successional species on the refuge was much smaller than woodland species under the present habitats (Fig. 1); mean total occupancy of scrub-successional species was 81.8 and woodland species total occupancy was

186.9 under the existing habitats (Fig. 1A). Eliminating meadows in favor of mixed deciduous forest resulted in a decrease in mean total occupancy of scrub-successional species, to 69.8. Woodland species total occupancy increased under the no meadows scenario to 189.7 (Fig. 1B). Mean difference in occupancy for these 2 habitat scenarios (using species as replicates) was -12.0 (95% CI: $-14.6, -9.3$) for scrub-successional species and 2.9 (0.3, 5.4) for woodland species; hence, on average, a scrub-successional species will occur at 12 fewer points on the refuge if meadows are eliminated.

Objective functions (i.e., summed total occupancies among species) provide a composite summary for total occupancy for all habitat scenarios (Fig. 2). For the 24 scrub-successional species, changing habitats from present conditions to an alternative scenario resulted in declines in the O_s from 2,006.4 (present habitats) to 1,727.6 (no meadow), 1,824.3 (no wetland), and 1,538.1 (no meadow or wetland; Fig. 2A). Direct calculation of differences in O_s allowed us to directly assess significance of changes by comparison of credible intervals. The no wetland scenario caused the smallest change in O_s (-182.1 , 95% CI: $-217.9, -147.5$), the no meadow scenario caused a significantly larger change in O_s (-278.8 , 95% CI: $-326.6, -232.5$), and the no meadow and wetland scenario caused an overall change of in O_s -468.2 ($-532.1, -406.5$). All changes represent significant declines in O_s ; removal of meadows and wetlands decreased the size of O_s by 23.3% (95% CI: 20.3–26.5).

The objective function O_w for woodland species increased as a consequence of eliminating meadows and wetlands (Fig. 2B). In the present habitats, O_w was 5,004.9; it increased by 62.7 (11.9, 113.4) under the no meadow sce-

nario, increased by 37.3 ($-9.37, 85.6$) under the no wetland scenario, and increased by 100.2 (25.5, 176) under the no meadow or wetland scenario. Removal of meadows and wetlands caused only a 2% (0.5, 3.5) increase in O_w for woodland birds.

For the larger and more heterogeneous groups of bird species, changes in the habitats generally resulted in reduced total occupancy. Decreases occurred in O_{sw} (the objective function based on all of the 51 scrub-successional and woodland species) for all management options relative to present management. Under present conditions, O_{sw} was 7,011.3; it was 6,643.2 under the no meadows or wetlands scenario and had intermediate values for other treatments (Fig. 2C). The objective function for all 90 species, O_a , changed from 8,830.7 based on the present habitats to 8,229.9 based on the no meadow or wetland scenario (Fig. 2D).

DISCUSSION

Although a large variety of decision support tools are available to land managers for defining present and predicted future habitat and biological resources (e.g., Korschgen et al. 2005), integrating this information with field data to provide statistically based metrics for use in structured decision making is a daunting task for land managers. The multi-species occupancy model presented here provides a quantitative framework for structured decision making. It directly uses survey data for estimation of occupancy, incorporates present habitats and predictions of changes in habitats as predictors of occupancies, and provides statistical estimates of the overall consequences of management actions on the species of interest. Our implementation of this procedure for the Patuxent Research Refuge demonstrated that the multi-

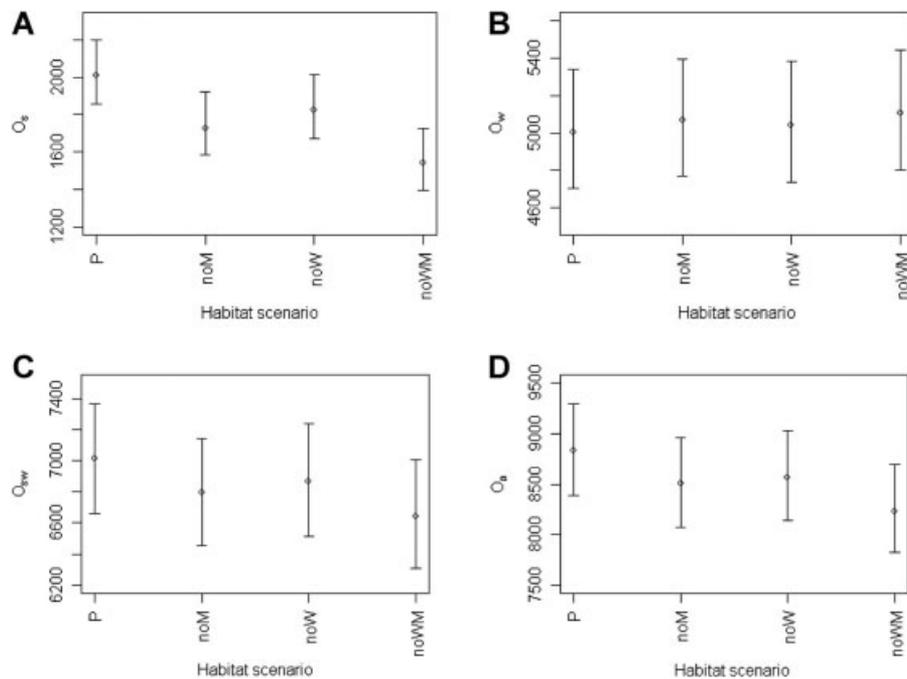


Figure 2. Values of the objective functions and 95% credible intervals associated with present (P), no wetland (noW), no meadow (noM), and no wetland or meadow (noWM) habitat scenarios for (A) scrub-successional species (O_s), (B) woodland species (O_w), (C) woodland and scrub-successional species (O_{sw}), and (D) all bird species (O_a) on the Patuxent Research Refuge, 2008.

species occupancy model controlled for detection issues in sampling and provided quantitative information on the magnitude and strength of the associations along with insights into magnitude and significance of habitat associations for species. It provided prediction of species-specific occupancy due to changes in the modeled covariates of occupancy with sufficient precision to detect differences in our objective functions associated with realistic habitat management scenarios. The utility of occupancy models is well established in the statistical literature, and many replicate surveys are increasingly used for population monitoring of a variety of wildlife resources that could be easily incorporated in multi-species occupancy analyses. The model we used in our analysis is similar to that used for occupancy analyses and species richness estimation (Royle and Dorazio 2008). Bayesian analyses of these models are becoming widespread among biologists (e.g., Russell et al. 2009, Ruiz-Gutierrez et al. 2010); this common approach to estimation and modeling of monitoring data should facilitate the use of these models in both analysis of monitoring data and structured decision making.

Refuge Bird Populations, Habitat Associations, and Management Scenarios

For scrub-successional and woodland birds on the Patuxent Research Refuge, habitat associations showed clear group-specific patterns, suggesting that effects of changing the habitats via management would lead to predictable changes in overall response to the groups. Within woodland species, we found heterogeneity in response to forest type, with species such as pine warblers highly associated with evergreen forest and some species showing a clear preference of woody wetland habitats. Scrub-successional species show similar individualistic responses to habitats. The relationships also contain some uncertainty, as our analysis is based on remotely sensed data and likely underestimates heterogeneity in habitats around individual points. These associations and accompanying uncertainty are clearly reflected in summaries of objective functions, as functions based on woodland (O_w) and scrub-successional species (O_s) groups show expected changes in response to habitat manipulations (Fig. 2).

We analyzed only proportions of habitats within 100 m of the points, and view this collection of habitat variables as a starting point for more complicated analyses of the effects of habitats on occupancy. Other metrics merit investigation. Features of the landscape near the points may influence occurrence at points; a large variety of landscape metrics exist (e.g., Flather and Sauer 1996) that could be used to further explore habitat features that influence occupancy. Counting at sample points is an inexact activity, and we document differences in detection rates associated with observers, hence the effective counting radius for some observers was likely <100 m.

Several species, such as the 4 woodpeckers, yellow-billed cuckoo (*Coccyzus americanus*), and worm-eating warbler, are predicted to have high and imprecisely estimated occupancies. These high occupancies are associated with low estimated detection rates (Fig. 1), and some of these species

(e.g., hairy woodpecker [*Picoides villosus*] and worm-eating warbler) were rarely encountered in the survey. Species with imprecise results are an unavoidable consequence of omnibus survey analyses (Sauer and Link 2002); surveys should be designed to ensure that species of critical management interest are well surveyed, or special surveys could be conducted that better sample these species. Hierarchical models mitigate the consequences of imprecise estimates by sharing information among species (Sauer and Link 2002), and alternative model structures can be chosen to better inform estimates of some species by assuming common underlying parameters with related species likely to share similar occupancy or detection (e.g., Ruiz-Gutierrez et al. 2010).

Examination of results from the alternative objective functions suggest that the consequences of the alternative management scenarios differ greatly between different objective functions. For example, changes in O_a , the objective function associated with all bird species included in the analysis, show that any of the management scenarios involving removal of wetlands or meadows lead to declines in occupancy; the no meadow or wetland scenario leads to a 6.8% decline in O_a . Under the current habitats, woodland birds have much higher occupancy on the refuge than scrub-successional species (5,004.9 vs. 2,006.4, respectively), and change in habitats to eliminate meadows or wetlands have significantly larger effects on scrub-successional species. Removal of meadows and wetlands decreases the objective function O_s by 23.3% for scrub-successional species, but increases the objective function O_w by only 2% for woodland birds. For that treatment, loss of scrub-successional birds is thus proportionately larger than the gain in woodland birds.

These results show the influence of choice of objective function. Objective functions reflect a goal for management, and provide a quantitative measure of the relative value of alternative management options for achieving that goal. The value of this approach is that the objective function is an explicit description of goals that encapsulates the manager's statements about which species should be targeted for management. Maximizing occupancy of all species, including non-native and nuisance species, is likely not a useful metric for predicting the success of management. In our example, objective functions based on categorization of birds as woodland or scrub-successional provided 2 alternative sets of goals. Our results emphasize that managers need to be sensitive to the competing needs of species; the management scenarios eliminating meadows and wetlands have significant effects for both collections of species, but have much larger effects for scrub-successional species.

Although our scenarios and species groups were relevant to the planning process for the Patuxent Research Refuge when the analysis was conducted, modifying the analysis to accommodate changes in objectives and scenarios as planning continues is simple. For example, prairie warbler (*Setophaga discolor*), wood thrush, worm-eating warbler, and Kentucky warbler (*Geothlypis formosa*) are listed as species of management concern in the New England-Mid Atlantic Coast Bird Conservation Region (U.S. Fish and Wildlife Service 2008), and an objective function based only on these species of

management concern would show an increase of 31.6 (95% CI: 2.7, 58.4; 5.8%) associated with changing meadows and wetlands to mixed deciduous forest.

Alternative Objective Functions

An objective function based on the summed total occupancy among species has many possible extensions for assessment of effects of habitat alteration on wildlife. The refuge analysis shows that this metric provides summary statements of ecological interest; it provided a comparative metric of the overall influence of the 2 collections of species on objective functions (i.e., O_w based on woodland birds was 2.5 times greater than O_s based on scrub-grassland birds) and amount of change in objective functions associated with alternative management scenarios.

Use of a multi-species occupancy model provides a convenient framework for aggregation of additional taxa into the model. If replicate survey data with comparable habitat covariates and sampled areas is available for a taxon, predicted occupancy can be estimated for the taxon and added to the objective function. Estimation for several analyses can be conducted simultaneously in WinBUGS, and predictions can be summarized as an additional part of the derived statistics that are estimated from the model. Also, the Bayesian approach to estimation permits great flexibility in incorporating estimates of occurrence from a variety of external sources; information from other taxa could be derived from existing decision support systems that make qualitative predictions of changes in wildlife resources (e.g., Korschgen et al. 2005). This would allow incorporation of non-bird taxa for which information may only exist for a few specialized habitats. Weighting of species occupancy in objective functions is easily accomplished, and permits results to reflect some externally derived measure of importance such as conservation scores (Watts 1999). Occupancy is a reasonable metric for species such as breeding birds, but we note that replicate survey analyses can model abundance (Royle and Dorazio 2008), permitting alternative formulations of objective functions that contain summed abundance and weightings.

Sources of Uncertainty in Modeling and Prediction

Prediction is always risky. Williams et al. (2002:650) define structural uncertainty, partial observability, partial controllability, and environmental variation as the 4 sources of uncertainty facing managers, and all of these could potentially limit the worth of the predictions about the magnitude of the objective functions under different management scenarios. Structural uncertainty affects prediction because predictions are dependent on the appropriateness of the model and on the range and configuration of habitats encountered by the sampling. Simple models condition on habitat configuration, and modifying habitats may change these lurking relationships and limit the predictive ability of the model. Partial observability is another source of uncertainty in habitat classification and effective areas surveyed during counting. Point counts are ubiquitous as a data collection technique among ornithologists, but are often criticized because counting is influenced by many features (Ralph et al. 1995). Our

occupancy analysis controlled for species-specific variation in detection; habitat-specific detectability could also be accommodated in the model if indicated. Another issue is partial controllability associated with prediction of future habitat. Often, management is conducted on specific units, allowing reasonable prediction of habitat changes. In general, however, habitats change due to management and chance, and the modeling could be extended to contain this source of variation through creation of replicate habitat predictions to include in the estimation of the objective functions. Environmental variation is also an issue, as wildlife populations fluctuate, and only a portion of variation in occupancy over time is related to local habitat factors. Collection of data in additional years will allow additional exploration into these sources of uncertainty; we intend to collect additional data to evaluate the model, refine our estimates of model parameters, reduce uncertainty in model structure, and provide improved predictions.

MANAGEMENT IMPLICATIONS

We provided a quantitative approach for implementing the elements of structured decision making in the context of a multi-species occupancy model. Multi-species occupancy models allow land managers to directly use survey data to inform models that predict the consequences of changes in management for collections of species via occupancy-based objective functions. Results for the Patuxent Research Refuge showed that implementation of the approach permitted statistical comparisons of the consequences of alternative management activities; removal of wetlands and meadows was likely to have negative consequences for scrub-successional birds and only mildly positive effects for woodland birds, providing clear guidance on consequences of management for bird species. The modeling is extremely flexible, and Bayesian approaches to implementing the models and estimating objective functions in terms of summed total occupancy can easily be extended to include occupancy-based surveys and estimates for other taxa (e.g., waterbirds and amphibians) likely to be objectives of management.

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Appendix 1. Means (α_h) and 95% credible intervals (CII, CIu) of the coefficients associating (on the logit scale) occupancy with mixed deciduous, evergreen, and woody wetland habitats for scrub-successional and woodland species encountered in 2008 on the Patuxent Research Refuge, Laurel, Maryland, USA. The mixed deciduous forest estimates represent an intercept, interpreted as logit occupancy at a site where only mixed deciduous habitats occur. Negative values indicate occupancy <0.5, positive values indicate occupancy >0.5. Other coefficients with credible intervals that do not overlap 0 describe significant changes in occupancy associated with increases in that habitat type relative to mixed deciduous forest. Estimates with asterisks have credible intervals that do not include 0. Total count is the summed number of individuals of the species encountered during the 805 counts.

Species	Total count	Mixed deciduous			Evergreen			Woody wetland		
		α_h	CII	CIu	α_h	CII	CIu	α_h	CII	CIu
Scrub-successional										
Mourning dove (<i>Zenaidura macroura</i>)	161	0.7	-0.2	2.5	2.4	-0.4	5.9	-3.1*	-5.6	-1.2
Eastern kingbird (<i>Tyrannus tyrannus</i>)	25	-4.1*	-5.8	-2.6	-1.4	-4.9	1.8	-1.3	-5.4	2.0
Tree swallow (<i>Tachycineta bicolor</i>)	81	-4.2*	-5.8	-3.0	-2.2	-5.9	1.0	-0.7	-3.9	2.0
Barn swallow (<i>Hirundo rustica</i>)	16	-4.7*	-7.0	-2.7	-1.5	-5.5	2.0	-1.7	-6.9	2.3
Carolina wren (<i>Thryothorus ludovicianus</i>)	271	0.1	-0.5	0.7	0.0	-1.5	1.6	4.3*	2.1	7.6
Eastern bluebird (<i>Sialia sialis</i>)	79	-2*	-2.9	-1.2	0.0	-2.1	2.0	0.9	-0.7	2.4
Gray catbird (<i>Dumetella carolinensis</i>)	42	-2.6*	-3.7	-1.6	-1.2	-4	1.4	-1.3	-4.5	1.2
Northern mockingbird (<i>Mimus polyglottos</i>)	58	-2*	-2.8	-1.2	-0.8	-3.1	1.3	-3*	-6.7	-0.3
Brown thrasher (<i>Toxostoma rufum</i>)	17	-2.4*	-3.7	-1.2	-1.9	-5.2	0.9	-2.8	-7.2	0.4
White-eyed vireo (<i>Vireo griseus</i>)	87	-1.8*	-2.5	-1.1	-0.6	-2.6	1.2	0.5	-0.8	1.8
Prairie warbler (<i>Setophaga discolor</i>)	59	-3.1*	-4.0	-2.3	0.9	-1.2	3.0	0.2	-1.8	2.0
Common yellowthroat (<i>Geothlypis trichas</i>)	112	-2.5*	-3.3	-1.7	-1.4	-3.8	0.9	1.8*	0.5	3.1
Yellow-breasted chat (<i>Icteria virens</i>)	65	-2.3*	-3.1	-1.5	-0.2	-2.3	1.9	0.7	-0.8	2.1
Northern cardinal (<i>Cardinalis cardinalis</i>)	318	-0.2	-0.8	0.3	0.9	-0.5	2.3	1.3*	0.0	2.8
Blue grosbeak (<i>Passerina caerulea</i>)	53	-2.1*	-2.9	-1.2	-1.9	-4.7	0.5	-3.2*	-7.2	-0.3
Indigo bunting (<i>Passerina cyanea</i>)	192	-1.4*	-2.0	-0.9	-1.5	-3.3	0.2	-0.3	-1.6	0.9
Eastern towhee (<i>Pipilo erythrophthalmus</i>)	188	-1.1*	-1.7	-0.6	0.6	-0.7	2.0	-5*	-8.5	-2.3
Field sparrow (<i>Spizella pusilla</i>)	99	-2.3*	-3.0	-1.6	-0.6	-2.6	1.2	-1.9	-4.5	0.1
Grasshopper sparrow (<i>Ammodramus saviannarum</i>)	11	-7.2*	-10.7	-4.5	-0.9	-4.8	2.6	-0.7	-6.0	3.7
Song sparrow (<i>Melospiza melodia</i>)	12	-2.7*	-4.5	-0.9	-1.2	-4.8	2.1	-1.4	-5.6	1.8
Red-winged blackbird (<i>Agelaius phoeniceus</i>)	118	-3.1*	-4.1	-2.3	-1.7	-4.6	0.8	-2.2	-5.4	0.3
Eastern meadowlark (<i>Sturnella magna</i>)	18	-4.9*	-7.1	-2.9	-1.0	-4.7	2.3	-1.5	-6.2	2.5
Orchard oriole (<i>Icterus spurius</i>)	42	-3.0*	-4.1	-2.1	-0.3	-2.8	2.2	-0.9	-3.7	1.4
American goldfinch (<i>Spinus tristis</i>)	194	0.5	-0.2	1.3	0.1	-1.6	2.0	-1.1	-2.5	0.3
Woodland										
Red-shouldered hawk (<i>Buteo lineatus</i>)	13	-2.0	-3.5	0.1	0.5	-2.0	3.1	-1.1	-4.4	1.7
Yellow-billed cuckoo (<i>Coccyzus americanus</i>)	86	2.5*	0.6	5.4	-1.3	-4.6	2.7	0.8	-2.8	5.7
Ruby-throated hummingbird (<i>Archilochus colubris</i>)	11	-0.9	-2.9	2.8	-1.4	-4.6	1.6	1.3	-2.1	4.9
Red-bellied woodpecker (<i>Melanerpes carolinus</i>)	209	1.0*	0.3	2.0	-1.2	-3	0.5	3.6*	0.9	7.4
Downy woodpecker (<i>Picoides pubescens</i>)	134	2.8*	1.1	5.7	0.5	-2.5	3.9	1.2	-2.4	5.7
Hairy woodpecker (<i>Picoides villosus</i>)	43	2.3*	0.0	5.9	-0.6	-3.6	2.8	1.6	-2.1	6.2
Pileated woodpecker (<i>Dryocopus pileatus</i>)	96	1.7*	0.4	3.9	-2	-4.9	1.2	2.9	-0.9	7.6
Acadian flycatcher (<i>Empidonax virens</i>)	519	1.0*	0.5	1.4	-1.7*	-2.9	-0.5	5.2*	2.5	8.9
Great crested flycatcher (<i>Myiarchus crinitus</i>)	80	2.4*	0.3	5.6	0.7	-2.5	4.3	-2.2	-6.4	3.3
Carolina chickadee (<i>Poecile carolinensis</i>)	471	3.2*	1.2	6.7	1.5	-2.0	4.9	1.2	-2.6	5.9
Tufted titmouse (<i>Baeolophus bicolor</i>)	725	4.8*	2.8	7.4	0.6	-2.7	4.3	1.7	-2.3	6.7
White-breasted nuthatch (<i>Sitta carolinensis</i>)	242	1.5*	0.7	2.8	-0.2	-2.5	2.6	3.2*	0.7	6.7
Blue-gray gnatcatcher (<i>Poliophtila caerulea</i>)	244	1.2*	0.2	2.9	0.6	-1.7	3.0	3.7*	0.5	7.7
Wood thrush (<i>Hylocichla mustelina</i>)	551	1.4*	0.8	2.1	0.6	-1.0	2.4	-0.1	-1.3	1.3
Yellow-throated vireo (<i>Vireo flavifrons</i>)	105	-0.8*	-1.4	-0.1	-1.4	-3.2	0.3	3.5*	1.5	6.5
Red-eyed vireo (<i>Vireo olivaceus</i>)	1038	3.2*	2.4	4.1	-2.2*	-3.9	-0.3	2.9*	0.1	6.5
Northern parula (<i>Setophaga americana</i>)	104	-0.7	-1.4	0.1	-2.1*	-4.4	-0.3	4.5*	2.4	7.2
Pine warbler (<i>Setophaga pinus</i>)	185	-0.2	-0.7	0.5	4.3*	2.1	7.1	-4.6*	-7.3	-2.4
American redstart (<i>Setophaga ruticilla</i>)	77	-2.4*	-3.2	-1.6	-3.0*	-6.2	-0.3	4.4*	2.9	6.2
Prothonotary warbler (<i>Protonotaria citrea</i>)	20	-4.1*	-5.9	-2.7	0.3	-2.6	3.2	3.2*	1.1	5.7
Worm-eating warbler (<i>Helminthos vermivorus</i>)	13	0.7	-1.9	4.6	0.5	-2.8	3.8	-1.2	-5.7	4.1
Ovenbird (<i>Seiurus aurocapillus</i>)	610	1.7*	1.1	2.4	3.0*	0.7	5.9	-1.7*	-2.8	-0.7
Louisiana waterthrush (<i>Parkesia motacilla</i>)	20	-2.1*	-3.5	-0.6	-2.6	-6.2	0.3	3.3*	1.3	6.4
Kentucky warbler (<i>Geothlypis formosa</i>)	30	-0.8	-2.1	2.2	0.1	-2.1	2.4	-0.1	-2.3	2.8
Hooded warbler (<i>Setophaga citrina</i>)	127	-0.2	-0.7	0.3	-1.1	-2.5	0.3	-1.0	-2.2	0.1
Summer tanager (<i>Piranga rubra</i>)	36	-0.4	-1.7	1.7	0.6	-1.8	3.6	-1.4	-4.1	1.2
Scarlet tanager (<i>Piranga olivacea</i>)	277	2.3*	1.1	4.2	0.8	-1.9	3.8	-0.8	-2.9	2.0

Appendix 2. Means (α_h) and 95% credible intervals (CII, CIu) of the coefficients associating (on the logit scale) occupancy with scrub, wetland, and meadow habitats for scrub-successional and woodland species encountered on the Patuxent Research Refuge, Laurel, Maryland, USA in 2008. Estimates are scaled so coefficients are interpreted as measuring deviations from a baseline occupancy associated with mixed deciduous habitat. Estimates with asterisks have credible intervals that do not include 0.

Species	Scrub			Wetlands			Meadows		
	α_h	CII	CIu	α_h	CII	CIu	α_h	CII	CIu
Scrub-successional									
Mourning dove	6.5	-1.5	21.3	9.9*	1.1	24	6.6*	0.4	16.2
Eastern kingbird	9.7*	1.9	22.6	13.0*	5.6	24.4	7.9*	3.7	13.9
Tree swallow	3.3	-2.1	8.4	12.5*	5.5	23.2	5.7*	2.5	10.9
Barn swallow	-2.7	-17	7.4	8.7*	3.2	18.4	9.9*	3.5	18.0
Carolina wren	8.5*	0.6	26.8	10.2*	0.5	26.3	6.3*	0.8	16.0
Eastern bluebird	5.5	-0.1	15.9	14.9*	5.2	29.0	9.0*	4.2	16.3
Gray catbird	16.4*	8.5	26.5	12.1*	4.4	24.8	7.2*	0.9	17.5
Northern mockingbird	12.5*	3.7	23.8	4.0	-0.4	12	9.9*	4.7	17.4
Brown thrasher	14.3*	6.5	25.1	6.2*	1.4	14.3	-2.2	-9.2	3.3
White-eyed vireo	10.6*	4.0	21.6	5.6*	0.8	16.5	6.2*	2.4	11.7
Prairie warbler	19.5*	11.2	31.0	-6.8	-20.0	1.4	5.6*	2.8	9.6
Common yellowthroat	11.1*	6.3	17.9	13.2*	6.0	23.9	12.3*	7.4	18.6
Yellow-breasted chat	16.3*	8.0	28.9	-0.9	-6.0	2.9	4.2*	1.0	9.3
Northern cardinal	14.4*	3.6	29.1	11.1*	2.1	24.3	13.4*	6.7	22.6
Blue grosbeak	9.2*	4.0	18.5	-0.2	-4.7	4.2	12.8*	5.8	22.2
Indigo bunting	17.1*	8.8	29.0	7.1*	1.7	17.9	15.5*	8.9	24.2
Eastern towhee	22.7*	12.7	35.5	0.2	-2.8	2.9	3.1*	0.7	6.4
Field sparrow	14.8*	8.6	23.2	-10.0*	-24	-0.6	6.0*	2.4	11.3
Grasshopper sparrow	-0.3	-14	9.5	-1.8	-16	8	7.5*	3.6	12.5
Song sparrow	10.1*	1.8	23.4	10.8*	2.3	23.8	3.6	-4.2	13.8
Red-winged blackbird	1.0	-3.8	4.6	18.9*	10.2	28.4	3.4*	1.2	5.8
Eastern meadowlark	5.4	-3.2	20.8	-2.9	-16	5.4	5.6*	2.2	10.9
Orchard oriole	3.1	-2.1	10.0	12.4*	6.1	23.3	8.2*	3.8	14.1
American goldfinch	8.6	-0.9	23.2	9.1*	1.9	21.1	7.2*	0.2	18.2
Woodland									
Red-shouldered hawk	4.5	-2	17.4	-1.2	-13	13.5	-3.9	-14	4.9
Yellow-billed cuckoo	5.2	-4.6	21.5	-4.3	-16	16.4	0.3	-8.4	13.4
Ruby-throated hummingbird	9.0	-3.6	25.1	-3.4	-19	14.8	5.3	-1.8	15.9
Red-bellied woodpecker	-6.4*	-12	-2.3	7.4	-3.9	25.6	-0.7	-3.7	4.2
Downy woodpecker	2.7	-7.3	18.9	5.0	-4.6	21.3	-6.7	-13	2.3
Hairy woodpecker	2.7	-11.0	21.0	-2.1	-18.0	18.7	1.5	-9.4	14.8
Pileated woodpecker	-4.6	-14.0	12.5	5.3	-4.0	19.5	-1.2	-7.0	9.8
Acadian flycatcher	-3.6*	-6.7	-1.0	-3.5*	-6.4	-1.0	-5.5*	-8.5	-2.9
Great crested flycatcher	7.6	-4.1	23.6	8.0	-3.4	23.5	1.4	-7.6	15.2
Carolina chickadee	7.9	-3.5	23.5	6.8	-5.1	22.9	4.9	-3.6	16.3
Tufted titmouse	7.2	-4.0	23.8	-4.2	-9.3	10.5	-0.6	-6.6	11.3
White-breasted nuthatch	-2.7	-7.2	4.7	-6.9*	-12	-2.8	-1.4	-4.4	3.9
Blue-gray gnatcatcher	7.0	-4.4	24.5	6.7	-2.0	22.1	4.7	-2.3	15.7
Wood thrush	-3.2*	-5.8	-0.3	-2.0	-4.3	0.2	-2.1*	-4.2	-0.1
Yellow-throated vireo	-0.6	-4.6	3.1	7.8*	1.7	18.3	-1.3	-4.6	1.5
Red-eyed vireo	-2.6	-5.4	0.8	-3.9*	-6.4	-1.4	-4.4*	-6.6	-2.3
Northern parula	-0.7	-5.2	3.7	-4.1	-9.3	0.5	7.5*	2.0	15.2
Pine warbler	-4.7*	-9.2	-0.9	-6.0*	-14	-1.0	-3.0*	-6.1	-0.4
American redstart	-4.7	-15.0	2.2	3.3	-0.1	10.0	-1.5	-6.7	2.1
Prothonotary warbler	-3.9	-18.0	5.2	13.8*	5.7	28.9	-3.5	-14.0	3.5
Worm-eating warbler	5.0	-6.7	21.1	-1.3	-18	16.7	-3.2	-15	12.0
Ovenbird	-4.9*	-7.9	-1.9	-4.9*	-7.9	-2.3	-2.8*	-4.7	-0.9
Louisiana waterthrush	-5.3	-19	3.9	1.2	-6.9	15.9	-1.2	-8	4.9
Kentucky warbler	-7.6	-22	8.1	-4.8	-16.0	9.6	-0.5	-6.1	8.8
Hooded warbler	-0.9	-3.9	1.9	-3.9*	-8.9	-0.2	-4.4*	-8.6	-1.2
Summer tanager	10.0*	0.5	25.8	-8.0	-21.0	2.1	1.6	-4.2	11.6
Scarlet tanager	4.1	-2.5	18.7	-3.5	-7.5	2.1	-1.9	-5.8	7.4