

# Bayesian Spatial Modeling of Data from Avian Point Count Surveys

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We present a unified framework for modeling bird survey data collected at spatially replicated survey sites in the form of repeated counts or detection history counts, through which we model spatial dependence in bird density and variation in detection probabilities due to changes in covariates across the landscape. The models have a complex hierarchical structure that makes them suited to Bayesian analysis using Markov chain Monte Carlo (MCMC) algorithms. For computational efficiency, we use a form of conditional autoregressive model for modeling spatial dependence. We apply the models to survey data for two bird species in the Great Smoky Mountains National Park. The algorithms converge well for the more abundant and easily detected of the two species, but some simplification of the spatial model is required for convergence for the second species. We show how these methods lead to maps of estimated relative density which are an improvement over those that would follow from past approaches that ignored spatial dependence. This work also highlights the importance of good survey design for bird species mapping studies.

**Key Words:** Binomial counts; CAR models; Detection histories; Detection probability; MCMC; Population density estimation.

## 1. INTRODUCTION

The analysis of data from large surveys of bird populations is often based on models that make simplifying assumptions and ignore important aspects of the survey design. The goals of such bird surveys include the estimation of density, mapping the distribution of animals across a region, and modeling the relationships between bird density and habitat variables such as elevation and vegetation. Although surveys typically involve making observations on many line or point transects (“survey sites”), data are often aggregated over all sites for analysis (Farnsworth et al. 2002; Alldredge et al. 2007) or the analysis ignores spatial structure in the data by assuming survey sites are spatially independent (Simons et al. 2000). Ignoring spatial dependence will influence estimates of the effects of

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any covariates on bird density (Cressie 1993), while accounting for such dependence can lead to improved prediction of density at unsurveyed locations. Further, uncertainty in the detection of animals has either been ignored or dealt with in an ad-hoc manner (Simons, Farnsworth, and Shriner 2000; Lichstein et al. 2002). Detection probability will vary across the landscape, with the time of the year, according to the local weather conditions, between individual observers and between different bird species. Not allowing for such variation may lead to over or underestimation of relative bird density at some locations, affecting inference from fitted models, or resulting in misleading comparisons of bird species populations or inaccurate assessment of population changes over time. We present a unified modeling framework for the analysis of repeated count and capture–recapture data from bird surveys carried out at spatially replicated sites that allows for both imperfect detection and spatial dependence in the data.

Although some surveys involve a simple count of birds of each species along a line transect or at a point transect (Royle et al. 2002; Wikle 2002), count data alone are not sufficient to distinguish variation in density from variation in detectability. Motivated by a large bird survey dataset collected between 1992 and 1999 in the Great Smoky Mountains National Park (Simons, Farnsworth, and Shriner 2000; Simons et al. 2006), we consider two types of survey data gathered by making a sequence of independent observations during multiple survey periods at each site: repeated counts, in which all birds seen or heard are counted in each survey period; and “capture–recapture” data, in which observed birds are again identified individually and a record is kept of whether an individual was observed in each survey period or not, thus forming a detection history (Allredge et al. 2007). Our use of quotation marks here is to indicate that the data conform to this particular type, even though birds are generally not physically captured. In the Smoky Mountains example, the original data are in the form of detection histories at multiple sites, and from these we can extract the appropriate statistics for repeated count analysis of the data. In both the repeated count and capture–recapture cases, the data at each survey site can be summarized in the form of a vector of animal counts, the form and distribution of which depends on the survey design. There is great potential for errors in such surveys, particularly when individuals are identified by sound, as was the case for almost all detections in the Smoky Mountains survey. Although we discuss this throughout our work, the models we present assume that observations are made without error.

With an additional closure assumption, we can make use of binomial models for repeated count data from multiple survey sites, in which the model for the data at a site contains distinct parameters for abundance and detection probability. Within a hierarchical framework, we can use Poisson-lognormal mixture models for relating site abundances to covariates, and logistic-linear models to do the same for the detection component of the binomial model. Importantly, the latter allows us to account for variation in detection probability between the survey sites. Royle (2004) described this hierarchical framework for repeated count data, while Wyatt (2002), Dorazio et al. (2005), and Forsyth et al. (2005) applied similar models to closely related removal data (Zippen 1956). Our approach is the same for “capture–recapture” bird survey data, as closed population models for such data also depend on the same abundance and detection probability parameters (see also Royle and Dorazio 2006). Closed population capture–recapture models have been extensively

studied (see Pollock et al. 1990), including those which attempt to model heterogeneity in detectability between individual animals (e.g., Norris and Pollock 1996; Coull and Agresti 1999; Pledger 2000; Dorazio and Royle 2003; Pledger 2005; Holzmann et al. 2006). In the surveys of multiple sites that form the focus of our work, we only model such heterogeneity using logistic-linear models that allow site differences and changes in detectability across the multiple survey periods to be modeled as a function of covariates. This approach is similar to that taken by Huggins (1989) and Alho (1990), who considered logistic models with covariates measured on individual animals, and this allows us to fit capture–recapture models within the same framework as models for repeated count data. Modeling heterogeneity between individuals within sites as a random effect is a more difficult problem, and as shown by Link (2003), can be highly dependent on the choice of model, and we do not consider this class of heterogeneity models.

The hierarchical structure of these models means that they are relatively easily implemented using Bayesian modeling with Markov chain Monte Carlo (MCMC) algorithms, for example, by combining Gibbs Sampling (Geman and Geman 1984) with Metropolis-Hastings steps (Hastings 1970). Accounting for spatial structure with large datasets requires specifying models that lead to efficient MCMC algorithms. Algorithms based on conditional autoregressive (CAR) models (Besag 1974) are much faster than those for geostatistical models described by Cressie (1993), and have been used by Royle, Link, and Sauer (2002) for modeling bird point count data. Lichstein et al. (2002) used a CAR model for modeling bird survey data, but their approach required fitting preliminary geostatistical models to estimate the distance at which spatial dependence between two points becomes negligible. We propose the use of a variation of standard CAR models for spatial modeling in two-dimensional space (Hrafinkelsson and Cressie 2003), in which this distance becomes a parameter of the models.

We fitted the hierarchical spatial models to both repeated count and “capture–recapture” versions of data from the Great Smoky Mountains bird survey. Comparison of repeated count and capture–recapture modeling is particularly interesting given that it is likely that errors in the data occur due to the misidentification of individual birds, but these may have a lesser effect when data are aggregated in the form of counts than when we require individuals to be distinguished for analysis of detection history data using capture–recapture models. Parts of this dataset were analyzed previously by Shriner (2001), Shriner et al. (2002), Farnsworth et al. (2002), and Alldredge et al. (2007), while Lichstein et al. (2002) looked at a similar dataset from the adjacent Pisgah National Forest, North Carolina. Past analyses focused on certain aspects of the modeling while neglecting others, in particular either the spatial structure or variation in detection probability. Our modeling framework allowed us to simultaneously model all components of the data structure, including covariates, detection probabilities, and spatial dependence.

In Section 2 we describe our hierarchical models for bird density and detection probability, and in Section 3 we discuss spatial modeling of bird survey data. We present detailed analyses of data for two species from the Great Smoky Mountains bird survey, including maps of the spatial distribution of relative bird density in Section 4. Finally, the implications of our work and possible avenues of future research are discussed in Section 5.

## 2. POPULATION AND DETECTION MODELS

In this section we present models for data from surveys in which a sequence of independent observations are made at multiple survey locations within a region of interest. Thus, we suppose that some number,  $L$ , of sites are surveyed, and that the data consist of observations made during  $T$  survey periods at each site. We assume that over the course of the  $T$  periods, the population is closed to migration, births, and deaths. In bird surveys this assumption is often reasonable, as repeated observations are usually made within a very short time period (e.g., 10 minutes for Farnsworth et al. 2002). Let  $N_i$  be the “abundance” of animals at survey site  $i$ , and  $p_{ij}$  the probability an animal is detected at site  $i$  on occasion  $j$ . In fact, in most situations  $N_i$  is a measure of *relative* abundance, as we discuss in the following. The first stage of our hierarchical models involves specifying a model for the data at site  $i$  in terms of these parameters.

In a repeated count survey, a record is kept of the number of animals observed at a site on each of the  $T$  survey periods and these counts are assumed to be made independently in each period. Let  $y_{ij}$  be the observed bird count site  $i$  for period  $j$ , so that at each site we observe a data vector  $\mathbf{Y}_i = [y_{i1}, \dots, y_{iT}]'$ . We assume that these bird counts are made without error. We can apply a binomial model to the observed counts, so that for  $i = 1, \dots, L$  and  $j = 1, \dots, T$ ,

$$y_{ij} | N_i, p_{ij} \sim \text{Bin}(N_i, p_{ij}). \quad (2.1)$$

This type of binomial model was used previously by Royle (2004) for repeated count data, and by Wyatt (2002) and Forsyth et al. (2005) for removal data.

In surveys that yield the capture–recapture type of data, a record is kept of whether each observed bird was detected in a given survey period or not. We assume that no errors are made in the identification of birds, for example, single birds are not misidentified as being more than one bird, multiple birds are not recorded as being the same individual, and species are always correctly identified. For our models, which allow detection probability to vary between sites and between periods within a site, we can summarize the detection histories of birds as a vector of counts for each site, with each count being the number of birds with a particular unique detection history (Otis et al. 1978). For example, for  $T = 3$  periods, there are eight possible detection histories,  $\omega = 111, 110, 101, 100, 011, 010, 001$ , and  $000$ . Let the number of birds with history  $\omega$  at site  $i$  be denoted by  $Y_{i\omega}$ , and let  $\mathbf{Y}_{i\omega} = [Y_{i,111}, Y_{i,110}, \dots, Y_{i,000}]$  for the three period example. If  $\boldsymbol{\pi}_{i\omega} = [\pi_{i,111}, \pi_{i,110}, \dots, \pi_{i,000}]$ , where

$$\begin{aligned} \pi_{i,111} &= P(\omega = 111) = p_{i1}p_{i2}p_{i3}, \\ \pi_{i,110} &= P(\omega = 110) = p_{i1}p_{i2}(1 - p_{i3}), \\ &\vdots \\ \pi_{i,000} &= P(\omega = 000) = (1 - p_{i1})(1 - p_{i2})(1 - p_{i3}), \end{aligned}$$

then  $\mathbf{Y}_{i\omega}$  has a multinomial distribution given by

$$\mathbf{Y}_{i\omega} | N_i, \mathbf{p}_{i\omega} \sim \text{multinomial}(N_i, \boldsymbol{\pi}_{i\omega}). \quad (2.2)$$

Note that  $Y_{i,000}$  is unknown since birds with detection history 000 are unobserved, and in constructing a likelihood function, we replace this with  $Y_{i,000} = N_i - \sum_{\omega \neq 000} Y_{i\omega}$ . It is also worth noting that in maximum likelihood estimation of single-site capture–recapture data, where detection varies only between the  $T$  occasions, the sufficient statistics are the  $T$  counts,  $y_{i1}, \dots, y_{iT}$  (for site  $i$ ) and the number of unique birds detected at that site,  $M_{i,T+1}$ . Thus the additional information contained in the “capture–recapture data,” but not in repeated count data, comes from  $M_{i,T+1}$ , and in general we would expect more precise estimation when modeling the detection histories.

Although the data models differ for count and detection history data, in both cases the distribution of the data at a site depends on the same set of parameters,  $N_i$  and  $p_{i1}, \dots, p_{iT}$  for  $i = 1, \dots, L$ . The next step in our hierarchical modeling is to specify models for these parameters. For  $N_i$  we use a Poisson-lognormal mixture to model variation in abundance across the sites as a function of covariates and spatially dependent Gaussian errors (see Diggle et al. 1998). As well as being very flexible, this mixture model allows for overdispersion in the site abundances, which is often present in animal data due to the clustering of animal populations (Seber 1982, p. 25). The model is as follows:

$$\begin{aligned} N_i | \lambda_i &\sim \text{Poisson}(\lambda_i) \\ \log(\lambda_i) &= \mu_i + \phi_i. \end{aligned} \quad (2.3)$$

Here  $\phi_i$  is a zero-mean Gaussian error term through which we model spatial dependence (Section 3) and  $\mu_i$  represents the covariate model, most commonly of linear form,  $\mu_i = \mathbf{X}'_i \boldsymbol{\alpha}$ , where  $\mathbf{X}_i$  here represents the vector of covariates measured on unit  $i$ , and  $\boldsymbol{\alpha}$  is the corresponding parameter vector. In the case where the animals are observed within a well-defined area around the survey site, we may replace  $\lambda_i$  in Equation (2.3) with  $A_i \lambda_i$ , where  $A_i$  is the surveyed area around site  $i$ , and  $\lambda_i$  becomes the density of birds per unit area. In most surveys, however, there is no clear boundary beyond which birds are unobservable. The  $N_i$  and  $\lambda_i$  in this case correspond to measures of relative abundance and density, but unlike simple count surveys, by modeling detection probability directly, we can still make appropriate inference on the parameters of the covariate model and of variation in density across space, between species, or over time.

For detection probability, we use a linear logistic model to allow for variation due to covariates,

$$\text{logit}(p_{ij}) = v_{ij},$$

where  $v_{ij}$  is a function of covariates that vary between sites and across the  $T$  periods within the sites. For example, if we have values of the covariates at each of the  $L$  sites and we fit a linear model, then  $v_{ij} = \mathbf{Z}'_i \boldsymbol{\beta}$ , where  $\mathbf{Z}_i$  is the covariate vector for site  $i$ , and  $\boldsymbol{\beta}$  is a vector of parameters. In this work we do not consider models that allow for a random effect in the detection model as per Forsyth et al. (2005). Our experience is that it can be difficult to distinguish random variation in detectability from that due to density, particularly when there are few survey periods [i.e.,  $T$  is small, common for bird surveys but not the case for the opossum survey of Forsyth et al. (2005)], and attempting to do so does not improve the fit of the models.

### 3. BAYESIAN SPATIAL MODELS

#### 3.1 MODELING SPATIAL DEPENDENCE

Due to our models' complexity and hierarchical structure, we use Bayesian modeling to make inference on the model parameters through MCMC algorithms based on Gibbs sampling (Geman and Geman 1984) with Metropolis or Metropolis-Hastings steps (Hastings 1970) to generate samples from the posterior distributions of the parameters. For these algorithms to be computationally efficient for large datasets, we must take care in our choice of model for the spatial dependent random effect,  $\phi_i$ . The most intuitive approach would be to use a standard geostatistical model to describe the spatial structure, such as an exponential or the more general Matérn variogram model. Within a Gibbs sampling algorithm, however, updates require the inversion of  $L \times L$  matrices, which creates an enormous computational burden when  $L$  is large.

A more practical alternative is to use conditional autoregressive (CAR) models (Besag 1974), which have become popular in recent years because MCMC iterations are very efficient to perform due to the conditional nature of the model specification. In a CAR model,  $\phi_i$  is assumed to be normally distributed with the mean defined to be the weighted average of the elements of the vector of errors with the  $i$ th omitted,  $\phi_{-i} = [\phi_1, \dots, \phi_{i-1}, \phi_{i+1}, \dots, \phi_L]'$ . Following Banerjee, Carlin, and Gelfand (2004), we begin by defining a symmetric  $L \times L$  matrix of weights,  $\mathbf{W}$ , with elements  $w_{ii'}$ . Now define  $w_i = \sum_{i'=1}^L w_{ii'}$ , the row totals of  $\mathbf{W}$ . A 'proper' Gaussian CAR model then follows by specifying the distribution of  $\phi_i$  conditionally as

$$\phi_i | \phi_{-i}, \gamma, \sigma_\phi^2 \sim N \left( \gamma \sum_{i' \neq i} \frac{w_{ii'}}{w_i} \phi_{i'}, \frac{\sigma_\phi^2}{w_i} \right). \quad (3.1)$$

Unconditionally,  $p(\boldsymbol{\phi})$ , the joint probability density of the vector  $\boldsymbol{\phi} = [\phi_1, \dots, \phi_L]'$ , is given by

$$p(\boldsymbol{\phi} | \gamma, \sigma_\phi^2) \propto \exp \left\{ -\frac{1}{2\sigma_\phi^2} \boldsymbol{\phi}' \mathbf{M}^{-1} (\mathbf{I} - \gamma \mathbf{C}) \boldsymbol{\phi} \right\}, \quad (3.2)$$

where  $\mathbf{M}$  is a diagonal matrix with  $i$ th diagonal element  $1/w_i$ , and  $\mathbf{C} = \mathbf{M}\mathbf{W}$ , the scaled weight matrix. Equation (3.2) specifies the kernel of a multivariate normal distribution with mean vector  $\mathbf{0}$  and covariance matrix  $\boldsymbol{\Sigma}_\phi = \sigma_\phi^2 (\mathbf{I} - \gamma \mathbf{C})^{-1} \mathbf{M}$ . Let  $\tau_\phi = 1/\sigma_\phi^2$  be the precision parameter of the model. With weights defined above,  $\boldsymbol{\Sigma}_\phi^{-1} = \tau_\phi \mathbf{M}^{-1} (\mathbf{I} - \gamma \mathbf{C})$  will be symmetric, and provided that  $|\gamma| < 1$ , this matrix will also be nonsingular and  $\boldsymbol{\Sigma}_\phi$  will be a valid covariance matrix. In this case, (3.1) defines a proper prior distribution in Bayesian hierarchical modeling.

Although the parameter  $\gamma$  governs the strength of spatial dependence, it is difficult to interpret the magnitude of a nonzero  $\gamma$ , and in general any degree of spatial dependence will lead to a large value for  $\gamma$  (Banerjee, Carlin, and Gelfand 2004). For this reason, some authors prefer to fix  $\gamma = 1$ , leading to what is known as an intrinsic CAR model. Such a formulation leads to computational difficulties with our MCMC algorithms, in particular,

the full conditional densities for  $d_{\max}$  and  $\alpha$  become improper. We do not consider this model further in this work.

As each value of  $\phi_i$  is a function of its neighbors, the CAR model has been most widely used when the survey region is divided into contiguous subregions because in such cases the neighborhood structure is straightforward to define. For example, the simplest case would be to let  $w_{ii'} = 1$  if sites  $i$  and  $i'$  share a common boundary, and zero otherwise. When the data are observed at points in continuous space, more care must be taken in specifying the neighborhood structure. A convenient approach, and the one we take here, was proposed by Hrafnkelsson and Cressie (2003), who introduced a neighborhood radius (which we call  $d_{\max}$ ) as an additional model parameter: only points within  $d_{\max}$  of a survey point are considered neighbors of that point and are assigned positive weights, with the magnitude of the weight being a decreasing function of distance from the survey point.

Let  $r_{ii'}$  be the Euclidean distance of site  $i$  from site  $i'$ , and let  $\delta$  be the magnitude of the spatial dependence at  $r_{ii'} = d_{\max}$ . Hrafnkelsson and Cressie (2003) defined the weights,  $w_{ii'}$ , assuming a minimum distance between two survey points of 1 unit. For an arbitrary minimum distance,  $r_{\min}$ , let

$$\psi = -\frac{\log(\delta)}{\log(d_{\max}/r_{\min})}.$$

Then the  $w_{ii'}$  for site  $i$  are given by

$$w_{ii} = 0, i = 1, \dots, L$$

$$w_{ii'} = r_{ii'}^{-\psi}, r_{ii'} \leq d_{\max}$$

$$w_{ii'} = 0, r_{ii'} > d_{\max}.$$

The parameter  $\delta$  is fixed at a low value so that the discrete drop in the weight function at distance  $d_{\max}$  is small. We follow Hrafnkelsson and Cressie (2003) by setting  $\delta = 0.05$ . Depending on the value of  $d_{\max}$ , some points may be without neighbors and would need to be excluded from the analysis unless additional unsurveyed points were added to the observed data and prediction made at these points. When fitting a model with covariates, that approach would require covariate measurements at each of the unsurveyed points, which may not always be available. Alternatively, we could set a lower bound on  $d_{\max}$  ( $d_L$ , say) such that at most only a small number of points have no neighbors within this distance. We do this in our example in Section 4.

Hrafnkelsson and Cressie (2003) also demonstrated that if the underlying spatial model is in fact of geostatistical form, such as a Matérn model (Cressie 1993), then the above CAR specification is likely to be a good approximation. This is an attractive feature if one feels more comfortable using geostatistical models for data in continuous space. The Matérn model in particular includes a smoothness parameter governing the continuity of the spatial process, and the work of Hrafnkelsson and Cressie (2003) implies that using their modified CAR model will also allow for the degree of smoothness of a given underlying spatial process. However, as we shall see in the following example, with sparse animal survey data, it can be unreasonable to fit a spatial model of such parametric complexity.

### 3.2 BAYESIAN MODELS

Given the form of the spatial model above, we can proceed with the Bayesian modeling by writing down the form of the posterior in terms of the likelihood and the prior distribution. Let  $\mathbf{Y}$  be the data matrix (repeated counts or detection history counts for all sites) and  $\mathbf{X}$  and  $\mathbf{Z}$  be the covariate matrices for the abundance and detection components of the model, respectively. In our algorithms, we chose to work with  $u_i = \log(\lambda_i) = \mu_i + \phi_i$ , and with other parameters as defined previously, the joint posterior distribution can be written as

$$p(\mathbf{N}, \mathbf{u}, \boldsymbol{\alpha}, \boldsymbol{\beta}, \gamma, d_{\max}, \tau_\phi | \mathbf{Y}, \mathbf{X}, \mathbf{Z}) \\ \propto p(\mathbf{Y} | \mathbf{N}, \boldsymbol{\beta}, \mathbf{Z}) p(\mathbf{N} | \mathbf{u}) p(\mathbf{u} | \boldsymbol{\alpha}, \mathbf{X}, \gamma, d_{\max}, \tau_\phi) p(\boldsymbol{\alpha}, \boldsymbol{\beta}, \gamma, d_{\max}, \tau_\phi),$$

where  $\mathbf{N} = [N_1, N_2, \dots, N_L]'$  and  $\mathbf{u} = [u_1, u_2, \dots, u_L]'$ . Note that the detection probabilities are only a function of the covariate parameter vector,  $\boldsymbol{\beta}$ , and corresponding data matrix,  $\mathbf{Z}$ , and therefore do not need to appear explicitly in the posterior. The likelihood component,  $p(\mathbf{Y} | \mathbf{N}, \boldsymbol{\beta}, \mathbf{Z})$ , has binomial form for repeated count data, and multinomial form for capture–recapture data, while  $p(\mathbf{N} | \mathbf{u}) = \prod_i p(N_i | u_i)$  is the product of Poisson densities, and  $p(\mathbf{u} | \boldsymbol{\alpha}, \mathbf{X}, \gamma, d_{\max}, \tau_\phi)$  is a proper Gaussian CAR density with nonzero mean. The term  $p(\boldsymbol{\alpha}, \boldsymbol{\beta}, \gamma, d_{\max}, \tau_\phi)$  is the joint prior density. In updating  $\mathbf{u}$  using Gibbs sampling, we work with the full conditional densities for the  $u_i$ , that is  $p(u_i | u_1, \dots, u_{i-1}, u_{i+1}, \dots, u_L, \dots)$ , allowing us to avoid the inversion of large covariance matrices that would be required in a standard geostatistical model.

Samples from the posterior can be generated using an MCMC algorithm based on Gibbs sampling with Metropolis–Hastings steps for some parameters, with the exact algorithm depending on the form of the priors. More details for our particular example are given in the next section. After discarding data generated prior to convergence of the algorithms (the “burn-in”), the MCMC samples can be used to estimate posterior summary statistics such as means, standard deviations, quantiles or the form of densities themselves (e.g., using kernel density estimation). For a discussion of convergence assessment and other diagnostics, we refer the reader to Gelman et al. (2004).

## 4. EXAMPLE: GREAT SMOKY MOUNTAINS BIRD SURVEY

An extensive multispecies survey of the bird population of the Great Smoky Mountains National Park was carried out from 1992 to 1999. More than 4,000 distinct point survey sites were positioned around low-use hiking trails. The survey at each point lasted 10 minutes, during which time observers recorded all individual birds that were seen or heard, with 95% of detections being based on auditory cues. A three-period capture history was created for each individual by dividing the observation period into three smaller intervals, the first of three minutes, the second of two minutes and the third of five minutes duration, and recording whether a bird was observed in each interval or not. This design was created to allow comparison with previous bird surveys which used single counting intervals of

three, five, or ten minutes (Ralph, Droege, and Sauer 1995), although we would recommend a simpler division into equal intervals for future work. From the detection history data, we also computed the count statistics required for analysis by repeated count survey models.

We restrict ourselves here to analyzing data from 1,750 survey points monitored in 1997, and focus on two species as examples: the Black-throated Green Warbler (BT) and the Black and White Warbler (BL). Both species are long-distance neotropical migrants that winter in the Caribbean and from southern Mexico to northern South America. They are common breeders in coniferous and mixed coniferous-deciduous forests of eastern North America and are found in the Smoky Mountains between late March and early October. BT is found up to the highest elevations in the park (1,800 m), and BL is found below 1,500 m (Alsop 1991). Sampling was conducted during the peak of the breeding season (late May–early July) when breeding birds occupy discrete breeding territories. BT is common and has a loud, easy-to-detect song, and our 1997 data come from observations of 1,445 distinct birds. By contrast, BL is less abundant and more difficult to detect due to its faint, high-pitched song. For this species, data come from only 469 individuals. Our interests in analyzing these data include exploring the relationships between density and habitat characteristics and determining if failure to allow for factors affecting detection probability affects model inference, and in developing maps predicting density of a species across the park. Our analyses will also improve upon the methods that Shriner (2001), Lichstein et al. (2002), and others have applied to these and similar survey data.

The most important factors affecting density at a survey site can be summarized with two variables—elevation above sea level and topographic relative moisture index (TRMI). The latter is an index based on forest moisture gradients and has been shown to be related to forest species composition (Pinder et al. 1997), and we use it here instead of more complex categorical variables for forest composition. Using a simple linear model, we model the relative bird density at the  $i$ th point transect using

$$\log(\lambda_i) = \alpha_0 + \alpha_1 E_i + \alpha_2 \text{TRMI}_i + \phi_i,$$

where  $E_i$  and  $\text{TRMI}_i$  are, respectively, the elevation and TRMI values for the  $i$ th site. The survey sites are not surrounded by a clearly defined area beyond which we cannot detect birds, which means that “density” at a transect,  $\lambda_i$ , should be interpreted as an index of relative bird density as noted in Section 2. The term  $\phi_i$  represents the spatially dependent error which we model using the proper CAR model of Section 3.

We compare two logistic models for detection probability. The first is a base model with no covariates, that is, one that ignores variation in detection probability across the park. The second model includes a contrast between detection probabilities in spring and in summer. We expect this to be important, as detection probability is affected by singing rate, which can vary substantially during the nesting cycle, and the sites were surveyed at different times from spring to summer. The two models are:

$$(1) \text{logit}(p_{ij}) = \log(\mathcal{T}_j) + \beta_0, \text{ and}$$

$$(2) \text{logit}(p_{ij}) = \log(\mathcal{T}_j) + \beta_0 + \beta_1 \mathcal{S}_i.$$

The term  $\log(\mathcal{T}_j)$  is an offset, where  $\mathcal{T}_j = 3, 2,$  or  $5$  minutes for period  $j = 1, 2,$  or  $3,$  respectively. This allows the probability of detection to vary with the duration of survey period in such a way that the odds ratios are proportional to the ratios of the period lengths,  $\mathcal{T}_j$ .  $\mathcal{S}_i$  takes the value  $0$  if a point was surveyed prior to June 21, and  $1$  otherwise.

We used mutually independent, vague or noninformative prior distributions for all parameters. Specifically, we used  $N(0, 1,000)$  priors for the covariate coefficients in both the density and detection models, for  $\text{logit}((\gamma + 1)/2)$ , and for  $\log(d_{\max} - d_L)$ . The spatial neighborhood radius parameter was constrained to be greater than  $d_L = 0.5\text{km}$ , which led us to exclude only 24 survey sites for having no neighbors within distance  $d_L$ . We sampled values from the posterior of  $\tau_\phi = 1/\sigma_\phi^2$ , for which we used a prior density of  $p(\tau_\phi) \propto \tau_\phi^{-3/2}$ , which corresponds to a uniform prior on  $\sigma_\phi$  as recommended by Gelman (2006). As a check, we also fitted models with alternative prior densities, in particular, independent flat priors on the covariate coefficients, a  $\text{Uniform}(-1, 1)$  prior on  $\gamma$ ,  $\text{Gamma}(0.001, 0.001)$  prior for  $\tau_\phi$  and for  $d_{\max} - d_L$ , and a  $\text{Beta}(0.5, 0.5)$  prior for detection probability in models with no seasonal covariate. All but the three CAR parameters were insensitive to the choice of priors, and even for the CAR parameters, the effect of the choice of prior on the posterior distribution was minor.

Our algorithms were programmed in Matlab 7.1, and it took approximately an hour to run 1,000 iterations. When running our algorithms, we monitored two independent MCMC chains for each model, and convergence was assessed based on the behavior of time series plots of the posterior samples for these chains. In the case of BL, the results we present come from models fitted using three independent MCMC chains in WinBUGs (see below). Within our algorithms, only the parameters  $\alpha$  and  $\tau_\phi$  could be sampled directly from their full conditional densities, which were multivariate normal and gamma, respectively, while the remaining parameters required Metropolis or Metropolis-Hastings steps. We ran 20,000 iterations for each chain in the BT models, following a burn-in period of at least 10,000 iterations. For the sparser BL data, we used 30,000 iterations for each of the three chains following burn-in.

Table 1 gives the posterior means and 95% credible intervals (the 2.5 and 97.5 percentiles of the posterior density) of key parameters from modeling the Black-throated Green Warbler (BT) data. As a measure of relative detection probability for the surveyed sites, we also computed the mean detection probability for the first three-minute survey period, averaged over all  $L$  survey sites, and denote this by  $\bar{p}_3$ . Detection probabilities were higher in summer than in spring for BT ( $\beta_1$  credible interval excludes 0). There is a clear negative relationship between density and elevation, and thus this species is more abundant at lower elevations, but the coefficient of this relationship,  $\alpha_1$ , does not change when we account for seasonal differences in detectability. The posterior mean of  $\alpha_1$  is, however, slightly lower for the capture–recapture models, for which we estimate detection probability to be slightly higher ( $\hat{\bar{p}}_3 = 0.65$  compared with 0.62 for repeated count models). Given the difficulty in distinguishing individual birds in this survey, we think it is likely that errors in the data would be most serious for capture–recapture data. If this is the case, the higher probabilities might imply that observers are mistaking multiple birds for the same bird across the three survey periods and, therefore, they record too few distinct individuals.

Table 1. Posterior means and 95% credible intervals of parameters for modeling of BT data.

Parameter	Count		Capture-Recapture	
	Model 1	Model 2	Model 1	Model 2
$\beta_1$ (Season)	–	0.27 (0.05, 0.49)	–	0.23 (0.05, 0.41)
$\bar{p}_3$	0.62 (0.60, 0.64)	0.62 (0.60, 0.65)	0.64 (0.63, 0.66)	0.65 (0.63, 0.66)
$\alpha_1$ (Elev)	–0.70 (–0.86, –0.55)	–0.70 (–0.85, –0.55)	–0.66 (–0.81, –0.51)	–0.66 (–0.81, –0.51)
$\alpha_2$ (TRMI)	0.081 (0.012, 0.149)	0.081 (0.011, 0.149)	0.086 (0.019, 0.154)	0.082 (0.015, 0.151)
$\sigma_\phi^2$	3.2 (1.8, 4.8)	3.3 (2.0, 4.9)	2.1 (1.0, 3.6)	2.1 (1.0, 3.3)
$\gamma$	0.995 (0.989, 0.998)	0.994 (0.989, 0.997)	0.995 (0.990, 0.998)	0.995 (0.991, 0.998)
$d_{\max}$	0.69 (0.57, 0.91)	0.70 (0.58, 0.91)	0.77 (0.62, 0.94)	0.76 (0.62, 0.96)

However, any differences between the two analyses are very small, so that if any errors exist, their effect is largely the same on both versions of the data. Another explanation for differences in posterior means of detection probability is suggested by the results of the BL analyses below. BT density is positively related to TRMI, although the magnitude of the posterior mean of  $\alpha_2$  and the wide credible intervals (they almost include 0) show that TRMI is a less important predictor than elevation.

The last part of Table 2 shows the posterior means and credible intervals of the three parameters of the spatial model,  $\sigma_\phi^2$ ,  $d_{\max}$ , and  $\gamma$ . For BT, it is apparent that the conditional variance parameter,  $\sigma_\phi^2$ , is higher for count data than capture–recapture data, which we might expect given that repeated count data contain less information than the full detection histories. The estimates of other parameters differ only slightly across the two models and methods: the parameter  $\gamma$  is consistently estimated to be around 0.995, with relatively tight credible intervals, while  $d_{\max}$ , the neighborhood radius, has posterior means ranging from 0.69 to 0.77 km. For the latter, we are reassured that the posterior distribution does not approach the selected lower bound of 0.5 km: if it had, we would have reevaluated our choice of  $d_L$ . Examination of the MCMC samples showed a significant degree of correlation between posterior values of the three spatial parameters, and it is possible that for this type of data, it is reasonable to simplify the structure of the spatial model.

For the much sparser BL data, we were indeed forced to simplify the spatial model. Convergence of the BL models was much more difficult. Fewer birds were observed, and from our previous experience with fitting models to similar datasets, convergence of MCMC algorithms can be much slower when detection probabilities are relatively low and the number of observation periods at each sampling site is small (recall  $T = 3$  here). More importantly, the generated samples from the posteriors of the three CAR parameters were

Table 2. Posterior means and 95% credible intervals of parameters for modeling of BL data, with  $\gamma = 0.995$  and  $d_{\max}=0.75$ .

Parameter	Count		Capture-Recapture	
	Model 1	Model 2	Model 1	Model 2
$\beta_1$ (Season)	–	–1.5 (–2.3, –0.4)	–	–1.2 (–1.9, –0.2)
$\bar{p}_3$	0.53 (0.49, 0.57)	0.45 (0.41, 0.52)	0.55 (0.52, 0.58)	0.49 (0.44, 0.55)
$\alpha_1$ (Elev)	–0.84 (–1.03, –0.66)	–0.76 (–0.95, –0.58)	–0.84 (–1.03, –0.66)	–0.78 (–0.97, –0.59)
$\alpha_2$ (TRMI)	–0.23 (–0.34, –0.12)	–0.23 (–0.33, –0.12)	–0.23 (–0.34, –0.12)	–0.23 (–0.33, –0.12)
$\sigma_\phi^2$	1.8 (0.9, 2.8)	1.3 (0.7, 2.3)	1.7 (0.9, 2.7)	1.3 (0.7, 2.3)

highly correlated, and for BL there appears to be insufficient information to distinguish the three parameters in the spatial model. Given the convergence difficulties, and that even in the case of BT, the spatial model may be overparameterized, we chose to simplify the model by fixing  $\gamma = 0.995$  in the proper CAR model, similar to the posterior mean values for BT and other species we examined. This is close to an intrinsic CAR model, but setting up an algorithm directly for such a model is more difficult when  $d_{\max}$  is a parameter, as its full conditional density would now depend on the improper joint prior density for the residual vector  $\phi$ . This simplification improved matters in some cases, but even then, there was still strong correlation between the posterior values of  $\sigma_\phi^2$  and  $d_{\max}$ , and for some repeated count models, the algorithms still failed to converge. This led us to make one further simplification, that  $d_{\max} = 0.75$  based on the results for BT and other species. We note that fixing  $d_{\max} = 0.75$  also permitted us to fit these models using the WinBUGS software (Spiegelhalter et al. 2003), as the proper CAR formulation we used for these models required the matrices  $\mathbf{C}$  and  $\mathbf{M}$  (which depend on  $d_{\max}$ ) to be read in as data in WinBUGS (Thomas et al. 2004).

From Table 2, we can see that there is again evidence of a relationship between detection probability and season, but this time the posterior mean of  $\beta_1$  is negative, and thus birds are more difficult to detect in summer. Accounting for this relationship has a small effect on our estimate of  $\alpha_1$ , with lower posterior means for Model 2 than Model 1. TRMI seems to be a more important variable for this species, with a much larger value (in this case negative) for the posterior mean of  $\alpha_2$ . As expected, the estimated mean detection probabilities were lower on average for BL than for BT. There was also a larger decrease in average detection probabilities when we allow for the seasonal effect. Apart from differences in detection probabilities, the posterior values from repeated count and detection history analyses are almost identical. The sparseness of the BL data was such that more than one bird was detected at only 4% of the survey sites, compared with 24% of sites for

BT. Therefore, in the case of BL, the detection history data contain very little information that is not contained in the repeated count data. This would suggest that the differences in detection probabilities (slightly higher for capture–recapture models) are largely due to the different properties of the two estimators, something that may also be a factor in the corresponding differences observed in the BT analyses (Table 1)

We undertook a cross-validation exercise to check the consistency of the models with the observed data. Models were refitted with a random sample of 10% of the observations removed, that is, 175 of the original 1,750 survey sites were treated as if no data were available. The “missing” binomial repeated counts and multinomial capture history counts were predicted using the refitted model, and for each of these 175 survey sites we computed posterior means and 95% prediction intervals of the weighted average of the three counts for repeated count data, and the total number of unique observed birds for capture–recapture data. The MCMC chains for the predicted values converged quickly and behaved well, and we found it sufficient to run 3,000 iterations for computing posterior means and credible intervals. We found that in all cases, fewer than 5% of the prediction intervals failed to include the corresponding observation, and thus there is no evidence that our models are inconsistent with the observed data.

One of the most important goals of fitting spatial models to animal survey data is to produce maps of the population distribution in some region of interest, and for this example, we are interested in mapping bird density across the Great Smoky Mountains National Park. Although our models do not allow us to directly estimate density for these data, the Poisson intensity  $\lambda$  from Equation (2.3) provides an index of relative density, and maps of posterior values of  $\lambda$  will show how animal density varies across the region. Also of interest are maps of the spatially dependent error process,  $\phi$ , which show patterns of spatial variation once we have allowed for covariates in the density model. This can give us insight into other factors that may affect animal distribution, such as covariates that have not already been included in the model.

As examples of the type of maps that can be produced by fitting the models we have presented in our work, we generated prediction maps of bird distribution by fitting detection Model 2 to capture–recapture data for BL. The original 1,750 survey locations were augmented with a regular grid of 3,668 sites spaced 0.75 km apart within the boundaries of the Great Smoky Mountains National Park, and the model was refitted. Values of elevation and TRMI at these prediction locations were extracted from a Geographic Information System (GIS) database.

The first map in Figure 1 shows the posterior medians of the values of  $\lambda$ , providing a map of BL distribution. We used posterior medians here rather than means as posterior distributions of  $\lambda$  were highly skewed. Our map predicts patches of high density mainly along the south, west, and north of the park, with very low densities in the center and eastern regions. The map of posterior means of  $\phi$  (bottom left) shows that after allowing for elevation and TRMI, bird densities are greater mainly in the south and southwest. Identification of these areas of relatively high density may help the biologist to better understand the factors affecting the distribution of this species. It is important when attempting to interpret these maps to consider the adjacent maps of posterior standard deviations (sd). The

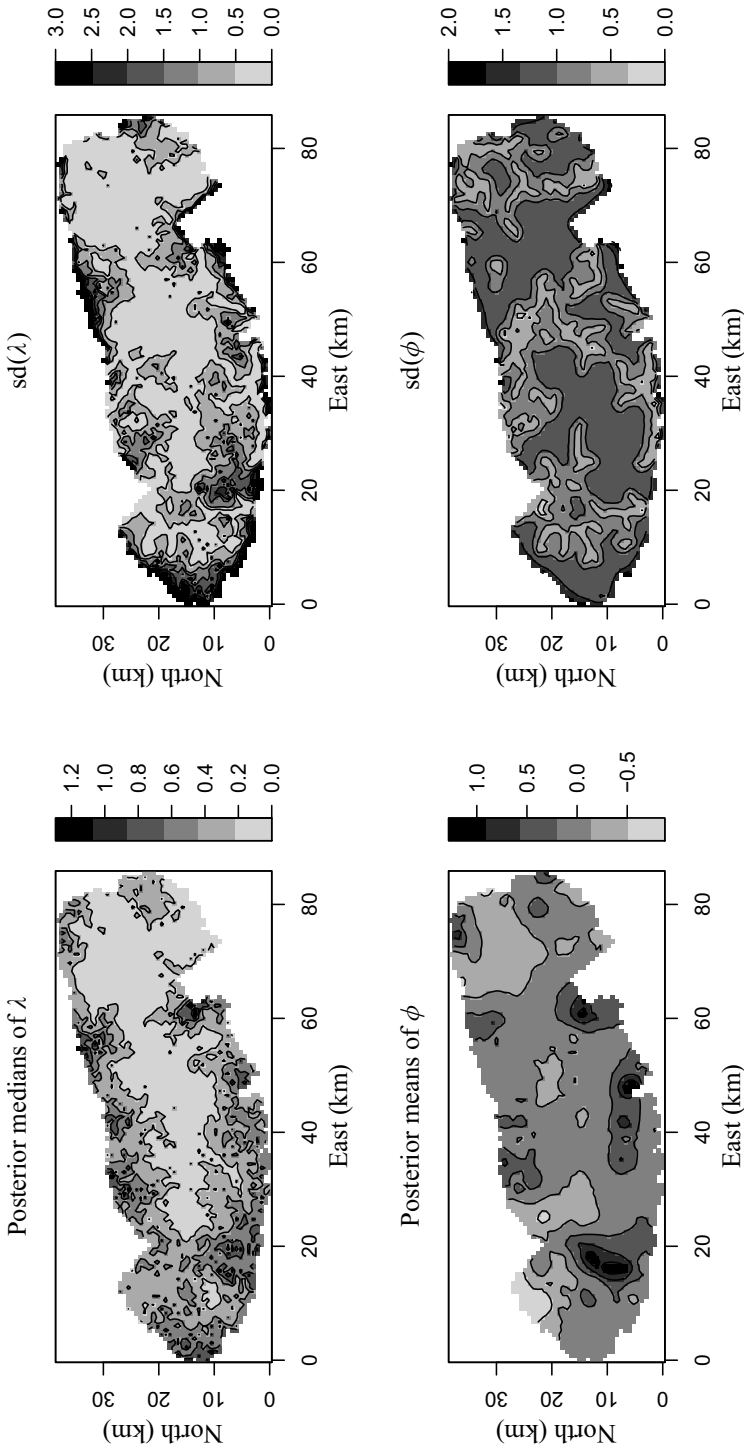


Figure 1. Maps of posterior medians of Poisson intensity,  $\lambda$  and posterior standard deviations (top), and the posterior means of the spatial error process,  $\phi$  with posterior standard deviations (bottom), derived from fitting detection Model 2 to capture-recapture data for the Black and White Warbler (BL).

map of  $\text{sd}(\lambda)$  shows that the regions of highest density are also those of greatest uncertainty in prediction, something we would expect from a lognormal model for  $\lambda$ . Of even more interest in this case is the map of standard deviation of  $\phi$ . The areas where prediction is precise (light shading) show up as a network of lines, which in fact correspond to the trails along which the survey points were located. That is, we only have precise values in the vicinity of the original survey sites, something that has very important implications for survey design.

## 5. DISCUSSION

We have described a framework for spatial modeling of closed-population bird survey data, where the observations come from repeated counts or capture–recapture data recorded at multiple sites within the survey region. The models simultaneously allow for variation in detection probability and for spatial dependence in distribution of birds, and thereby lead to more reliable inference on the causes of variation in bird density across the landscape. When covariates are available at unsurveyed locations, these models will lead to improved mapping of birds species distribution. We have found some evidence that for the Black and White Warbler, the hardest to detect species of those we examined, allowing for heterogeneity in detection probabilities by incorporating covariates in the detection model affects not only the mean detection probability across the survey sites, but also affects the estimates of coefficients in the density component of the model. Although the effect was not strong in our example, we believe that in general it is very important to account for variation in detection probability across a region when attempting to model the relationship between bird density and covariates, or when producing maps of relative density from spatial models. Further, the parameters of the detection model can be of interest in themselves: biologists can use the information on factors that affect detection probability to help design future studies, for example, by planning surveys of certain species when conditions are optimal for detection.

For the Great Smoky Mountains bird survey, the posterior statistics of the covariate parameters fit our previous understanding of the biology of the two warbler species. Both species are found at greatest abundance at lower elevations, consistent with the highly negative posterior means we obtained for the coefficient of elevation. We also expected the significant relationships with habitat, represented in our models by TRMI. The Black-throated Green Warbler is often present in moist, hemlock-lined ravines (Alsop 1991), habitat associated with high values of TRMI (Pinder et al. 1997). This is supported by our finding of a positive relationship between density and TRMI for this species. The Black and White Warbler is more likely to be associated with drier, mixed-deciduous sites supporting more oaks and pines and fewer hemlocks. Such sites would have lower values of TRMI, consistent with our observation of a negative relationship between density and TRMI for BL. Regarding detection probability, the singing rates of breeding birds vary with the stage of the nesting cycle, with generally more singing early in the cycle (McShea and Rap-pole 1997). This led us to expect a difference in mean detection probability between sites surveyed in summer and spring. We observed this for both species, and our results imply

easier detection of BT in summer and of BL in spring. BL is one of the first warblers to arrive in the spring (often by mid to late March), and presumably they start and finish nesting earlier than BT and most other warblers, which can arrive as much as a month later. Therefore, the peak of BL singing during pair formation and nest building occurs earlier for BL than for BT and other warblers.

Allowing for spatial dependence will improve the mapping of bird distribution. If we had simply fitted a covariate model for density and assumed independence of observations, we would have found that our maps largely reflected the relationship with elevation for the two species we considered. Accounting for additional covariates could further improve the mapping, but even without this, modeling spatial dependence has allowed us to identify apparent clusters of birds, along with regions of low density, that would not have been predicted by our covariate models alone.

Our mapping exercise also highlighted the importance of good survey design. The Smoky Mountains survey was conducted mainly along high-use trails, and although many sites were surveyed each year, they tended to be relatively close together. Such site location raises concerns of bias, as our results depend on the assumption that bird density in the vicinity of the trails does not systematically differ from density away from the trails. It also meant that large areas of the park went unsurveyed. The precision of our prediction maps was very much dependent on the design—precision was good only if we were predicting values fairly close to a survey site. We do note, however, that the 1997 data we examined are only part of the more extensive 1992–1999 survey, although significant areas of unsurveyed habitat still exist in the full survey. Although it may be impractical in difficult terrain to locate survey points in every part of the region of interest, ensuring more even coverage is important for good spatial prediction of bird density. A design based on an evenly spaced grid of points, however, may be undesirable, since if spatial dependence between sites exists at distances shorter than the grid spacing, we will fail to detect it. Instead, a clustered design may be most suitable for such surveys, whereby groups of relatively close survey points are distributed throughout the survey region. Ensuring each survey point has at least one near neighbor will also help in choosing a lower bound for  $d_{\max}$  that does not exclude data from the analysis.

In many instances, the bird population is surveyed over a number of years, and we may therefore wish to add a temporal component to the models presented in this work. Banerjee, Carlin, and Gelfand (2004) reviewed extensions of CAR models to allow for temporal effects and for spatio-temporal interactions. They presented examples of both aligned data, when the same survey sites are monitored over time, and misalignment across years, when the sites change over time. The Smoky Mountain survey data, for example, come from some sites that were monitored every year and others that were not.

We also restricted ourselves in this work to single-species modeling. Extending the models to allow for multiple species is also possible, possibly through use of a multivariate conditional autoregressive (MCAR) model (Gelfand and Vounatsou 2003; Banerjee, Carlin, and Gelfand 2004). Modeling the diversity of species can also be fitted into our framework. Instead of counts of the number of individual animals, our data would be based on counts of the number of unique species observed at each survey site, and modeling could

otherwise proceed as before. It may even be possible to combine diversity and abundance modeling in a single model, although the complexity of such a model and the quantity of data that would need to be analyzed will make such an exercise difficult in practice.

There are some important assumptions implicit in our models, some of which are quite questionable given the manner in which bird survey data are gathered. Of particular concern is the high chance of errors being made in detecting and identifying individual birds. In “capture–recapture” bird surveys of the type we have discussed, birds are generally not marked, and the accuracy of the capture histories depends entirely on an observer’s ability to correctly identify and distinguish individual birds over the  $T$  survey periods. This is an extremely difficult task, particularly given that birds are often observed in dense forest and that many species are identified by sound alone (Simons et al. 2007). One might suppose, however, that a repeated count survey would be less prone to error, as an observer needs only to track the individuals within each period in order to produce a count, which should be easier than identifying individuals across all  $T$  periods. Therefore, the lower bias induced by identification errors when using repeated count data may mean that this approach is preferable to attempting to record full detection histories. This is especially true when data are very sparse and any gains in the precision of parameter estimates made by using detection histories can be small, as was the case in our examples. We plan to investigate the effects of data errors on bird survey models in future work. We note, however, that the results of our analyses were very similar for both types of data, implying that for our data the effect of any errors is much the same, regardless of the form of the data being analyzed.

Our models do not allow for heterogeneity in detection probability between birds at the same site on the same survey occasion. In the capture–recapture case, we previously noted the difficulties in trying to fit models accounting for individual heterogeneity (Link 2003), and given that the models we have presented are already complex and the data are fairly sparse, it is unlikely that attempting to fit such models will be worthwhile. However, as one referee noted, heterogeneity will exist due to variation in singing behavior between individual birds. Such heterogeneity could lead to positively biased estimators of detection probability and negative bias in estimators of relative abundance from the capture–recapture models (Pollock et al. 1990). Given that we are dealing with a relative measure of abundance, this might be of concern only if the degree of any biases induced by such heterogeneity varied across space or time due to varying patterns in bird behavior, or if comparisons between the relative abundance of different species was of interest. While this issue is worth further investigation, our feeling is that identification errors will have a more serious effect on inference from our models.

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