

## HIERARCHICAL SPATIAL MODELS OF ABUNDANCE AND OCCURRENCE FROM IMPERFECT SURVEY DATA

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*Abstract.* Many estimation and inference problems arising from large-scale animal surveys are focused on developing an understanding of patterns in abundance or occurrence of a species based on spatially referenced count data. One fundamental challenge, then, is that it is generally not feasible to completely enumerate (“census”) all individuals present in each sample unit. This observation bias may consist of several components, including spatial coverage bias (not all individuals in the population are exposed to sampling) and detection bias (exposed individuals may go undetected). Thus, observations are biased for the state variable (abundance, occupancy) that is the object of inference. Moreover, data are often sparse for most observation locations, requiring consideration of methods for spatially aggregating or otherwise combining sparse data among sample units. The development of methods that unify spatial statistical models with models accommodating non-detection is necessary to resolve important spatial inference problems based on animal survey data.

In this paper, we develop a novel hierarchical spatial model for estimation of abundance and occurrence from survey data wherein detection is imperfect. Our application is focused on spatial inference problems in the Swiss Survey of Common Breeding Birds. The observation model for the survey data is specified conditional on the unknown quadrat population size,  $N(s)$ . We augment the observation model with a spatial process model for  $N(s)$ , describing the spatial variation in abundance of the species. The model includes explicit sources of variation in habitat structure (forest, elevation) and latent variation in the form of a correlated spatial process. This provides a model-based framework for combining the spatially referenced samples while at the same time yielding a unified treatment of estimation problems involving both abundance and occurrence.

We provide a Bayesian framework for analysis and prediction based on the integrated likelihood, and we use the model to obtain estimates of abundance and occurrence maps for the European Jay (*Garrulus glandarius*), a widespread, elusive, forest bird. The naive national abundance estimate ignoring imperfect detection and incomplete quadrat coverage was 77 766 territories. Accounting for imperfect detection added approximately 18 000 territories, and adjusting for coverage bias added another 131 000 territories to yield a fully corrected estimate of the national total of about 227 000 territories. This is approximately three times as high as previous estimates that assume every territory is detected in each quadrat.

*Key words:* animal abundance; Bayesian analysis; detection probability; hierarchical models; monitoring data; occurrence probability; spatial coverage bias; spatial modeling.

### INTRODUCTION

Understanding spatial and temporal patterns of animal distribution and abundance is fundamental to much of ecological science, and is critical for the conservation and management of many species. Most field investigations of distribution and spatial patterns in abundance are based on survey data that are counts of animals over many relatively small sample units. For example, in avian studies, sample networks often consist of a large number of point count locations, routes, or areal units (e.g., the North American [Robbins et al. 1986], Swiss [Schmid et al. 2004], and British Breeding

Bird Surveys [Newson et al. 2005]), or networks of mist net stations (e.g., the Monitoring Avian Productivity and Survival [MAPS] Program [DeSante et al. 1995]). Aerial transect surveys, for example of marine mammals (Garner et al. 1999, Buckland et al. 2001) or waterfowl (Smith 1995), are another common method of animal sampling that yield spatially indexed counts. Using data from such surveys, interest is frequently focused on objectives that are relevant to the spatial organization of sample units. Examples include (1) relating abundance to landscape or habitat structure so that, for example, the effect of changes in land use practices may be assessed; (2) estimating the range of a species, or mapping occurrence probability; or (3) estimating abundance maps that depict spatial variation in abundance and, when aggregated over geographic

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regions, allow for estimates of actual (e.g., regional, national) population sizes to be obtained.

Because spatial replication is a prevalent feature of the data in many ecological studies and inferential problems are inherently spatial, the adoption of spatial statistical methods to facilitate inference is critically important. Recent years have seen explosive growth of statistical methods aimed at developing spatial and spatiotemporal models of count data, such as those arising from animal surveys. These approaches are based on the view that the counts derive from an inhomogeneous Poisson process, and focus on developing spatial models of the Poisson intensity. For example, log-Gaussian Cox process models (Diggle et al. 1998, Brix and Diggle 2001, Brix and Møller 2001, Wikle 2003) and Poisson-gamma random field models (Wolpert and Ickstadt 1998, Best et al. 2000) have been adopted in many application areas, including epidemiology, demographic and health surveys, and environmental assessment. Such models would seem to provide an ideal framework for conducting spatial inference about animal abundance and occurrence for animal surveys that yield abundance information.

Unfortunately, in virtually all animal sampling problems, these statistical procedures cannot be used directly because one cannot observe the abundance or occupancy state variables directly. Indeed, one of the most important considerations in animal sampling is that of imperfect detection and there exists a tremendous volume of literature describing formal procedures for estimating abundance and other demographic parameters in the context of imperfect detection (e.g., Seber 1982, 1986, Pollock 2000, Buckland et al. 2001, Williams et al. 2002, MacKenzie et al. 2006). Common approaches include distance sampling, "capture-recapture" methods based on capture or encounter data, and a myriad of related techniques based on sampling with multiple observers, or sequential "removal" of individuals. The majority of these varied sampling protocols yield multinomial data with index  $N$  (population size) and cell probabilities that are functions of various parameters that describe the detection process. In the context of spatial sampling, the multinomial sample counts,  $\mathbf{x}(s)$  for location  $s$ , are spatially indexed, with "local abundance," say  $N(s)$ , the number of animals available to be sampled at location  $s$ .

Formally accounting for detectability is important because observed counts are biased by imperfect detection. Factors which influence detectability may vary among sample locations or through time and may not have been measured or even recognized. Similarly, accounting for imperfect detection is essential when making inference about occurrence because observed zeros do not necessarily equate to absence. Despite the importance of bias induced by sampling, the issue of detectability is almost never considered explicitly in the vast majority of studies of spatial variation in abundance or occurrence (e.g., Gibbons et al. 1993, Lichstein

et al. 2002, Scott et al. 2002, Wikle 2003, Thogmartin et al. 2004, Guisan and Thuiller 2005, Araujo and Rahbek 2006, Elith et al. 2006, Thogmartin et al. 2006). Sometimes this may be an oversight, while sometimes, especially at very large spatial (e.g., continental) scales (e.g., Jetz and Rahbek 2002), it may rather be because data have not been collected in a manner that yields direct information about the detection process. The result is that spatial or other models can be difficult to interpret as they are not models of abundance or occurrence per se, but rather of some aggregate index that includes both variation in detection probability and in abundance. Therefore, such indices are frequently interpreted as describing "relative abundance" or "relative occurrence," supposed, hoped, or at least asserted to be proportional to abundance or occurrence, respectively. However, since this is virtually never tested, resulting models, at worst, describe patterns in the difficulty with which organisms are detected rather than real patterns in their abundance and occurrence. Thus, statistical methods which seek to address spatial inference problems on abundance and occurrence must seek to unify these two important elements of animal sampling: spatial sampling and imperfect detection. Recent applications of spatial models which do address the problem of imperfect detection to some extent include Doherty et al. (2003), who model detection-bias-adjusted estimates in a two-stage procedure, and Hooten et al. (2007) who develop information about detectability from independent data.

In this paper, motivated by spatial inference problems in the Swiss Survey of Common Breeding Birds (Monitoring Häufige Brutvögel [MHB]; Schmid et al. 2004) described in the next section, we develop a novel modeling framework of animal abundance from spatially referenced survey data collected in a manner that allows for explicit consideration of detection probability. Specifically, using the European Jay, a widespread but elusive forest bird as case study, we consider data resulting from repeated sampling that yields territory encounter history data. We specify a hierarchical model that consists of the multinomial sampling distribution for the data, and this is augmented by a spatial model describing variation in the abundance of territories. This yields a rigorous and generic modeling strategy for integrating spatially referenced survey data and addressing spatial inference problems such as mapping abundance and occurrence and assessing the effects of landscape or habitat structure on abundance and occurrence. We use this model to address several spatial inference problems such as estimation of national abundance and occurrence maps and national abundance of the jay in Switzerland. Although we are fortunate to have encounter history data available in our application, many other sampling protocols yield multinomial data and so the basic model structure is easily translated to many other spatial animal sampling problems (see *Discussion*).

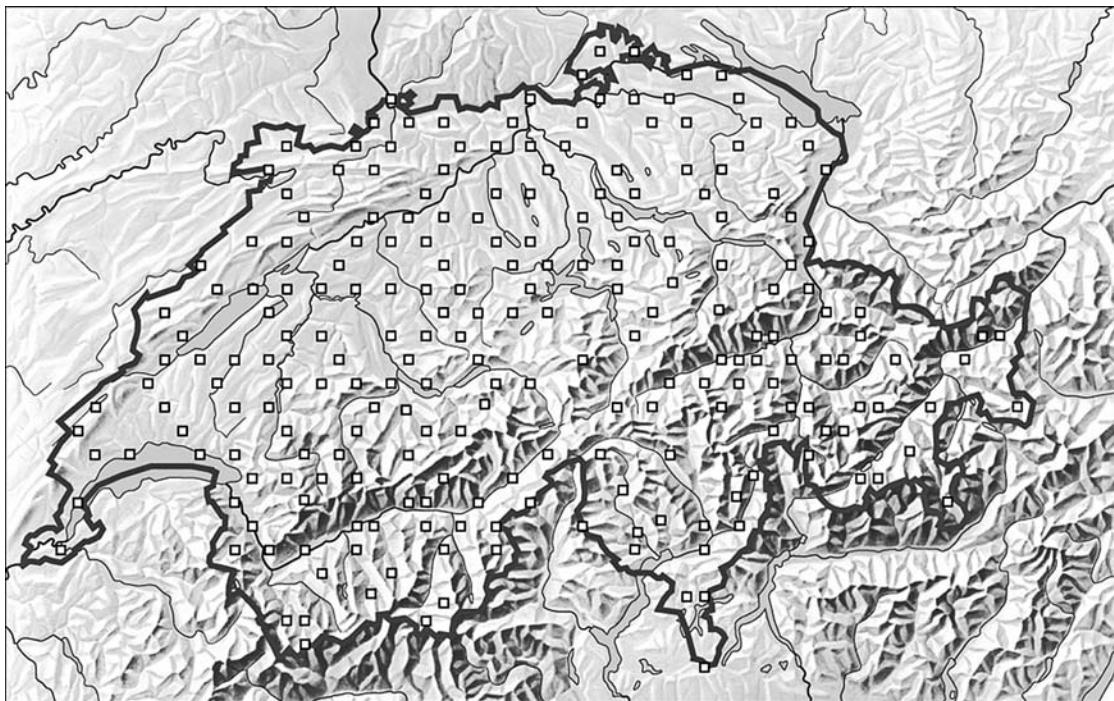


FIG. 1. Locations of 238 1-km<sup>2</sup> quadrats surveyed in 2002 in the Swiss Survey of Common Breeding Birds.

#### EXAMPLE OF A LARGE-SCALE SURVEY: THE SWISS SURVEY OF COMMON BREEDING BIRDS

Data for our study are from the Swiss Survey of Common Breeding Birds (Monitoring Häufige Brutvögel) conducted annually by the Swiss Ornithological Institute (Schmid et al. 2004). Our spatial sample contains 238 1-km<sup>2</sup> quadrats selected according to a systematic sample as a grid from among 41 365 possible quadrats in Switzerland (Fig. 1). Since 1999, quadrats are surveyed three times (twice for quadrats that lie mostly above the timberline at around 2000 m elevation) during the breeding season (15 April–15 July) by an experienced observer using the territory mapping method (Bibby et al. 1992). Each quadrat is surveyed along a quadrat-specific, irregular transect route that aims to cover as much as possible of the quadrat area and that averages 5.1 km in length (range 1.2–9.4). Transect location is not chosen at random but partly in response to habitat or other features, e.g., open water and excessively steep areas in the mountains are avoided. Mean survey duration is about 230 min (range 60–427 min) which translates into 48 min on average (range 15–167 min) spent per kilometer of transect length on each survey (Kéry and Schmid 2006). Repeated surveys in individual quadrats are typically spaced one month only apart, therefore we assume a closed population of territories for the (sedentary) species considered here. During each survey, observers mark every visual or acoustic contact with an individual of a potential breeding species on a map and note additional information such as sex, behavior, territorial

conflicts, location of pairs, or simultaneous observations of individuals from different territories. By overlaying these survey maps, putative territories are determined based on the knowledge of average territory size, clustering of observations, as well as on behavioral information such as territorial conflicts or simultaneous observations. As is customary for this method, the numbers of territories are often equated with the number breeding pairs.

In the present study, we used the maps from all quadrats surveyed in 2002 and derived “encounter histories” for individual territories by determining if a putative territory was or was not detected during a visit. Encounter histories consist of a string of three digits, such as “110,” which indicates that a particular, putative territory was detected on the first two, but not on the third survey. We assume, along with the various model assumptions described elsewhere in this paper, that each territory is recognized (but not necessarily detected) without error. Thus, for example, if encounter histories “110” and “001” are recorded in a quadrat, we assert that these represent two unique territories, and not an incorrect labeling of a single territory. The adequacy of this important assumption of correct territory recognition or labeling should be considered for each application of our model (see relevant discussion in *Application to the Swiss Survey of Common Breeding Birds Data: The Eurasian Jay* and *Discussion: Closure, territory identification, and parametric model assumptions*). The goals of our application are to produce abundance and occurrence maps and to generate estimates of total abundance



FIG. 2. Elevation (km) on a 1-km<sup>2</sup> grid in Switzerland.

where abundance is defined in terms of the number or density of territories. These goals involve prediction (e.g., of abundance) on all 41 365 quadrats in Switzerland.

We view the population of territories susceptible to sampling during the breeding season in a given year as being “closed” to demographic processes of recruitment and mortality. While this assumption and the perfect territory recognition assumption may be difficult to meet for some species and some sampling designs, for our species here and the Swiss bird data, we believe that both are adequate (see *Discussion*). We focus on the problem of developing a spatially explicit model for bird abundance (i.e., territories) across Switzerland while accommodating important sources of variation that affect detection probability and abundance. For example, the elevational gradient in Switzerland is severe (Fig. 2) and should be an important determinant of the abundance of most species. We also consider the distribution of forest cover (Fig. 3) as another likely factor influencing the abundance of a forest species like the jay. Data on elevation and forest cover were taken from databases of the Swiss federal statistical office.

#### THE MODEL

##### *Multinomial sampling distributions*

The data resulting from capture–recapture studies on a closed population are encounter (or capture) history frequencies,  $x_h$  for encounter history  $h$ , a possible sequence of encounter events. For sampling that occurs on  $T$  occasions, there are  $2^T$  possible encounter histories

(including that corresponding to “not encountered”). For example, in the Swiss Survey of Common Breeding Birds,  $T = 3$ , and all possible encounter histories are shown in Table 1 where  $x_0$  is the unobservable encounter history, and only  $\{x_h; h > 0\}$  are observable; the objective is to estimate the frequency  $x_0$ , the number of territories not occurring in the sample, or, equivalently, the population size  $N = \sum_h x_h$ . Hereafter, we adopt the conventional “bracket-notation” to refer to probability distributions. The distribution of the observed encounter history frequencies is multinomial, having probability mass function (pmf):

$$[\mathbf{x}|N, \boldsymbol{\pi}] \propto \frac{N!}{(N - x.)!} \left( \prod_{h=1}^7 \pi_h^{x_h} \right) (1 - \pi.)^{N - x.} \quad (1)$$

where  $x.$  is the number of unique territories observed (the sum of the observed encounter history frequencies) and  $\pi. = \sum_{h=1}^7 \pi_h$  is the net probability of encountering a territory in at least one of the  $T$  samples. The probability of not detecting a territory (at all) is  $\pi_0 = (1 - \pi.)$ . The cell probabilities  $\{\pi_h\}$  are probabilities of observing each encounter history,  $h$ , and are functions of various nuisance parameters that describe the detection process. For example, under a model where detection probability varies for each sample occasion,  $\pi_1 = \Pr(h = \text{“100”}) = p_1(1 - p_2)(1 - p_3)$  where  $p_t$  is the probability of encountering a territory in period  $t$ . The dependence of  $\mathbf{x}$  on detection probability parameters  $\mathbf{p} = (p_1, p_2, p_3)$  (via  $\pi_h$  in Eq. 1) will be indicated as  $[\mathbf{x}|N, \boldsymbol{\pi}(\mathbf{p})]$ , or just  $[\mathbf{x}|N, \mathbf{p}]$ . Many alternative (to capture–recapture)



FIG. 3. Forest cover (percentage of area) on 1-km<sup>2</sup> quadrats in Switzerland.

sampling protocols yield a likelihood that only differs from Eq. 1 by the manner in which the multinomial cell probabilities are parameterized (see *Discussion*).

*The likelihood under spatial replication*

Let  $\{s_i\}_{i=1}^R$  denote the locations of the  $i = 1, 2, \dots, R$  sample quadrats and let  $N_i \equiv N(s_i)$  be the unknown “local population” size of quadrat  $i$  and let  $\mathbf{x}_i = \{x_{ih}; h > 0\}$  denote the vector of observable capture history frequencies. The number of unique territories observed for quadrat  $i$  is  $x_i = N_i - \sum_{h=1}^7 x_{ih}$ . For convenience we will reference attributes of the spatial samples by the integer index  $i$  instead of by their locations  $s_i$ , except where necessary to avoid confusion.

The contribution to the joint likelihood of the data from quadrat  $i$  is

$$[\mathbf{x}_i | N_i, \boldsymbol{\pi}(\mathbf{p}_i)] \propto \frac{N_i!}{(N_i - x_i)!} \left[ \prod_{h>0} \pi_h(\mathbf{p}_i)^{x_{ih}} \right] \pi_0(\mathbf{p}_i)^{x_i}. \quad (2)$$

We suppose that, when conditioned on  $N_i$  and parameters of the cell probabilities  $\pi_h$ , the data are independent across quadrats so that the joint likelihood based on data from all  $R$  quadrats is

$$[\mathbf{x}_1, \mathbf{x}_2, \dots, \mathbf{x}_R | (N_i)_{i=1}^R, (\mathbf{p}_i)_{i=1}^R] \propto \prod_{i=1}^R \left\{ \frac{N_i!}{(N_i - x_i)!} \left[ \prod_h \pi_h(\mathbf{p}_i)^{x_{ih}} \right] \pi_0(\mathbf{p}_i)^{x_i} \right\}. \quad (3)$$

It will not generally be feasible to estimate the collection of abundance parameters  $\{N_i\}_{i=1}^R$  as distinct

parameters primarily because for most species the  $N_i$  are small owing to small sampled area, and low densities of many territorial birds. Consequently, the sample size (number of territories observed) at each site will also be small (often even 0) and there will be little point in attempting to obtain MLEs of the collection of local abundance and detection probability parameters. Our solution, providing practical motivation for considering spatial models on abundance, is to view the  $N_i$  parameters as latent variables, for which we can specify sensible spatial models based on considerations for the distribution of organisms in space. This is the topic of *Spatial models of abundance*. Note that the independence assumption represented by Eq. 3 is one of conditional (on  $N$ ) independence. We would typically expect the observed counts,  $\mathbf{x}_i$  to be spatially dependent for a variety of reasons. Subsequently, we introduce spatial correlation in the observed counts indirectly, by

TABLE 1. All possible encounter histories for the Swiss Survey of Common Breeding Birds with three sampling occasions.

Frequency	$t = 1$	$t = 2$	$t = 3$
$x_0$	0	0	0
$x_1$	1	0	0
$x_2$	0	1	0
$x_3$	0	0	1
$x_4$	1	1	0
$x_5$	1	0	1
$x_6$	0	1	1
$x_7$	1	1	1

parameterization of dependence on the unobserved abundance parameters,  $N_i$ .

#### Detection probability models

Note that  $\mathbf{p}_i$  have been described as spatially explicit here. We will now parameterize spatial variation in detection probability as a function of measurable covariates at each site, and possibly varying over the course of the breeding season (Kéry et al. 2005). For example, the sites may have been surveyed on different days and with varying effort, as is the case in our analysis of the Swiss bird survey data (see *Application to the Swiss Survey of Common Breeding Birds Data*). We will model such effects using a typical logistic regression formulation in which the probability of detection at site  $i$  and occasion  $t$  is  $p_{it}$ , and then

$$\text{logit}(p_{it}) = \mathbf{f}'_{it}\boldsymbol{\alpha} \quad (4)$$

where  $\text{logit}(p) = \log(p/(1-p))$  is the logit transformation,  $\mathbf{f}'_{it}$  is a vector of measured covariates at  $i$  and  $t$ . The dependence of the multinomial cell probabilities in Eq. 3 on  $\boldsymbol{\alpha}$  via Eq. 4 will be expressed as  $\pi_{it}(\boldsymbol{\alpha})$ .

#### Spatial models of abundance

A natural ecological framework for characterizing spatially referenced data and motivating the construction of spatially explicit models of abundance can be achieved by regarding the collection of sample locations as a snapshot in time of a metapopulation (Levins 1969, Hanski 1999). In the classical sense, a metapopulation consists of spatially referenced sub-populations that interact through time. Here we consider that this metapopulation has been sampled over a sufficiently short interval so that the local population structure is not affected by such interactions. Thus, for our practical purposes here, in the most fundamental sense, a metapopulation is simply “a population of (local) populations indexed by space”; i.e., a collection of spatially referenced populations. Note that, at least for our application, the spatial indexing of sample units yields a metapopulation by design rather than from its biology, which we have also employed in similar applications (Royle 2004a, b, Dorazio et al. 2005, Kéry et al. 2005). Also note that use of the present version of our model is limited to short periods within which the abundance and location of territories is static, i.e., to single season data.

It is natural to provide a probabilistic characterization of the metapopulation, by imposing a probability distribution on local population size  $N_i$ , say  $g(N; \theta)$ . The specification of such models facilitates a general description of patch occupancy: the event that patch  $i$  is occupied is equivalent to the event that  $N_i > 0$ , and patch occupancy is the metapopulation average  $\Pr_g(N > 0; \theta)$ . Thus, specification of a model for local abundance automatically yields a model of occurrence and inferences concerning both characteristics may be achieved within the same abundance modeling framework. In

addition, this metapopulation structure is, in essence, a prior distribution for the unobserved parameters  $\{N_i; i = 1, 2, \dots, R\}$ . This additional model structure provides the framework for combining a large number of spatially referenced count surveys, such as is the case in our motivating Swiss breeding bird survey.

An equivalent solution to managing the high-dimensional abundance parameter is to view  $\{N_i; i = 1, 2, \dots, R\}$  as a collection of latent variables: in effect, nuisance parameters to be removed from the likelihood by integration. Because this abundance process is related to the distribution of organisms in space, natural models can be imposed that may be sensibly interpreted in the context of most spatial animal sampling problems. For example, we might consider the obvious null model in which animals distribute themselves according to a homogeneous Poisson process so that, when aggregated into units of equal sized (i.e., 1 km<sup>2</sup> quadrats), we have that  $N_i \sim \text{Poisson}(\lambda)$  where  $\lambda$  is the expected number of territories per quadrat.

Of course,  $\lambda$  need not be constant and the extension to an inhomogeneous point process underling the distribution of animals is straightforward. In the case of the Swiss bird data, we have a number of landscape covariates thought to influence abundance and so we consider models of the form  $N_i \sim \text{Poisson}(\lambda_i)$  with

$$\log(\lambda_i) = \mathbf{m}'_i\boldsymbol{\beta} \quad (5)$$

where  $\mathbf{m}_i$  are measured covariates for quadrat  $i$  and  $\boldsymbol{\beta}$  is the parameter to be estimated.

Over small areas, it may be sufficient to consider the case where the spatial dependence in  $\lambda_i$  is only a function of measured spatial covariates. However, when the data are collected over large regions the possibility of latent spatial variation beyond that accounted for by covariates should be considered because it is unlikely that the mean structure given by Eq. 5 will be correctly specified. This generalization forms the basis of many models for spatially referenced counts (e.g., Moller et al. 1998, Wolpert and Ickstadt 1998, Best et al. 2000, Wikle 2003, Thogmartin et al. 2004).

*Models of latent spatial variation.*—One approach to accommodating spatial structure in models of count data is to embed a Gaussian random field model into Eq. 5 and we adopt that general strategy here. In the case where the data are counts derived from an inhomogeneous Poisson process, such models are often referred to as log-Gaussian Cox processes (Moller et al. 1998, Brix and Diggle 2001, Brix and Moller 2001). In the present case, the log-Gaussian Cox process governs the unobserved latent abundance parameters, providing the framework both for combining these spatially referenced data sets, and also facilitating the spatial inference problems of interest.

To parameterize spatial variation in mean abundance, define  $u(s) \equiv \log(\lambda(s))$  for some quadrat located (i.e., centered) at  $s$  and suppose that:

$$u(s) = \mathbf{m}(s)' \boldsymbol{\beta} + z(s) + \varepsilon(s) \tag{6}$$

where  $\varepsilon(s)$  is Gaussian noise with mean 0 and variance  $\sigma_\varepsilon^2$ , and  $z(s)$  is a latent Gaussian spatial process defined on the coordinate system indexed by  $s$ . In the present case,  $s$  is discrete, being the possible quadrat centers of the 41 365 1-km<sup>2</sup> nonoverlapping quadrats from which the MHB sample was drawn. Following our previously established notation, we index the coordinates of the sampled quadrats as  $s_i$ ;  $i = 1, 2, \dots, 238$ . The collection of random effects  $z(s_i)$ ;  $i = 1, 2, \dots, 238$  are surrogates for unmodeled spatial variation [i.e., not due to the fixed effects in (5)] while the uncorrelated noise term in Eq. 6 allows for unstructured site-specific effects beyond the variation provided for by the Poisson assumption.

The model in Eq. 6 is analogous to the “measurement error” model in classical geostatistics (Cressie 1991:112–113) and, as a prior for the log-mean of a Poisson distribution, is the Poisson-lognormal model (Banerjee et al. 2004:162–165) which is now in widespread use in many applied disciplines. Estimation and prediction under this model was first formalized by Diggle et al. (1998; see also Moller et al. 1998). Adopting the geostatistical “generalized linear prediction” formulation (Diggle et al. 1998),  $z(s)$  is a spatially correlated Gaussian process with correlation function  $k_\theta(\|s - s'\|)$  where  $\|s - s'\|$  is the distance (km) between quadrat centers and  $\theta$  is the unknown parameter to be estimated. We consider the exponential correlation model defined as  $k_\theta(\|s - s'\|) = e^{-\|s - s'\|/\theta}$ . Thus, the collection of spatial effects at the sample locations,  $\mathbf{z} = (z(s_1), z(s_2), \dots, z(s_{238}))$ , is multivariate Gaussian:

$$\mathbf{z} \sim \text{Gau}[0, \sigma_z^2 \boldsymbol{\Sigma}_0]$$

where

$$\boldsymbol{\Sigma}_0[i, j] = e^{-\|s_i - s_j\|/\theta}$$

Under this model, the variance components are poorly identified when priors are too diffuse (some relevant discussion of this can be found in Banerjee et al. [2004:164–165]). However, we prefer this formulation for two reasons. First, it appears more meaningful in terms of accommodating excess-Poisson variation when  $N(s)$  is viewed conditionally on the latent process  $z(s)$  (consistent with the manner in which we would interpret maps of abundance or occurrence). Consider that  $z(s)$  can be thought of as a latent covariate that describes variation in abundance across the landscape. Under the model without  $\varepsilon(s)$ , abundance at quadrats with the same  $z(s)$  is Poisson whereas, in the model containing the noise term, the marginal distribution of  $N(s)$  is over-dispersed relative to the Poisson. We would certainly expect demographic processes operating at very local scales to induce such over-dispersion, even though we may not be able to identify causal factors explicitly. Thus, while the variance components would not be identifiable in a frequentist sense (i.e., under flat priors), we believe that this does not imply a lack of

interpretability of the model. A second, practical, advantage to having the small-scale variance component is that it yields a simpler implementation of the MCMC algorithm for estimation and prediction (see Appendix A). If the interpretability of over-dispersion was in question, one could still achieve this benefit by setting  $\sigma_\varepsilon$  to be arbitrarily small.

For purposes of analysis by Markov chain Monte Carlo (MCMC), we reparameterized the model so that covariates thought to influence abundance were parameterized in the mean of  $z(s)$ , i.e.,  $E[\mathbf{z}] = \mathbf{M}\boldsymbol{\beta}$ . This hierarchical centering (Gelfand et al. 1995) yields a Markov chain with better mixing. Thus, the logarithm of the Poisson intensities are independent normal

$$u_i \equiv \log(\lambda_i) | z(s_i) \sim \text{Gau}[z(s_i), \sigma_\varepsilon^2] \tag{7}$$

for  $i = 1, 2, \dots, 238$  or, for the vector of log intensities,  $\mathbf{u} | \mathbf{z}, \sigma_\varepsilon^2 \sim \text{Gau}(\mathbf{z}, \sigma_\varepsilon^2 \mathbf{I})$  and, as before

$$\mathbf{z} | \boldsymbol{\beta}, \theta \sim \text{Gau}[\mathbf{M}\boldsymbol{\beta}, \sigma_z^2 \boldsymbol{\Sigma}_0].$$

*Modeling spatial coverage bias.*—An important feature of the Swiss Survey of Common Breeding Birds is that, partly owing to the topographically challenging terrain, sample plots were not exhaustively sampled. Instead, each observer traverses a quadrat-specific sample route through the quadrat (mean length = 5.12 km, minimum = 1.2 km, maximum = 9.4 km), with routes being consistent among surveys of the same quadrat. Our view is that route length affects the number of birds exposed to sampling; i.e., it is a surrogate for sample area. Consequently, one might include it as an additive offset in a model for  $\log(\lambda)$ . However, more likely there is perhaps a diminishing returns; as the route length increases the path tends to meander throughout the quadrat yielding some degree of redundant sampling. We therefore considered the following parameterization for the effect of route length:

$$\log(\lambda_i) = \beta_0 + \beta_1 \left( \frac{1}{\text{Length}_i} \right). \tag{8}$$

For  $\beta_1 < 0$ ,  $\lambda_i$  is an increasing function of sample route length,  $\text{Length}_i$ . In making predictions (e.g., at unsampled quadrats), we omit the  $\text{Length}_i$  term in Eq. 8 because  $\exp(\beta_0)$  is the density of the quadrat under exhaustive sampling (i.e., as  $\text{Length}_i \rightarrow \infty$ ), which we will refer to as “saturation density.”

We provide more discussion of this issue of spatial coverage bias, and parameterization of its effect, in Appendix B.

#### BAYESIAN ANALYSIS BY MARKOV CHAIN MONTE CARLO

Because the model contains latent structure in the form of a spatially indexed (and correlated) random effect, we adopt a procedure for fitting the model and prediction based on MCMC. The spatial effects pose some difficulty in attempting to numerically integrate the likelihood (as noted also by Diggle et al. 1998). To deal with these spatial

TABLE 2. Detection history frequencies for the Eurasian Jay (*Garrulus glandarius*) on 10 sample quadrats.

Quadrat	100	010	001	110	101	011	111
1	1	0	0	0	0	0	0
2	0	0	1	0	0	0	0
3	0	2	0	0	0	0	0
4	1	0	0	0	0	0	0
5	1	0	0	0	0	0	0
6	1	0	0	2	0	1	0
7	0	0	0	0	0	0	0
8	0	0	0	1	1	0	0
9	2	0	0	0	0	0	0
10	1	1	3	2	2	4	0

Note: Encounter histories consist of a string of three digits, such as “110,” which indicates that a particular, putative territory was detected on the first two surveys, but not on the third survey.

effects, we devised an MCMC algorithm for obtaining posterior samples of the model parameters. The algorithm was developed in the free software package R (Ihaka and Gentleman 1996, R Development Core Team 2005) using conventional methods based on the Metropolis-Hastings algorithm and Gibbs sampling, yielding a hybrid algorithm referred to generically as Metropolized Gibbs sampling (Robert and Casella 1999: section 7.3). Because the structure of the algorithm is fairly conventional, we avoid a detailed description of each component of the algorithm. Some details are given in Appendix A (see also Diggle et al. 1998). We believe that similar models could now be fitted conveniently using the freely available software WinBUGS.

To fully specify the model, we require prior distributions for the model parameters. We adopted priors that are customarily viewed as expressing little prior information about model parameters. We assumed constant priors for the parameters governing detection probability,  $[\alpha] \propto 1$ , and similarly for the parameters governing the abundance covariates  $[\beta] \propto 1$ . In addition, we have the variance components and correlation parameter  $\theta$ . Under the formulation of the model described in the previous section, the variance components are poorly identified and so prior distributions cannot be arbitrarily vague (Banerjee et al. 2004:164). Thus, for the variance components, we assumed the customary gamma priors for the precision parameters  $1/\sigma_z^2$  and  $1/\sigma_\epsilon^2$ , both having parameters shape = 0.1 and scale = 10, using the shape-scale parameterization of the gamma distribution in R. This yields a “u-shaped” prior with mass concentrated near 0 and 1, having expected value for the “signal to noise ratio” of 0.5, an ostensibly “fair” prior outcome (Banerjee et al. 2004:165). For the prior distribution for the correlation parameter  $\theta$ , we used the reference prior for Gaussian random field model suggested by Berger et al. (2001), but with the support of  $\log(\theta)$  discretized on a regular grid for reasons of computational efficiency. Additional details on estimation and prediction are contained in Appendix A.

Each iteration of the MCMC algorithm proceeds by sequentially drawing samples of the log-intensity pa-

rameters,  $\log(\lambda(s_i))$ , the vector of spatial effects  $\mathbf{z}$ , and remaining structural parameters ( $\alpha$ ,  $\beta$ ,  $\sigma_\epsilon^2$ ,  $\sigma_z^2$ ,  $\theta$ ) from their conditional posterior distributions. Operationally, the Poisson log-intensities  $u(s_i) \equiv \log(\lambda(s_i))$  (i.e., for sampled quadrat  $i$ ) are updated using a Metropolis-Hastings step (based on the integrated likelihood, see Appendix A). Given  $\mathbf{u} = \{u(s_i)\}_{i=1}^R$ , the vector  $\mathbf{z}$  is updated by drawing a sample from a multivariate normal distribution using the Cholesky factorization method. Then,  $\beta$  can be updated as a draw from a low-dimensional multivariate normal distribution. The detection probability parameters,  $\alpha$  are sampled by Metropolis-Hastings, and the variance components from conjugate inverse-gamma distributions. Finally, the logarithm of the correlation parameter ( $\theta$ ) is sampled using a Metropolis step, with candidate values generated by perturbing the current value of  $\log(\theta)$ . These steps are repeated a large number of times after a suitably long burn-in period required to ensure that sampling from the target posterior distribution is achieved.

#### APPLICATION TO THE SWISS SURVEY OF COMMON BREEDING BIRDS DATA

##### *The Eurasian Jay*

The Eurasian Jay (*Garrulus glandarius*), a small crow, is a medium-sized (140–190 g), widespread, typical, forest bird in Switzerland. It occurs up to the tree limit at about 2000–2200 m. According to results from the last Swiss breeding bird Atlas project (Schmid et al. 1998), highest observed density (without correction for imperfect detectability) is about 3 pairs/km<sup>2</sup> and occurs at around 800–1100 m elevation. Density declines somewhat below that and, above 1100 m, declines to zero at about 2200 m. The jay is recognized as a species whose elusive behavior and difficult habitat during the breeding season make abundance assessment particularly difficult (Schmid et al. 1998). Table 2 contains the example of the territory encounter history frequencies for 10 quadrats. We note the sparsity of the data largely motivates the need for a model-based means of integrating the information from among many sample quadrats.

We chose the jay in this case study for biological and for technical reasons. The jay is a representative of many other forest species, for which imperfect detectability is of particular concern in assessments of abundance. Furthermore, the jay did not challenge crucial assumptions of our model. It is sedentary in Switzerland and the distribution and number of territories can be assumed to be constant and static during the surveys. In addition, its density is not so great as to make individual territory recognition a challenge.

##### *Models of abundance and detection*

The encounter history frequencies for quadrat  $i$  are assumed to have a multinomial distribution (Eq. 2) with index  $N_i$  and cell probabilities  $\{\pi_{ih}\}_{h=0}^7$ . The latter are parameterized in terms of site-specific detection probabilities  $\{p_{ih}\}_{i=1}^3$  with covariate effects modeled according

TABLE 3. Posterior summaries of model parameters.

Parameters	Mean	Median	SD	$q_{0.025}$	$q_{0.975}$
<b>Detection</b>					
$\alpha_0$ (intercept)	-0.545	-0.544	0.087	-0.718	-0.373
Date (linear)	-0.087	-0.087	0.042	-0.169	-0.003
Date (quadratic)	0.041	0.041	0.023	-0.005	0.086
Rate	-0.170	-0.170	0.079	-0.322	-0.016
<b>Abundance</b>					
$\beta_0$ (intercept)	1.693	1.693	0.318	1.066	2.313
Elevation (linear)	-1.168	-1.164	0.166	-1.502	-0.853
Elevation (quadratic)	-1.320	-1.321	0.307	-1.922	-0.720
Forest cover	0.401	0.400	0.068	0.270	0.537
Route length	-4.239	-4.218	1.326	-6.874	-1.677
$\lambda_0$	5.719	5.433	1.866	2.905	10.104
$\sigma_e$	0.286	0.279	0.080	0.152	0.454
$\sigma_z$	0.340	0.333	0.097	0.177	0.540
$\log(\theta)$	2.512	2.530	0.949	0.668	4.678

Note: For abundance,  $\beta_0$  is the saturation density parameter on the log scale,  $\lambda_0$  is the saturation density on the arithmetic scale,  $\sigma_e$  is unstructured “noise” variance in log-abundance at the quadrat level,  $\sigma_z$  is the variance of the latent spatial process, and  $\log(\theta)$  is the logarithm of the spatial correlation parameter.

to Eq. 4. We consider two covariates on detection probability. First, a standardized metric of sample day to account for variation in detectability due to behavioral changes over the course of the breeding season. Second, sampling effort (duration of survey) varied among quadrats due both to variation in the length of the sample path chosen through each quadrat (see *Discussion*) and also the rate at which each observer traversed the route. Thus, we defined a standardized sampling intensity metric as the length of the sample route divided by the duration of the sample (henceforth sampling “rate”). Thus,  $\mathbf{f}'_i = [1, \text{Day}_{it}, \text{Day}_{it}^2, \text{Rate}_{it}]$  (the 1 represents an intercept). The local abundance parameters,  $N_i$ , are assumed to be Poisson with mean  $\lambda_i$  with  $\log(\lambda_i) = z_i + \varepsilon_i$ , where  $\{\varepsilon_i\}_{i=1}^R$  are independent errors with variance  $\sigma_\varepsilon^2$ , and  $z_i \equiv z(s_i)$  are spatially correlated random effects with mean  $\mathbf{m}'\boldsymbol{\beta}$ , variance  $\sigma_z^2$ , and exponential correlation parameter  $\theta$ . Elevation and forest cover were chosen as landscape covariates thought to influence density. Because of the very large elevational gradient in Switzerland, we suppose that the elevation effect is quadratic. A third covariate included in the model is route length. For reasons discussed previously (see *Modeling spatial coverage bias*), the inverse of route length was included in the linear predictor. Thus,  $\mathbf{m}_i = [1, \text{Elev}_i, \text{Elev}_i^2, \text{Forest}_i, \text{Length}_i^{-1}]$ .

*Results*

The MCMC algorithm outlined in *Bayesian Analysis by Markov Chain Monte Carlo* was run for  $1 \times 10^6$  iterations after a 100 000 iteration burn-in. Every 50th iteration was retained for purposes of inference and summarization. Posterior summaries of the model parameters are given in Table 3. For purposes of evaluating convergence, three shorter chains of length 210 000 were run (burn-in = 10 000) and convergence was assessed using the Brooks-Gelman-Rubin diagnostic (Gelman and Rubin 1992), using the facilities

provided in the **R** add-on library BOA (Smith 2005). Results indicated convergence, with scale reduction factors near 1 (1.0001–1.012) for all parameters, and the multivariate potential scale reduction factor was 1.0087.

The effect of sampling rate was negative, as expected (Eq. 2). That is, detection probability of an individual jay territory decreases with increasing sampling rate along a route. The estimated quadratic effect of date is not convex as expected (Fig. 4). We initially suspected a date by elevation interaction because higher elevation sites, where breeding activity commences later in the season, tended also to be sampled later in the season. Further analyses (not shown here) indicated this interaction to be unimportant. An alternative plausible explanation is that birds are more detectable early in the breeding season due to behavior associated with the establishment of territories and nest initiation. The timing of the minimal detectability in fact appears to coincide with the late nestling period, when parents are most busy foraging (Maumary et al., *in press*), and the slight increase later may be due to recently fledged nestlings.

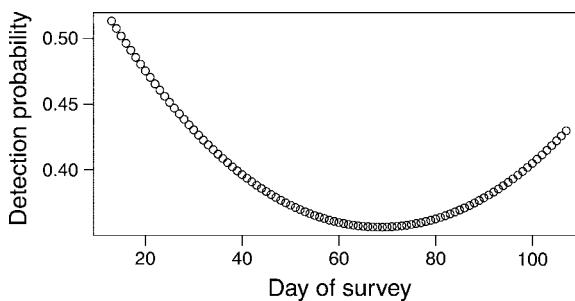


FIG. 4. Estimated response of detection probability (for European Jay) as a function of day from initiation of survey (1 = 1 April).

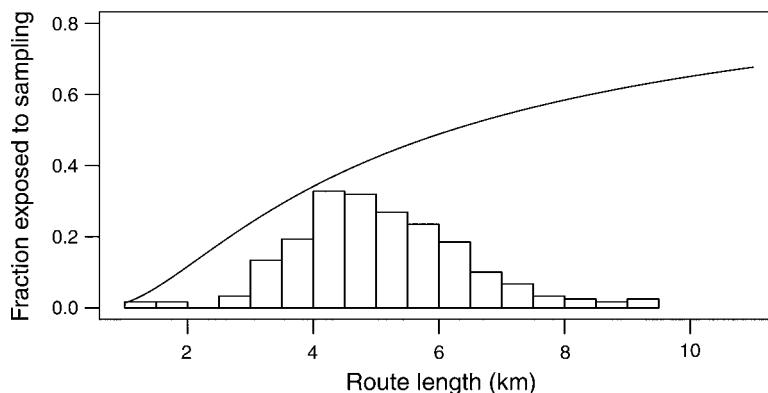


FIG. 5. Relative fraction of the quadrat population exposed to sampling as a function of route length (solid line). The histogram shows the distribution of the route length in sampled quadrats.

The posterior mean detection probability [i.e., of  $\text{expit}(\alpha_0)$ ], is 0.367 (SD = 0.0203), which is the probability of detecting a territory on the mean date of the surveys conducted (24 May), with an observer traversing a route at average rate. Thus, the probability of not detecting a territory at all, during three surveys, that is exposed to sampling by a prescribed route is about  $(1 - 0.367)^3 = 0.250$ .

The estimated effect of route length ( $\beta_1$  in Eq. 8) was negative (Table 3), indicating the expected diminishing return of jay territories exposed to sampling with increasing sampling route length (Fig. 5). The estimated saturation density ( $\lambda_0 = \exp(\beta_0)$ , Table 3), indicates roughly (posterior median) 5.43 territories per quadrat. Note that the average number of observed territories was 1.88. This adjustment of 1.88 to 5.43 (a net increase of 3.55) includes territories that were exposed to sampling by the sample route but not detected (non-detection bias), and territories present on the quadrat but not exposed to sampling along the route (spatial coverage bias).

The fitted curve (Fig. 5) allows us to partition the relative contributions of non-detection from spatial coverage bias. In particular, for example, the exposed territory density of a typical route of length 5.2 km is  $\exp(1.693) \exp(-4.239/5.2) = 2.41$  territories. At this route length, the model suggests that we exposed to sampling only about  $2.41/5.43 = 44.2\%$  of the available territories. Previously, we noted that about 75% of exposed territories are detected (in three visits at the mean survey date, by an observer traveling an average rate). Thus, for a route of average length, spatial coverage bias is by far the largest contribution to overall bias (see also *Discussion: The Swiss survey*).

*Landscape variation in territory density.*—There was a strong quadratic response of density to elevation (Fig. 6). This response surface achieved a maximum at around 720 m, i.e., at somewhat lower elevation than the observed maximum density (800–1100 m), emphasizing that observed counts are the combination of true abundance and detectability. Jay density was much

higher when forest cover was greater in a quadrat (Table 3).

The spatial structure in the model for abundance is governed by the correlated spatial process,  $z(s)$ . The estimated posterior of  $\log(\theta)$  (summarized in Table 3), implies a modal value of  $\theta$  of approximately 12.4 km. The parameter  $\theta$  is usually referred to as the correlation range parameter. It does not have an intuitive meaning. We can however restate this estimate in terms of the correlation between quadrats at any, arbitrary, distance. For example,  $\rho_1$ , the correlation between the abundance of neighboring quadrats (i.e., separated by 1 km), is  $\rho_1 = 0.92$  and for quadrats located 12 km distant,  $\rho_{12} = 0.38$ .

Normally, predictions of  $z(s)$  can be thought of conceptually as residuals in a fit of  $\log(\lambda(s))$  on the prescribed covariates. However, under the hierarchically centered parameterization (described in *The Model: Spatial models of abundance: Models of latent spatial variation*), in which  $E[z(s)] = \mathbf{m}(s)\boldsymbol{\beta}$ , the spatial process includes the nonzero mean,  $\mathbf{m}(s)\boldsymbol{\beta}$ , a function of elevation, forest cover, and route length. To depict the  $z(s)$  map, we thus used the centered values, i.e., having mean 0. These residual predictions for each of the 41 365 quadrats of Switzerland are shown in Fig. 7. This map shows clearly regions of under- and over-prediction relative to the regression model containing forest cover and elevation effects.

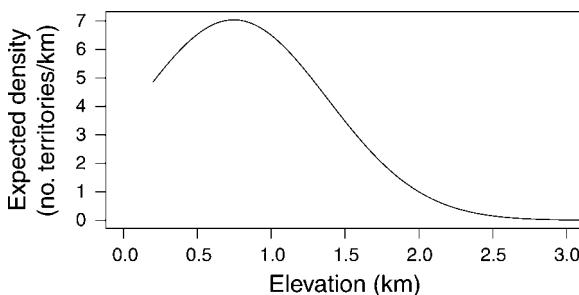


FIG. 6. Estimated response of European Jay density to elevation in Switzerland.

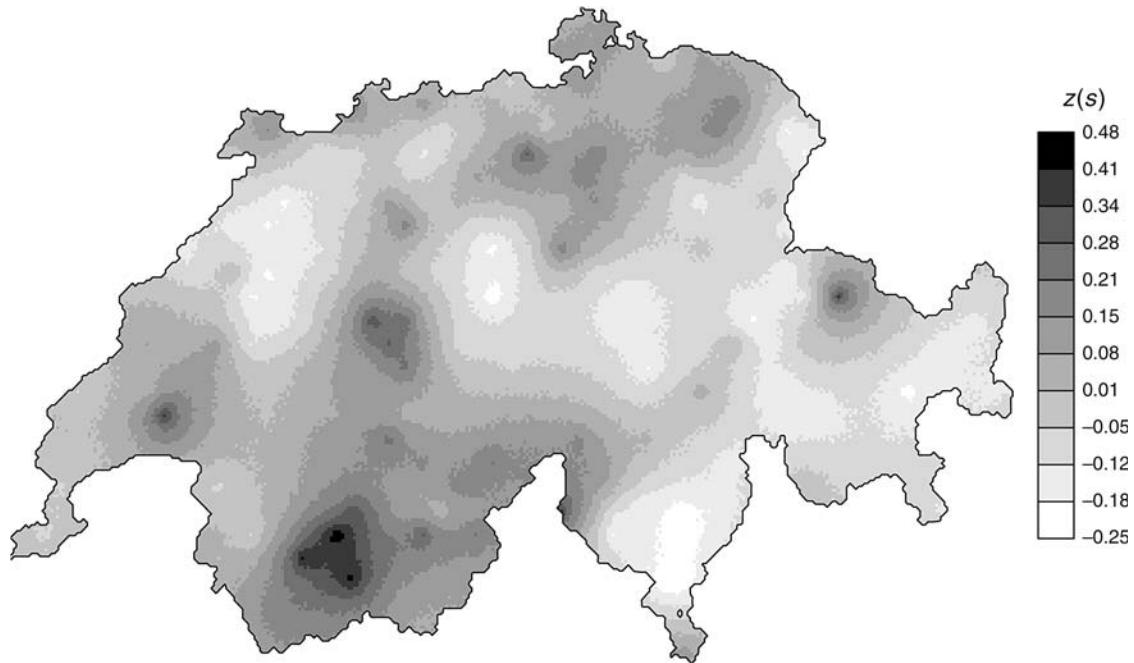


FIG. 7. Estimated posterior means of the spatial process,  $z(s)$ , centered about the regression mean containing elevation, forest cover, and route length as described in *Models of abundance and detection*.

The model yields quadrat-specific estimates of the number of territories,  $N(s)$ . The posterior means of each  $N(s)$  are shown in Fig. 8. We used this information to estimate the total number of jay territories in Switzerland. The posterior distribution of this quantity (Fig. 9) has mean 227 091 and 95% CI (133 169–369 521). This indicates approximately 5.48 territories per quadrat, roughly consistent with the posterior median of  $\lambda_0 = 5.43$ . We would probably expect a discrepancy due to slight biases in the sample with respect to the landscape covariates included in the model. For example, higher elevation quadrats, or those in rugged terrain, are sampled somewhat less in proportion to their availability because it is difficult to sample these quadrats. For comparison, the estimated total number of jay numbers in Switzerland when based on the effectively surveyed area of each quadrat was 95 786 with 95% posterior interval (84 544–108 524). To obtain that estimate, the model was rerun without route length in the model for  $\log(\lambda)$ . The naive estimate ignoring imperfect detection and incomplete quadrat coverage yields 77 766 territories. And, during the latest Atlas project, the total population was estimated at between 50 000 and 70 000 pairs (Schmid et al. 1998), again absent any adjustments for imperfect detection and incomplete sample coverage. Therefore, imperfect detection of jay territories and incomplete quadrat coverage may yield an almost threefold underestimation of true density in this species, with detectability bias (net, resulting from three surveys) responsible for approximately 12% and coverage bias for approximately 88% of the downward bias.

Maps provide a gross characterization of patterns in abundance and occurrence and might form the basis of some management and assessment activities. However, we may also use the model to obtain estimates or predictions of local population attributes, e.g., estimation of  $N$  for any particular quadrat. This objective might conceivably be of interest for some management and assessment problems and, for sparse data, this model-based small-area estimation can yield great improvements in the precision of predictions (Dorazio et al. 2005). Our model does permit estimation of abundance and occurrence probability at the scale of a single quadrat. For example, we selected one quadrat where four territories were detected, yielding three detection histories with frequencies  $x_{100} = 1$ ,  $x_{110} = 2$ , and  $x_{011} = 1$ . The estimated posterior probabilities of  $N = \{4, 5, 6, 7, 8, 9, \geq 10\}$  for that quadrat were (0.084, 0.173, 0.193, 0.176, 0.132, 0.095, 0.148). Thus, for example, a reasonable point estimate of  $N$  for this quadrat is the modal value  $N = 6$  (having probability 0.193). While the precision associated with such point estimates is not particularly remarkable, we do not see an effective method of conducting formal inference for such problems absent a modeling framework that permits the borrowing of information across space.

Finally, the posterior predictive means of  $\psi(s) = \Pr[N(s) > 0]$  for each quadrat are mapped in Fig. 10. This figure presents a probabilistic range map of the Jay in Switzerland. Unlike the myriads of species distribution maps produced (e.g., Scott et al. 2002, Araujo and Rahbek 2006, Coudun et al. 2006, Elith et al. 2006,

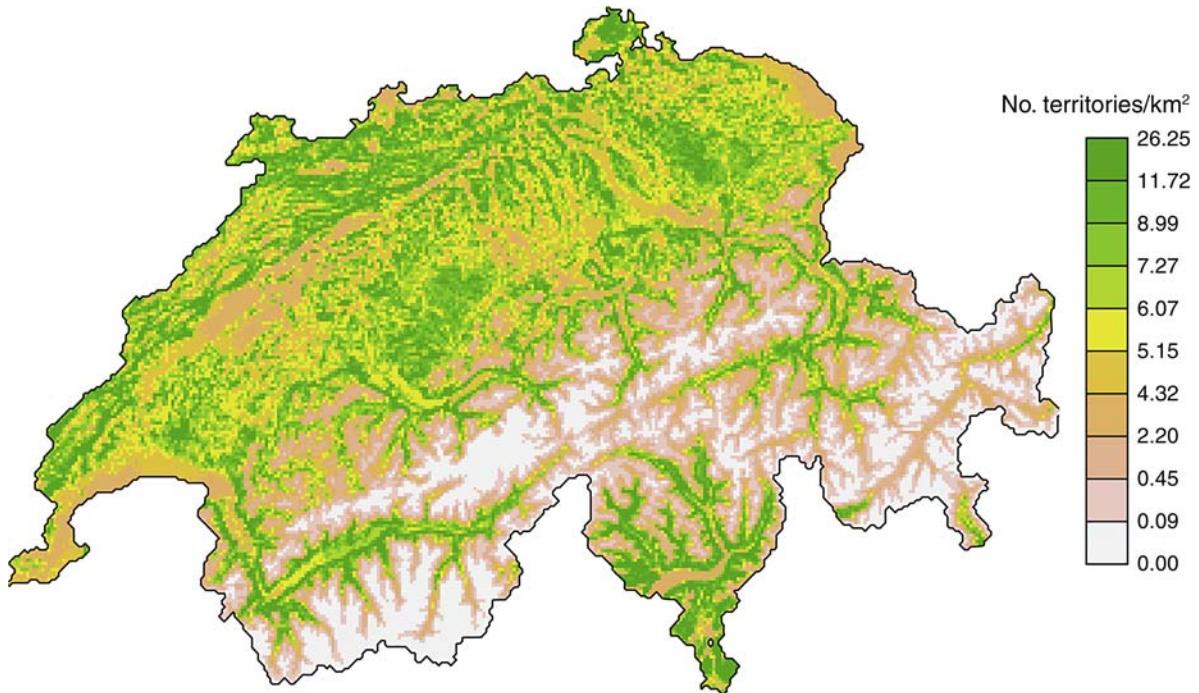


FIG. 8. Estimated abundance map [posterior means of  $N(s)$  for each quadrat] of the European Jay in Switzerland.

Latimer et al. 2006), it does take into account both landscape structure and possible non-detection in quadrats where the Jay did in fact occur and which renders observed zeros ambiguous.

#### DISCUSSION

A vast number of ecological studies aim at inference about spatial variation of abundance and occurrence of species based on replicate spatial samples. Virtually all such studies have neglected two issues that are fundamental to almost all animal and plant monitoring programs: that the samples are spatially referenced and therefore, closer samples may be more similar to each other than more distant samples, and that, typically, not all animals or plants exposed to sampling are detected (“imperfect detection”).

We have developed a hierarchical spatial model that provides a rigorous and flexible framework for addressing spatial inference problems about abundance and occurrence from survey data. This model simultaneously addresses these two fundamental considerations of sampling animal or plant populations. Within this framework for modeling abundance, a unified treatment of inference for both abundance and occurrence is achieved. Commonly, inference about these two quantities is approached independently. For example, count data are often quantized (e.g., MacKenzie et al. 2002, Dorazio and Royle 2005) in order to develop models of occurrence. This represents some loss of information. In addition, this treatment also disregards the probabilistic linkage between abundance and occurrence (i.e., that

occurrence is the event  $N > 0$  [Royle and Nichols 2003]). It has been proposed that occurrence of, and abundance given occurrence of a species, are best modeled as two separate processes (e.g., Cunningham and Lindenmeyer 2005). We agree that this might be useful in some cases where one or a few limiting factors determine the occurrence of a species, and a different set of factors determine variation in abundance. However, we believe that this is unlikely to occur frequently in practice and that in the vast majority of species both occurrence and abundance are the result of the combined action of multiple factors.

In our application, we adopt a spatial model for abundance based loosely on the consideration that territories are distributed spatially according to an inhomogeneous Poisson process. This model serves as a prior distribution governing local abundance, which is unobserved. We believe that this is the most interesting

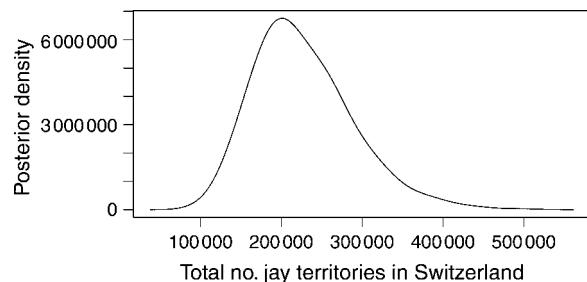


FIG. 9. Posterior distribution of the total number of European Jay territories in Switzerland.



FIG. 10. Estimated probability of occurrence of the European Jay in Switzerland (posterior mean of  $\Pr[N(s) > 0]$  for each quadrat).

aspect of our application. That is, while spatial sampling and imperfect detectability are nearly universal commonalities in animal sampling problems, the two ideas have not been addressed simultaneously to any great extent. While many inference problems are inherently spatial, we believe that the need for model-based estimation is especially acute in many avian surveys because the density of territorial species is low, leading to sparse data with observed zeros at many sites. In such cases, one cannot estimate local abundance effectively in the absence of a model that allows for the combination of information among spatial samples. The model proposed here allows for the estimation of local abundance at the scale of a quadrat, or abundance aggregated over multiple quadrats (e.g., all quadrats in Switzerland; see Fig. 9). The model also permits, directly, characterizations of patterns in abundance and occurrence (i.e., estimation of range or distribution maps), which can provide useful summaries of species range, and the relationship between these quantities and landscape structure such as can be useful for conducting formal assessments of landscape change, management requirements or tests of ecological relationships.

*Closure, territory identification, and parametric model assumptions*

In order to achieve a clear interpretation of the data and of model parameters, we have assumed that the population is closed to demographic processes and movement, i.e., that the number and location of

territories stays constant during the breeding season. Furthermore, we assume that each sighting can be unequivocally assigned to an identifiable territory, i.e., that territory “identification” is perfect. This is analogous to the assumption that “marks are not lost and read perfectly” in classical capture–recapture. Conducting temporal repeats in a time period as short as possible, and spending more time on a quadrat for each repeat would be one way of ensuring that these important assumptions are met. The European Jay in Switzerland is sedentary and individuals are present for detection throughout the sampling season. The species does not nest at high densities, therefore territory identification will have been assessed adequately in most cases. Furthermore, even though the total survey duration was three months, the three surveys in individual quadrats were spaced much less in time, and typically within about one month. In summary, we believe that in our application both the assumption of a static population and that of perfect territory identification were adequately met. We note however, that our model may not be applicable for more dynamic species, for surveys conducted over longer time intervals, and for species nesting at high densities or having large territories. However, it is clear that for such species the validity of any assessment of abundance, also the naive one that disregards imperfect detection, will be questionable.

One particular manner in which the assumption of a static and closed population may be violated is when a

migratory species has not yet fully arrived to the breeding grounds by the start of the survey period. Such a closure violation may be addressed by either replacing the respective data with missing values or by modelling a quadratic effect of season into detection probability. At the start of the season, detectability may then be close to zero and abundance estimates should be unaffected.

We made a number of purely subjective modeling decisions that we did not formally evaluate. Although we agree with a referee that one should be aware of potential sensitivities to such modeling choices, we have chosen to avoid certain of these, focusing instead on developing the basic formulation of the model and investigating its application. For example, we assumed the customary logit and log-linear relationships between covariates and detection probability (Eq. 4) and mean abundance (Eq. 5), respectively. Secondly, we made a parametric assumption about the form of the correlation model (see *The Model: Spatial models of abundance: Models of latent spatial variation*). In both cases, we see no formal basis for consideration of any particular parametric form and so did not consider alternative parameterizations for that reason. With specific regard to the model for the correlation function, while other parametric functions are in fairly widespread use, our view is that the parametric form is irrelevant given the level of the random effect in the hierarchy. In the present case,  $z(s)$  is not a real process (i.e., that could conceivably be observed), and so the mathematical properties induced by choice of correlation functions (e.g., its differentiability) are practically irrelevant. A more fundamental assumption that underlies almost all animal sampling problems is that the observed “encounter histories” are multinomial. This is justified when the detection/non-detection events can be regarded as independent Bernoulli trials. A number of plausible departures are evident (see previous paragraph), including nonindependence among individuals, and across surveys by the same observer. We believe that certain model extensions (e.g., nonindependence among individuals) would require additional information, whereas others (e.g., nonindependence among samples) might be achievable by modifications to the structured multinomial cell probabilities, although we have not considered such extensions in the present work.

Regardless of the many modeling decisions that are adopted, the adequacy of a particular model, i.e., how well it fits the data, should typically be of some concern. In the present case, we assessed the goodness of fit using the Bayesian  $P$  value (Gelman et al. 1996). To implement this, some discrepancy measure (a fit statistic) between the observed data and the expected data under the model in question is computed at each iteration of the MCMC algorithm (using the current values of the parameters). This is compared to a reference distribution, which is based on the distribution of the discrepancy measure computed from simulated data

(again, using parameter values at each iteration of the MCMC algorithm). If the model is correct, the distribution of the fit statistic should be centered around 0.50, and poor fit is indicated by extreme values (say, near 0 or 1). In the present application, we used the sum of the squared Pearson residuals for the fit to the total number of territories observed [i.e.,  $n(s)$ ] as the fit-statistic, yielding a  $P$  value of 0.346 when averaged across three MCMC runs of length 200 000 (post burn-in), providing some evidence of model adequacy.

#### *The Swiss survey*

Our motivating application, the Swiss Survey of Common Breeding Birds, produces encounter history data on territories that may be viewed as conventional capture-recapture data. This yields a multinomial data model with a spatially indexed abundance parameter. We focused on developing abundance and occurrence maps for a species that made use of covariates that influence abundance and also detection probability. The model yielded a formal adjustment of the number of observed territories in each quadrat to compensate for imperfect detection, and also that the quadrats were not completely sampled (i.e., that route length did not achieve saturation of the quadrat).

It may be argued that one weakness of the Swiss survey is that quadrats are sampled with varying effort: sample route length varies among quadrats. This leads to what we referred to as spatial coverage bias. Our solution to dealing with this sampling problem was to accommodate route length as a covariate on the fraction of the quadrat population exposed to sampling, using a parameterization that yields an estimate of the quadrat population size under saturation sampling, i.e., as route length tends to infinity. While this sampling situation is not ideal, it is necessary because it would be difficult to implement a large-scale survey based on volunteer observers for which the protocol dictated substantial expenditures of effort by every observer. We note that effort adjustments are critical considerations in other large-scale animal surveys that lack a fully standardized protocol, such as the large-scale “Christmas bird count” survey in North America (e.g., Link and Sauer 1999). Our model-based adjustment has a clear interpretation if habitat is homogeneous within a quadrat and transect routes are placed randomly within the quadrat. However, routes were not really randomly placed, and therefore, if route length and placement varies in response to habitat heterogeneity (e.g., the amount and distribution of forests), then our adjustment might “over-correct” to yield an estimate of the abundance that would be expected were all quadrats covered entirely by the same type of habitat as where the route is located. Therefore, we suspect that our estimated “accumulation” of territories might actually be too slow because observers probably pick exceptional routes through the quadrats, i.e., avoiding lakes, villages, roads, and so on (thus, less desirable habitats remain

unsampled). We discuss this issue of spatial coverage bias further in Appendix B.

The naive estimate of the national total number of jay territories was about 78 000. Accounting for imperfect detection added approximately 18 000 territories and adjusting for coverage bias added another 131 000 territories to yield a fully corrected estimate of the national total of about 227 000 territories. The national abundance estimate was thus almost three times higher than previous estimates that did not account for these important factors. These results emphasize the importance of adjusting analyses of abundance for imperfect detection and incomplete coverage of the spatial samples in the Swiss Survey of Common Breeding Birds. While varying spatial coverage may not be an issue in other ecological studies or large-scale monitoring or mapping studies, that of imperfect detectability undoubtedly is. Our study demonstrates that abundance may be grossly underestimated when simple counts are used.

Many would question the need for actually estimating population size and argue that most applications are only interested in comparisons of abundance (or occupancy) over time (e.g., population trends), regions (e.g., to direct conservation efforts, or pest management actions, preferentially to high-density areas), habitats or other classifications. If such comparisons are really the only objective of a study and if the expectation of detection probability and of the degree of coverage bias are both constant over the dimensions of comparison, then this approach is valid. If on the other hand any of the myriad of factors that affect detection probability or the degree of coverage bias changes, then resulting "relative abundance" or "relative occurrence" indices will yield biased comparisons. Formally accounting for detectability and coverage in the model confers an insurance against any such unexpected and perhaps even unmeasurable effects. Furthermore, even if relative abundance indices are used, the important assumption of stationary detectability and degree of coverage bias ought to be tested, perhaps for a subsample of quadrats and at some points in time in a longer running monitoring program.

In other cases, however, unbiased estimates of abundance or occurrence of a species are required. For instance, real abundance estimates are required to evaluate the extinction probability of small populations of a rare species, to target pest management of overabundant species or to decide on culling levels of harvested species. Then, disregarding issues of detectability and/or coverage bias in the data on which conclusions and decisions are based may imperil threatened or harvested species and lead to inefficient management. One (hypothetical) example with the Jay might be an investigation into the impact of Jay predation on populations of small passerines. The Jay may be hunted in Switzerland partly for its perceived negative effect on small passerines. In a rigorous study of its impact on potential prey populations, it would

make a tremendous difference if average Jay abundance was assumed to be 1.88 territories per km<sup>2</sup> (the average naive density estimate) or rather 5.43 territories per km<sup>2</sup> (the best available density estimate accounting for both imperfect detectability and incomplete sample coverage).

Often, count or detection/non-detection data are available that do not contain information about the sampling process, i.e., about detection probability or effective sampling area. We would not argue that such data are a priori useless for inference about relative abundance or occurrence. Especially if they are all that is available for a given species, geographic area, or time period, we agree that such data should be analyzed in the best possible way. However, we suggest that the results be interpreted with due caution. Unfortunately, data for which there is no direct information about observation processes is often all that is available. This entices many researchers to neglect these important sampling issues (and also at the design state of a study). There are still countless studies, ecological or more applied, e.g., monitoring programs, that are initiated without taking into account observation processes that induce error in the form of detection bias or spatial coverage bias. This, in our view, is irresponsible and leads to bad science or management.

We believe that the MHB is unique among large scale monitoring programs in some important ways that foster the development and application of unique assessment and inference to MHB data. Important among these are that it is based on multiple sample occasions, and it yields a (territory) map with locational information relating to individual bird detections. This is unlike the North American Breeding Bird Survey (as well as other monitoring programs) which only records gross counts of adult individuals, for a single survey occasion, and without a precisely defined sample unit. Intuitively, there is additional information in such data (i.e., replication as in the MHB) that should be exploited. Rendering the data into encounter histories is one way to do that, but perhaps not the only, or best. We note, however, that while we think that data resulting from territory mapping is potentially highly informative about avian population status because it yields direct information on the detection process, we do not necessarily advocate territory mapping to the exclusion of other data collection protocols. Indeed, the basic modeling strategy that we employed here is directly applicable to many other common animal sampling protocols. For example, sampling with multiple observers (Nichols et al. 2000) yields a multinomial likelihood with cell probabilities that are functions of detection probability parameters that are specific to each observer. Other protocols in common use that yield multinomial data include removal sampling (Farnsworth et al. 2002, Royle 2004b, Dorazio et al. 2005) wherein individuals are physically (or passively) removed from the population in successive sampling intervals, and distance sampling (Buckland et al. 2001,

Royle et al. 2004) in which the frequency of individuals in distance classes from a point (or transect) of observation are recorded. Thus, our model may provide a very general and unifying framework for abundance and occurrence estimation problems based on many spatially replicated sampling schemes.

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#### APPENDIX A

Integrated likelihood and Bayesian analysis (*Ecological Archives* M077-013-A1).

#### APPENDIX B

Statistical adjustment of spatial coverage bias (*Ecological Archives* M077-013-A2).