

# Hierarchical Models and Bayesian Analysis of Bird Survey Information<sup>1</sup>

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## Abstract

Summary of bird survey information is a critical component of conservation activities, but often our summaries rely on statistical methods that do not accommodate the limitations of the information. Prioritization of species requires ranking and analysis of species by magnitude of population trend, but often magnitude of trend is a misleading measure of actual decline when trend is poorly estimated. Aggregation of population information among regions is also complicated by varying quality of estimates among regions. Hierarchical models provide a reasonable means of accommodating concerns about aggregation and ranking of quantities of varying precision. In these models the need to consider multiple scales is accommodated by placing distributional assumptions on collections of parameters. For collections of species trends, this allows probability statements to be made about the collections of species-specific parameters, rather than about the estimates. We define and illustrate hierarchical models for two commonly encountered situations in bird conservation: (1) Estimating attributes of collections of species estimates, including ranking of trends, estimating number of species with increasing populations, and assessing population stability with regard to predefined trend magnitudes; and (2) estimation of regional population change, aggregating information from bird surveys over strata. User-friendly computer software makes hierarchical models readily accessible to scientists.

*Key words:* Bayesian methods, bird surveys, hierarchical models, Markov chain Monte Carlo, North American Breeding Bird Survey, ranking, trends.

## Introduction

Bird survey results provide basic information for most of our conservation activities. We use surveys to (1) identify declining species; (2) rank species to assign priority for management; (3) model bird habitat associations; and (4) assess results of management activities. Unfortunately, bird survey data are often difficult to interpret and use. In particular, there are no definitive surveys for most species. Often, information is provided by several surveys such as the North American Breeding Bird Survey (BBS; Robbins 1986), the Christmas Bird Count (Dunn and Sauer 1997), or one of several waterfowl surveys (such as the Spring Breeding Ground Survey; Smith 1990). These sources provide information of varying quality, and large differences in quality of estimates can occur among species within any of the multispecies surveys.

For most surveys, there are also underlying concerns related to flaws in the survey designs. With few exceptions, bird surveys tend to provide incomplete coverage, missing portions of populations both locally (e.g. off roads) and rangewide (e.g., northern portions of species ranges), and unmodeled detectability of birds in most surveys is a large potential source of bias in estimation (Barker and Sauer 1995). To produce a credible analysis of these count data, it is necessary to use covariates to model factors associated with known differences in detectability (such as observer differences; Sauer et al. 1994), adding a great deal of complexity to the analysis. A variety of competing analyses have been proposed, based on distinct model assumptions and using alternative statistical models (e.g., generalized linear models, Link and Sauer 1997; generalized additive methods, Fewster et al. 2000). Naturally, their results are not entirely consistent. Our experience, however, is that given similar sets of explanatory variables the discrepancies tend to be relatively small; when they are not, the inconsistency is often attributable to differences in methods of combining estimates of varying quality.

Conservation activities often require summaries of these rather equivocal sources of information over space (e.g., for mapping abundances), time (e.g., for estimation of population change for individual species), and over species (e.g., for estimation of change for species groups). All of these problems can be reasonably and profitably evaluated as hierarchical models: data, the highest level of the hierarchy, provide an

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imperfect view of parameters, which comprise an intermediate level of the hierarchy. The parameters are stochastically related (that is, weakly, rather than deterministically). Characteristics of this stochastic relation are the object of summary analyses; these are described as “hyperparameters,” the lowest level of the hierarchy. In the past, relatively inefficient approaches such as route regression (Geissler and Sauer 1990) have used weightings to combine information over space in population change estimation. However, hierarchical models (Spiegelhalter et al. 1995) provide a convenient structure for the analysis of data that contain several levels of interest. Analytical tools such as Markov chain Monte Carlo (Gilks et al. 1996) are available for fitting hierarchical models. In this paper, we introduce the idea of hierarchical models for use in avian conservation, and discuss two general topics in which we have successfully applied these models: (1) Estimation of population change for individual species; (2) Summaries of estimates of population change for groups of species. We also provide a brief summary of hierarchical approaches to analysis of spatial pattern of abundance.

## Hierarchical Models

It is not uncommon to find considerable variation in precision in collections of parameter estimates; some parameters are very poorly estimated, but some are very well estimated. All summaries of attributes of these collections are limited by precision of the estimates. Simple averages of trend estimates may be wildly imprecise due to the inclusion of a few poorly estimated values; estimated rankings of parameters are corrupted by the tendency for poorly estimated quantities to appear extreme relative to the group (Link and Sauer 1996). The proportion of positive trend *estimates*, a natural estimate of the proportion of positive trend *parameters*, is biased towards 0.50, and the precision of the estimate cannot be assessed without hierarchical structure.

It is useful to consider how we conceptualize the analysis of collections of estimates. Often, we view data ( $Y$ ) as though they are governed by a fixed, unknown parameter ( $\theta$ ), and our statistics  $F(Y|\theta)$  are based on distribution of data, given the unknown parameter. This view of parameters of species is limiting in most survey analyses, as our interest is actually in the attributes of collections of the parameters, not in the collections of the estimates. New analytical opportunities arise if parameters are viewed as random variables, themselves sampled from unknown distributions. This conceptualization, in which data and parameters are both random variables, is a hierarchical model.

Hierarchical models, like conventional fixed effects models, begin with the specification of sampling distributions for data; these distributions are determined by fixed values of parameters. The richer structure of hierarchical models arises from the assumption that the parameters themselves can be thought of as sampled from probability distributions. Although frequentist approaches exist to analysis of hierarchical models, they are often difficult to implement for complex situations. Analysis of hierarchical models is conveniently and rigorously accomplished through Bayesian methods. The goal of hierarchical analysis is to make probability statements about the distribution of  $\theta$ , given the data and our assumptions about how the parameters are distributed. This indicates that a Bayesian analysis of a hierarchical model must specify the distributions:

- (1)  $f(Y|\theta)$ , the sampling distribution of the data given the unknown parameter,
- (2)  $\pi(\theta|\Psi)$ , the distribution of the parameters, in which  $\Psi$  is a hyperparameter (the parameter governing the distribution of the parameters).

From (1) and (2), an additional distribution is implied:

- (3)  $f(\theta|Y)$ , the distribution of the parameters, conditional on the observed data.

In a Bayesian analysis,  $\pi(\theta|\Psi)$  is referred to as the prior distribution, and  $f(\theta|Y)$  is called the posterior distribution; inference about  $\theta$  is based on the posterior distribution. Historically, Bayesian analyses have been of limited use for many practical applications. The posterior distributions are very difficult to calculate unless quite simple models are specified, and in part this complexity has led to concerns about the need to make assumptions about the prior distributions of the parameters (Gelman et al. 1994).

Another issue for Bayesian analysis is the necessity of specifying a prior distribution reflecting knowledge (or lack of knowledge) of likely values of the hyperparameters. This requirement is the focus of what we regard as much unreasonable and even hysterical criticism of Bayesian methodology as lacking in scientific objectivity. The choice of reasonable noninformative prior distributions for hyperparameters and the evaluation of alternative choices of prior specifications should lay to rest all such concerns. Unless either the inferential value of the data is very low or the prior specification for hyperparameters expresses a great deal of prior knowledge, the choice of prior is likely to have limited consequences for a Bayesian analysis.

Markov chain Monte Carlo (MCMC) procedures allow investigators to avoid the difficulties of calculating posterior distributions by using simulation-based approximations. Monte Carlo simulations are a widely-

used, stochastic approach to solving complex problems in mathematical modeling, in which independent values are randomly drawn from distributions of interest and the outcomes are summarized to characterize the model system. The only difference between MCMC, in its various formulations, and conventional Monte Carlo simulation methods is that the analyst draws correlated sequences, or first order Markov chains, in MCMC. In Bayesian applications, the distributions sampled are the posterior distributions of the parameters and hyperparameters; all Bayesian inference is based on these distributions. Features of the posterior distributions (means, medians, modes, quantiles, etc.) are approximated by the corresponding features of sampled values, just as in conventional Monte Carlo simulations.

Hierarchical models have great potential for application in bird conservation because so many of the problems are naturally hierarchical. Our research on hierarchical models began when we studied methods for summary of estimates of population change for groups of bird species (Link and Sauer 1998, Sauer and Link 2002). We recognized that standard procedures such as route regression estimation of population change were ad-hoc approaches to a hierarchical modeling situation (Link and Sauer 2002), and that many spatial problems were hierarchical in nature (e.g., Royle et al. 2002). Here we provide brief summaries of these hierarchical models.

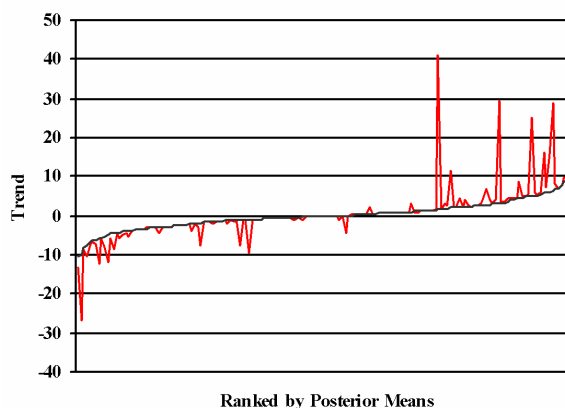
### Example I: Summary of Attributes of Groups of Species

Groups of species are often of interest in conservation biology. Conservation activities are often motivated by comparative analyses of population change and abundance for taxa such as Neotropical migrants (Robbins et al. 1989) or grassland birds. Taxa-level management is also traditional for groups such as waterfowl, and has led to development of coordinated conservation activities such as the North American Waterfowl Management Plan.

Common summaries of group attributes include average population trend, number of “declining” species, ranks of species by population trend, and identification of species with extreme changes. Any summary requires that the collection of species is meaningful, that some common characteristic of the species permits summary of population attributes among species. Complications associated with the summary are both practical (quality of information may vary greatly among species, making simple averages and summaries of estimates misleading) and conceptual (all groups are composites of many characteristics that are not neces-

sary critical). Imprecise information creates a variety of problems. For example, it is unwise to develop criteria based on estimated magnitude of population trend, because an imprecise trend estimate may be quite large while still having a confidence interval large enough to include zero. Statistical significance is also a flawed measure, as a very small rate of change may be identified as “statistically significant” but be of little practical significance. Separating notions of statistical significance from magnitude of trend is a difficult conceptual issue, and most investigators adopt ad-hoc approaches that constrain analyses of magnitude to significant trends.

For example, for the 167 bird species in the Appalachians (Bird Conservation Region [BCR] 28; Commission for Environmental Cooperation 1997) for which population change data could be estimated from North American Breeding Bird Survey, 46 percent have trends >0, 33 percent of species have significant ( $P < 0.05$ ) negative trend estimates, and 26 percent of species have significant positive trend estimates (fig. 1). Species with large estimated declines include Bewick’s Wren (*Thryomanes bewickii*, 26.67 percent/yr), Henslow’s Sparrow (*Ammodramus henslowii*, 12.13 percent/yr), and Horned Lark (*Eremophila alpestris*, 10.53 percent/yr).



**Figure 1**— Graph of unadjusted trend estimates for 168 species of birds in the Appalachians (jagged curve) plotted against ranked posterior means (smooth line).

Hierarchical analyses of these data begins by supposing that the trend estimate  $\hat{\beta}_s$  for species  $s$  is normally distributed with mean  $\beta_s$  (the true value) and variance  $\sigma_s^2$ . The actual variance is unknown, but an estimate  $\hat{\sigma}_s^2$  is available; it is assumed that  $(v_s / \sigma_s^2) \hat{\sigma}_s^2$  has a chi-squared distribution with  $v_s$  degrees of freedom, independent of the distribution of  $\hat{\beta}_s$ . Further, it is assumed that the sampling distributions are independent among species. Additional structure is added by assum-

ing that the (unobserved) values  $\beta_s$  are themselves a sample from a normal distribution, with mean  $\mu$  and variance  $\tau^2$ . To complete the specification of the model, we placed standard noninformative priors on  $\mu$ ,  $\tau^2$ , and the variances  $\sigma_s^2$ : for  $\mu$ , we used a normal distribution with mean of zero and variance 1000<sup>2</sup>; for the variances  $\tau^2$  and  $\sigma_s^2$ , we used gamma priors with mean of 1 and variance of 1000. See Sauer and Link (2002) and Link and Sauer (2002) for discussion regarding choice of priors and noninformative priors.

We fit this model using program BUGS (Spiegelhalter et al. 1995). We ran the simulation, discarding the first 10,000 iterations to allow the results to converge on the posterior distributions. We then took means and variances from the simulation results to get estimates of parameters and hyperparameters. Posterior means of interest include the Bayes trend estimate for species  $s$ . These estimates represent the estimate for the species in the context of the group, and differ from the  $\hat{\beta}_s$  in that they are “shrunk” toward the prior mean  $\mu$ , with the amount of shrinkage relative to the amount of information associated with the original estimate. They are similar to empirical Bayes results (Link and Sauer 1987), but also take into account uncertainty in estimates of precision. One important feature of the MCMC procedure is the ease with which composite results can be constructed based on the posterior means. For example, at each step of the MCMC sampling, we may count the number of species for which the latest value sampled from the posterior distribution of  $\beta_s$  is positive, and call this quantity  $N_{inc}$ . The resulting chain of values  $\{N_{inc}\}$  is then a sample from the posterior distribution of this composite parameter, allowing legitimate inference to be made about the number of increasing trends in the population. Similarly, we may keep track of the rank of sampled values from the posterior distribution of trend for a particular species, relative to those for other species. The result once again is a sample from the posterior distribution of a composite parameter. Inference based on this posterior distribution properly accounts for all sources of variation in the estimates, removing essentially insurmountable difficulties inherent to conventional (non-Bayesian) analyses.

### Defining Population Stability

We also use the MCMC replicates to estimate a measure of population stability. The natural approach to determine whether populations are stable is to define a range of values in which the population is considered “stable,” then to determine the probability that the species’ estimate is in the region. We say that a population is stable if  $\beta_s \in (-\delta, \delta)$ , where  $\delta$  is a maximum acceptable deviation of trend from 0. Since  $\beta_s$  is unknown, we cannot state with certainty whether  $\beta_s \in (-\delta, \delta)$ ; however, we can compute the posterior probability of stability using the MCMC sample, as

$$\Pr(\beta_s \in (-\delta, \delta) | Y).$$

This probability can be enumerated directly from the MCMC replicates.

### Results for the Appalachians

For the 167 species, the posterior mean number of species with positive trend estimates was 78.54 (95 percent confidence interval: [71,86]). The estimate based on the observed trend estimates was 77. We present results for selected species (table 1). For species with extreme estimates of change, the analysis suggests that the actual estimated trends have little value in predicting the actual rank of the species. Bewick’s Wren has the most extreme estimated trend of -26.7, but the posterior mean trend was -10.1, and the analysis estimates an average rank of 6 (i.e., it is the 6<sup>th</sup> most extreme declining trend). Dickcissel (*Spiza americana*), with an estimated trend of -13.3, has an average rank of 3.3. Often, large differences in point estimates of trends have little meaning, and the MCMC analysis reorders these estimates to accommodate differences in precision. We also present a list of unstable (probability of stability to be less than  $p = 0.05$ ) with regard to the interval of [-2, 2]) increasing and declining species for the stratum (Appendix 1). This information provides a reasonable way of defining species with unstable populations, and allows managers to more confidently describe priority species based on scientific information. We note that some of the estimates of number of declining species from the MCMC

**Table 1--** Estimated trends, posterior mean trends,  $N$  of survey routes, estimated ranking, and probability of stability for four species in the Appalachian BCR.

Species	Trend %/yr	N	Posterior mean (CI)	Rank	Stability Pr( $\beta_s \in (-2,2)   Y$ )
Henslow’s Sparrow	-12.1	34	-5.0 (-11.5, 1.7)	26.0	0.17
Bewick’s Wren	-26.7	23	-10.1 (-18.3, -2)	6.0	0.02
Horned Lark	-10.5	105	-7.9 (-12.1, -3.6)	22.0	0.00
Dickcissel	-13.3	8	-10.4 (-14.4, -4.5)	3.3	0.01

Note: CI refers to a 95% credible interval

analysis (78.5) are not greatly different from the number estimated from the unadjusted trend estimates (77). Consistency in numbers based on “naïve” analyses and more sophisticated analyses is comforting, and often indicates that many of the species have trends that are quite precisely estimated. However, the MCMC estimate is based on appropriate models, and in other situations the estimates can be very different.

### Example II: Estimation of Population Change

Estimation of population change from survey data is sometimes controversial due to the need to aggregate information over space. The BBS is a good example of a difficult-to-analyze survey. The BBS is a roadside survey, based on data from survey routes composed of 50, 3-min point counts conducted once each year. The sum of counts of individuals of each species over the 50 stops is generally used as the dependent variable in analyses (Robbins et al. 1986). Started in 1966, the BBS covers almost all of the 37 BCRs North of Mexico, but some provide very poor information and some provide huge amounts of information. Combining information from these regions has always been problematic, and often ad-hoc weightings are used to accommodate regional differences in population abundance and precision of estimates (e.g., ter Braak et al. 1984; Geissler and Sauer 1990; Link and Sauer 1998, 2002). Modeling of regional population change is also complicated by the need to accommodate differences in detectability among the observers conducting the survey. Often, it is possible to construct year effects models at the scale of BCRs that accommodate differences in observer quality and survey information with regions, but combining information among regions to obtain overall estimates requires additional modeling (Link and Sauer 1998). However, hierarchical models provide a reasonable way of accommodating the constraints of the survey in a regional summary (Link and Sauer 2002).

The model:

$$\log(\lambda_{i,j,t}) = S_i + \beta_i(t-t^*) + \omega_j + \eta I(j,t) + \gamma_{i,t} + \varepsilon_{i,j,t}$$

provides an approach for modeling regional population change from the BBS. In this description,  $\lambda_{i,j,t}$  is the expected value of  $Y_{i,j,t}$  (the count for year  $t$  for stratum  $i$  and observer-route  $j$ , this structuring is needed because segments of routes surveyed by an individual observer are the “comparable” units). Stratum-specific intercept ( $S_i$ ), slope  $\beta_i$ , and year effects ( $\gamma_{i,t}$ ), observer/route effects ( $\omega_j$ ), and overdispersion effects ( $\varepsilon_{i,j,t}$ ) all can influence counts, as can a start-up effect ( $\eta$ ) that allows an initiation effect for new observers to have lower counts the first year they conduct a survey on a route

( $I(j,t)$  is a dummy variable to index the first year of counting by an observer). Finally,  $t^*$  is a baseline year for change estimation. The model is hierarchical in that the effects are themselves treated as variables governed by hyperparameters. Here, observer/route effects, year effects, and overdispersion effects are treated as mean zero normal random variables. Each set of effects were identically distributed, with common variances  $\sigma_{\omega}^2$  for observer effects and  $\sigma_{\varepsilon}^2$  for overdispersion, and with stratum-specific variances  $\sigma_{\gamma,i}^2$  for year effects. The variance hyperparameters all were given flat inverse gamma distributions (Link and Sauer 2002). It has been noted that, after controlling for various covariate effects, counts are more variable than indicated by Poisson distribution, hence the overdispersion parameter is needed (Link and Sauer 1998). Note that year effects are constrained to show variation around a slope parameter, allowing accommodation of yearly differences in precision. For the complete model description and a discussion of alternative model formulations, see Link and Sauer (2002).

Within this model, we define annual indexes as the year effects, scaled by the baseline regional intercept and slope, and exponentiated, then multiplied by an additional factor to accommodate the proportion of routes on which the species was encountered ( $z_i$ ), or:

$$n_{i,t} = z_i \exp(S_i + \beta_i(t-t^*) + \gamma_{i,t})$$

Trend ( $B_i$ ) for any interval  $t_a$  to  $t_b$  can be defined as the ratio of the annual indices, to the appropriate power:

$$B_i = \left\{ \frac{n_{i,t_b}}{n_{i,t_a}} \right\}^{\frac{1}{t_b - t_a}}$$

Regional indexes are sums of regional totals, or the indexes multiplied by the regional areas ( $A_i$ ):

$$N_t = \sum_i A_i n_{i,t}$$

and composite trend ( $B$ ) is calculated as:

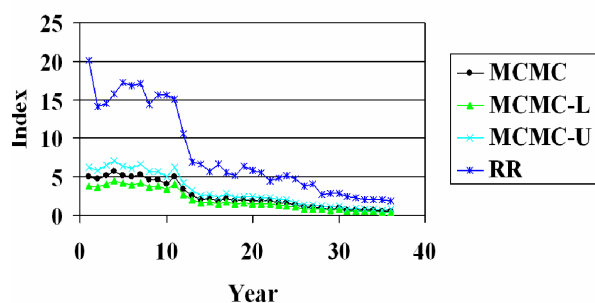
$$\bar{B} = \left\{ \frac{N_{t_b}}{N_{t_a}} \right\}^{\frac{1}{t_b - t_a}}$$

Means and credible intervals (percentiles of posterior distributions) are estimated for all of these quantities from the MCMC replicates.

### Sample Application: Northern Bobwhite in Appalachians

We used the hierarchical model to estimate trends for Northern Bobwhites (*Colinus virginianus*) in the Appa-

lachians. We divided the Appalachians into three strata (Northern [NY, PA, NJ], central [MD, WVA, VA], and southern [AL, GA, NC, TN, KY]), estimated trend and indexes separately for each strata, then estimated composite trend for the Appalachians. We also conducted an estimating equation route regression (Link and Sauer 1994) and residual indices (Sauer and Geissler 1990) for comparison. Route regression results indicated a trend of -5.77 percent/year,  $p < 0.001$ ,  $n$  routes = 195, while the posterior mean trend estimate from the MCMC result was -5.86 percent/year, (95 percent CI: -6.69, -5.02). General similarities also exist in patterns of population change over time from residual indices and annual indices from the hierarchical models (fig. 2). Primary differences exist in scaling of the results, possibly due to the naïve scaling of residual indices to a mean abundance in the midyear of the time series (Sauer and Geissler 1990, Link and Sauer 2002).



**Figure 2**— Population year effects for Northern Bobwhite in the Appalachian BCR from BBS data. RR indicates route regression residual indices, while MCMC represents the annual indices from the hierarchical models with 95 percent credible intervals.

### Hierarchical Spatial Modeling

Spatial dependence often arises in ecological data due to spatial structure in underlying habitat and landscape structure. In some instances, it is possible to model these sources of spatial dependence explicitly, for example within a regression framework. However, it is not always possible to define or characterize the appropriate suite of dependent variables which explain spatial patterns in data. Consequently, in problems dealing with spatially indexed data it may be desirable to model residual spatial variation which leads to dependence among observations. While one goal in developing spatial models may simply be to account for unexplained spatial dependence (yielding more appropriate inferences about model parameters), spatial dependence is often of direct interest in problems which involve mapping or spatial prediction.

Whatever the motivation, there are many approaches for developing models for spatial data, depending on the type of data at hand and the goals of the analysis. A fairly general and concise description can be developed

for most problems simply by considering the addition of a spatially indexed random effect within a hierarchical modeling framework. For normal data models, this approach yields the classical linear mixed model (e.g., Laird and Ware 1972) for which analysis may proceed using classical methods, but which we feel is more conveniently analyzed using Bayesian methods, especially when there is direct interest in estimating specific random effects (i.e., spatial prediction). In addition, the Bayesian hierarchical formulation often facilitates the analysis of non-normal data models, such as for count data, which are commonly collected in many ecological studies.

Spatial models arise by specification of a spatial dependence prior distribution on a collection of spatially indexed parameters. As an example, Royle et al. (2002) recently suggested a simple spatial association model for mapping relative abundance from BBS data. The BBS yields spatially indexed counts, say  $y(s)$ , which are naturally conceived of as realizations of a Poisson random variable with mean  $\lambda(s)$ . As in traditional log-linear models, it is natural to consider models for the logarithm of the Poisson mean. Thus, a simple spatial model for BBS counts is:

$$\log(\lambda(s)) = \mu + \alpha(s)$$

where  $\mu$  is a constant mean and  $\alpha(s)$  is the spatial effect (or route effect in the case of BBS data) for location  $s$ . Now, the spatial modeling task is to specify a model (a prior distribution) for these spatial effects which accommodates potential dependence among them and satisfies the goal of mapping and prediction.

To this end, there are dozens of possibilities for choice of spatial prior distributions. For example, in discrete space (such as if the sample region were composed of discrete spatial units), Markov random fields, or spatial autoregression models are appealing. This is the approach taken in applications to image analysis, and also in applications where data are indexed by discrete geopolitical units such as counties or physiographic strata such as BCRs (He and Sun 2000). This idea underlies the common autologistic model for mapping occurrence of a species, or range mapping (Wu and Huffer 1987, Hoeting et al. 2000). The method commonly known as “kriging” presents an alternative approach for spatial parameterizations of the random effects that is more natural for continuous spatial domains. The essence of most kriging models is to assume a multivariate normal distribution on the vector of random effects  $\alpha = (\alpha(s_1), \alpha(s_2), \dots, \alpha(s_n))$  with an  $n \times n$  variance-covariance matrix of the random effects,  $\Sigma(\theta)$ . The variance-covariance matrix is assumed to be completely specified by a covariance function which dictates the distance-associated covariance between any two locations,  $s$  and  $s'$ , and which depends on the parameter  $\theta$ ,

say  $k(s,s';\theta)$ . There are many common spatial covariance models in widespread use (see Cressie 1991, p. 61). Royle et al. (2002) made use of the exponential model given by:

$$k(s,s';\theta) = \exp(-d(s,s')/\theta)$$

where  $d(s,s')$  is the distance between locations  $s$  and  $s'$ . The parameters  $\mu$  and  $\theta$ , as well as the random effects, may be estimated using standard MCMC methods. In addition, prediction of random effects at locations where no data are available is possible because of the relationship implied by the spatial correlation model. A collection of predictions, such as on a regular grid over the study area, yields the desired map.

The importance of observer effects in BBS data is widely known and it is necessary to accommodate observer variation within this spatial model. This may be done by the addition of random observer effects which are assumed to be spatially *independent*. That is, the model for the Poisson mean becomes

$$\log(\lambda(s)) = \mu + \alpha(s) + \eta(s)$$

where  $\eta(s) = \text{Normal}(0, \sigma^2)$ . The observer effects play the role of measurement error (the “nugget” effect) in the classical kriging model and they are not of direct interest in the analysis but instead serve to soak up residual overdispersion. This model may also be expanded to accommodate spatial covariates such as habitat and temporal variation such as trends.

## Benefits of Hierarchical Models

Unfortunately, many of the questions that must be addressed in conservation biology cannot be easily answered using conventional statistical approaches. Even questions such as ranking species for magnitude of decline, which superficially appears to be a simple procedure, are complicated by the need to simultaneously address magnitude of change and significance of change. Hierarchical models are a natural way to approach these questions (e.g., Link and Sauer 1998, Sauer and Link 2002). Bayesian models provide an appropriate conceptual framework for dealing with collections of estimates, whether they arise from comparison of trends for a variety of species or from the need to summarize geographic patterns of population change from a single species. Earlier analyses of populations, such as the route regression method, provide ad-hoc approaches for accommodating error in summaries of estimates, but hierarchical models make the assumptions associated with those methods explicit, and provide the first reasonable means for appropriate aggregation of population change estimates over space or species. Hierarchical models also allow for estimation

of derived attributes, such as the population stability metric and rankings of population change. Finally, Bayesian approaches to analysis of hierarchical models are relatively easy to implement in programs such as BUGS. BUGS programs to implement the examples presented in the paper are available from the authors.

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## Appendix 1

List of posterior mean trends, estimated ranking, and probability that the population trend is within the range [-2,2 percent/yr] for species with unstable populations in the Appalachian BCR.

Species	Posterior mean	Estimated ranking	Pr( $\beta_s \in (-2,2)   Y$ )
<b>Unstable increasing species</b>			
Great Blue Heron ( <i>Ardea herodias</i> )	6.7	156.3	0.00
Canada Goose ( <i>Branta canadensis</i> )	13.9	165.3	0.00
Mute Swan ( <i>Cygnus olor</i> )	18.7	166.9	0.00
Wood Duck ( <i>Aix sponsa</i> )	5.2	148.9	0.01
Red-tailed Hawk ( <i>Buteo jamaicensis</i> )	4.2	143.8	0.01
Wild Turkey ( <i>Meleagris gallopavo</i> )	6.7	154.9	0.01
Ring-billed Gull ( <i>Larus delawarensis</i> )	10.6	164.1	0.00
Red-bellied Woodpecker ( <i>Melanerpes carolinus</i> )	4.2	144.2	0.00
Yellow-bellied Sapsucker ( <i>Sphyrapicus varius</i> )	8.8	161.3	0.00
Blue-headed Vireo ( <i>Vireo solitarius</i> )	4.3	144.4	0.01
Common Raven ( <i>Corvus corax</i> )	5.1	147.9	0.02
Tree Swallow ( <i>Tachycineta bicolor</i> )	5.5	151.6	0.00
Red-breasted Nuthatch ( <i>Sitta canadensis</i> )	4.9	147.4	0.02
Hermit Thrush ( <i>Catharus guttatus</i> )	4.6	146.6	0.00
Magnolia Warbler ( <i>Dendroica magnolia</i> )	4.8	147.6	0.00
Yellow-rumped Warbler ( <i>Dendroica coronata</i> )	5.9	151.1	0.03
House Finch ( <i>Carpodacus mexicanus</i> )	7.6	158.9	0.00
<b>Unstable declining species</b>			
Northern Bobwhite ( <i>Colinus virginianus</i> )	-5.7	10.9	0.00
Whip-poor-will ( <i>Caprimulgus vociferus</i> )	-6.0	11.6	0.01
Northern Flicker ( <i>Colaptes auratus</i> )	-3.5	24.1	0.00
Eastern Wood-Pewee ( <i>Contopus virens</i> )	-3.2	27.4	0.00
Horned Lark ( <i>Eremophila alpestris</i> )	-7.9	6.6	0.00
Bewick's Wren ( <i>Thryomanes bewickii</i> )	-10.1	6.5	0.02
Golden-winged Warbler ( <i>Vermivora chrysoptera</i> )	-8.1	4.7	0.00
Prairie Warbler ( <i>Dendroica discolor</i> )	-4.3	17.4	0.00
Cerulean Warbler ( <i>Dendroica cerulea</i> )	-2.9	32.4	0.03
Yellow-breasted Chat ( <i>Icteria virens</i> )	-3.6	23.4	0.00
Field Sparrow ( <i>Spizella pusilla</i> )	-3.8	20.9	0.00
Vesper Sparrow ( <i>Poocetes gramineus</i> )	-6.9	7.5	0.00
Grasshopper Sparrow ( <i>Ammodramus savannarum</i> )	-6.3	9.3	0.00
Dickcissel ( <i>Spiza americana</i> )	-10.4	3.3	0.01
Red-winged Blackbird ( <i>Agelaius phoeniceus</i> )	-2.7	33.8	0.00
Eastern Meadowlark ( <i>Sturnella magna</i> )	-3.6	22.9	0.00
Brown-headed Cowbird ( <i>Molothrus ater</i> )	-3.5	24.2	0.00
House Sparrow ( <i>Passer domesticus</i> )	-2.9	31.7	0.00