

Generalized estimators of avian abundance from count survey data

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Abstract

Generalized estimators of avian abundance from count survey data.— I consider modeling avian abundance from spatially referenced bird count data collected according to common protocols such as capture–recapture, multiple observer, removal sampling and simple point counts. Small sample sizes and large numbers of parameters have motivated many analyses that disregard the spatial indexing of the data, and thus do not provide an adequate treatment of spatial structure. I describe a general framework for modeling spatially replicated data that regards local abundance as a random process, motivated by the view that the set of spatially referenced local populations (at the sample locations) constitute a metapopulation. Under this view, attention can be focused on developing a model for the variation in local abundance independent of the sampling protocol being considered. The metapopulation model structure, when combined with the data generating model, define a simple hierarchical model that can be analyzed using conventional methods. The proposed modeling framework is completely general in the sense that broad classes of metapopulation models may be considered, site level covariates on detection and abundance may be considered, and estimates of abundance and related quantities may be obtained for sample locations, groups of locations, unsampled locations. Two brief examples are given, the first involving simple point counts, and the second based on temporary removal counts. Extension of these models to open systems is briefly discussed.

Key words: Abundance estimation, Avian point counts, Detection probability, Hierarchical models, Metapopulation models, Population size.

Resumen

Estimadores generalizados de abundancia en aves a partir de datos de estudios de recuento.— En el presente estudio se analiza la modelación de la abundancia en aves mediante datos de recuento de aves, referenciados espacialmente y obtenidos a partir de protocolos comunes, como los de captura–recaptura, muestreo por observadores múltiples, muestreo por eliminación y recuentos de puntos simples. Las muestras de pequeño tamaño, así como el amplio número de parámetros, han propiciado numerosos análisis que no tienen en cuenta la indexación espacial de los datos y, por consiguiente, no proporcionan un tratamiento adecuado de la estructura espacial. En este trabajo se describe un marco general para la modelación de datos replicados en el espacio, que considera la abundancia local como un proceso aleatorio, todo ello basado en el punto de vista de que el conjunto de poblaciones locales referenciadas espacialmente (en los lugares de toma de muestras) constituye una metapoblación. De este modo, la atención puede centrarse en el desarrollo de un modelo para la variación en la abundancia local que sea independiente del protocolo de muestreo que se esté utilizando. La estructura del modelo metapoblacional, en combinación con el modelo de generación de datos, define un modelo jerárquico simple que puede analizarse mediante el empleo de métodos convencionales. El marco de modelación propuesto es de carácter general, en el sentido de que permite considerar amplias clases de modelos metapoblacionales, covariantes del nivel del emplazamiento sobre datos de detección, y la abundancia, pudiendo obtenerse estimaciones de abundancia y cantidades relacionadas para emplazamientos de muestreo, grupos de emplazamientos y emplazamientos no muestreados. A tal efecto, se incluyen dos breves ejemplos; el

primero trata de los recuentos de puntos simples, mientras que el segundo se basa en los recuentos por extracción temporal. También se apunta la posibilidad de ampliar estos modelos a sistemas abiertos.

Palabras clave: Estimación de la abundancia, Recuentos de puntos aviares, Probabilidad de detección, Modelos jerárquicos, Modelos metapoblacionales, Tamaño poblacional.

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Introduction

The detectability of individuals is a fundamental consideration in many studies of animal populations. The need to properly account for detectability has given rise to an extensive array of sampling protocols and statistical procedures for estimating demographic parameters in the presence of imperfect detection (Williams et al., 2002).

Conventional capture–recapture methods in which individual animals are marked, released, and recaptured (or resighted) constitute the most useful class of methods in terms of the information content provided by the data, and the complexity of detection process models that may be considered. In studies of avian populations, implementation of capture–recapture methods is often difficult in field situations. Because of this, there has been considerable recent interest in methods based on avian point counting that are capable of controlling for imperfect detection while remaining efficient to implement in field situations. These methods include those based multiple observer sampling (Cook & Jacobson, 1979; Nichols et al., 2000), temporary removal (Farnsworth et al., 2002), distance sampling (Rosenstock et al., 2002) and even simple point counts (Royle, 2004a). These and similar methods are also widely used in the study of other organisms including marine mammals, ungulates, and amphibians. My motivation derives from studies of bird populations, and so subsequent discussion and examples focus on bird sampling problems.

Many small–scale studies of animal populations and large–scale monitoring efforts rely on sampling designs in which one (or more) of these common sampling protocols is replicated *spatially*. This is partly out of necessity—many species exist at low densities, and effective sampling areas are small—but often there is direct interest in characterizing spatial variation in abundance. These replicated surveys yield spatially indexed count data \mathbf{y}_i for sample location (or site) $i = 1, 2, \dots, R$. In most sampling protocols for which it is possible to estimate abundance in the presence of imperfect detection, $\mathbf{y}_i = \{y_{ik}; k = 1, 2, \dots, K\}$ is a vector of counts. As an example, if a removal protocol is used then $\mathbf{y}_i = (y_{i1}, y_{i2}, y_{i3})$ are the number of animals first observed (and "removed" from further counting) in consecutive time intervals of say 3 minutes. The precise nature of the count statistic under other common sampling protocols is described in "Notation and preliminaries" section.

There are two objectives considered in many studies of animal populations that are demographically closed. First is estimation of "abundance", population size, or density. In the context of spatially replicated surveys, this is often defined as total or average abundance of the sampled area. The second objective is estimation of the effects of (site–specific) covariates on abundance or density. Typical covariates of interest are those that describe habitat or landscape structure. Interestingly, there have been few general suggestions for ac-

commodating site–specific covariates in these common sampling protocols. Royle et al. (2004a) describe an approach for incorporating abundance covariate effects in distance sampling models that is related to the models described here.

One important difficulty present in most spatially replicated bird counting surveys (of breeding birds) is that typical abundance at individual sampled locations is very small. Consequently, site–specific sample sizes (number of *observed* birds) are small. The general small sample situation is problematic when it comes to estimation because the likelihood contains many (abundance) parameters each of which is ill–informed by the available sparse data. Estimation of spatially explicit abundance is usually infeasible. A common solution is to aggregate data across sites and apply conventional estimation methods to the aggregate counts. In doing so, site–specific information is lost so that, for example, estimation and modeling of site–specific covariate effects on abundance and detection is infeasible. In addition, spatial scale becomes a concern when deciding how data should be aggregated. While it may be reasonable to combine multiple samples within a small forest or woodlot, additional considerations should be relevant at larger scales. Finally, the use of aggregated counts cannot generally be justified based on the likelihood for the observed data, i.e., the site–specific counts. That is, the aggregated counts are not sufficient statistics for the objective (total) abundance "parameter" under a sampling scheme involving spatial replication. Additional assumptions are required to formally justify aggregation of count statistics among sites; this is elaborated on in "The likelihood under spatial replication" section. These deficiencies motivate the need for a more general approach to dealing with spatially replicated count survey data.

In this paper, I describe a general framework for modeling and estimation of abundance from spatially replicated animal count data. The key idea is introduction of a metapopulation model that characterizes the (spatial) variation in abundance of the spatially referenced populations being sampled. The metapopulation view provides a concise framework for combining the data collected at multiple sample locations, regardless of the sampling protocol used to collect data. Specification of a metapopulation model is a great advantage because it allows the biologist to focus on explicit formulation of the abundance model *at the level of the sample unit*, independent of the detection process. The main benefit of adopting the metapopulation view is that a broad class of more complex models are possible including models which describe variation in site–specific abundance explicitly (e.g., with covariates), and models which allow for latent spatial variation (overdispersion, spatial correlation) that is not modeled explicitly by covariates. These metapopulation models form the basis for the development of generalized estimators of abundance based on any of the previously mentioned protocols. These are generalized in the sense that they can accommodate variation in site–specific abundance,

factors that influence detectability, and additional considerations described in "The metapopulation view" section.

Under this metapopulation formulation, local abundance is regarded as a "random effect", and the general model structure is commonly referred to in statistics as a *hierarchical model*. Hierarchical models are commonly analyzed by either integrated likelihood or Bayesian methods. This is described in "Estimation and inference" section. Modeling abundance effects, estimating density, estimating local population size, and even predicting abundance at unsampled locations are straightforward problems under this hierarchical modeling framework.

Notation and preliminaries

Let N_i be the number of birds available to be counted at location i ; $i = 1, 2, \dots, R$. Sampling yields the vector of counts \mathbf{y}_i for each sample location. The precise nature of the data vector \mathbf{y}_i depends on the sampling protocol used. For several of the more common sampling protocols, the data structure is as follows:

(1) For independent double or multiple observer protocols, k indexes an "observer detection history". For example, with two independent observers, $K = 3$ and y_{i1} , and is the number of birds seen by observer 1 (but not observer 2), y_{i2} is the number seen by observer 2 (but not 1), and y_{i3} is the number seen by both observers. In general, with T observers, there are $K = 2^T - 1$ observable observer histories.

(2) For a removal protocol, k indexes the time interval of (first) detection. i.e., y_{i1} is the number of birds first seen in interval 1, y_{i2} in interval 2, and y_{i3} in interval 3, etc.

(3) For distance sampling, the count statistics are indexed by distance, so that y_{ik} is the number of birds seen in distance class k at site i .

(4) For conventional "capture-recapture" experiments, the data structure is analogous to that obtained under multiple observer sampling except that the capture history is organized in time. For example, in a two period study, $K = 3$, and let y_{i1} be the number of individuals with capture history "10" (seen in the first interval, but not the second), y_{i2} be the number of individuals with capture history "01", and y_{i3} be the number of individuals with capture history "11".

Various other protocols may also be considered, including that based on simple point counts (see "Point counts" section).

A final bit of notation will be useful. In some applications that involve spatial replication, putative interest lies in estimation of the total abundance at the sampled sites: $N_{total} = \sum_i N_i$. The familiar "dot notation" will be used to indicate various sums. Let $y_{i0} = N_i - y_i$ be the number of birds not detected at each site where $y_i = \sum_{k=1}^K y_{ik}$ (the total number detected at site i). Thus, N_{total} can be

expressed as the total count $\sum_i y_i$ plus the sum of the unobserved individuals at each location $y_{i0} = \sum_i y_{i0}$.

The likelihood under spatial replication

Hereafter, I assume that the observations \mathbf{y}_i are *independent* when conditioned on local population size N_i and parameters of the detection process. Under this assumption, the sampling distribution of the data $\mathbf{y} = \{\mathbf{y}_i; i = 1, 2, \dots, R\}$ under most common sampling protocols is the product multinomial

$$f(\mathbf{y} | \{N_i; i = 1, 2, \dots, R\}, \mathbf{p}) = \prod_{i=1}^R \frac{N_i!}{y_{i1}! y_{i2}! y_{i3}! y_{i0}!} \pi_1^{y_{i1}} \pi_2^{y_{i2}} \pi_3^{y_{i3}} \pi_0^{N_i - y_i} \quad (1)$$

for a sampling protocol yielding 3 observable frequencies (e.g., 3 period removal, 2 observers, etc). The cell probabilities, π_k , are functions of one or more detection probability parameters \mathbf{p} (the precise function depends on the protocol being used) and $\pi_0 = 1 - \sum_{k=1}^K \pi_k$ (the probability that an individual is not captured). For example, under a removal sampling protocol with three removal periods, the cell probabilities have the following form when detection probability is assumed constant:

$$\begin{aligned} \pi_1 &= p \\ \pi_2 &= (1 - p)p \\ \pi_3 &= (1 - p)^2 p \\ \pi_0 &= (1 - p)^3. \end{aligned}$$

For other sampling protocols, these cell probabilities are different functions of various detection probability parameters but their precise form is not relevant in any of the following discussion.

While the product multinomial likelihood (1) is not inherently intractable, in many practical situations there are important considerations that render it so. In particular, there are usually many unknown abundance parameters (the N_i 's), in addition to the parameters that describe the detection process. Also, local population sizes are frequently very small and, consequently, the sample sizes (number of captured individuals) for each location are small. In many surveys, there may in fact be many zero counts. One common solution to dealing with these problems is to aggregate the counts (i.e., pool data from multiple sample locations). This is discussed subsequently.

Spatial aggregation of count statistics

A common goal of many studies is estimation of the total abundance, N_{total} across all sampled locations. Ignoring the fact that the *data* are indexed by sample location, one might focus on the likelihood of the aggregated count statistics:

$$f(\mathbf{y}|\mathbf{N},\mathbf{p}) = \frac{N_{total}!}{(\sum_i y_{i1})!(\sum_i y_{i2})!(\sum_i y_{i3})!(\sum_i y_{i0})!} \pi_1^{\sum_i y_{i1}} \pi_2^{\sum_i y_{i2}} \pi_3^{\sum_i y_{i3}} \pi_4^{\sum_i y_{i0}} \quad (2)$$

To be more concise, using the notation introduced in "Notation and preliminaries" section, Eq. (2) is

$$f(\mathbf{y}|\mathbf{N},\mathbf{p}) = \frac{N_{total}!}{y_{.1}! y_{.2}! y_{.3}! y_{.0}!} \pi_1^{y_{.1}} \pi_2^{y_{.2}} \pi_3^{y_{.3}} \pi_4^{y_{.0}} \quad (3)$$

Interestingly, the use of aggregated counts cannot be justified under the (correct) likelihood for the disaggregated data given by (1) without some additional assumptions elaborated on shortly. While it is true that Eq. (3) is the correct likelihood for the total counts if the site-specific counts are unknown, it is not equivalent to the likelihood based on the disaggregated site-specific counts. That is, given the site-specific counts y_{ik} , the totals $y_{.k} = \sum_i y_{ik}$ are not the sufficient statistics for N_{total} when the N_i are viewed as fixed but unknown parameters.

I believe that the idea of pooling the site-specific sufficient statistics is partially motivated by convenience. The main support for use of (3) over (1) seems to be that there are too many N_i parameters in the joint likelihood (1) and this motivates one to consider them as nuisance parameters. However, estimation based on aggregated data does not appear consistent with usual notions of the treatment of nuisance parameters. For example, integration of the nuisance parameters from the likelihood under a suitable prior distribution, or conditioning on sufficient statistics, both of which are fairly conventional treatments of nuisance parameters.

It can be demonstrated that if N_i are assumed to have a Poisson distribution with mean λ , then one can justify aggregation (i.e., (3)) from likelihood (1). In this sense, estimation based on aggregated counts can be viewed as having implied a Poisson assumption on N_i with constant mean. Importantly, it precludes other possibilities: That N_i are overdispersed relative to the Poisson, or that the mean is not constant. Thus, technical details aside, the important reason that one should not aggregate data is that it renders impossible the consideration of covariate effects on both abundance and detection probability, and consideration of more complex variance structure.

The conditional likelihood under spatial aggregation

As an alternative to using the likelihood (1), it is common to use so-called "conditional" estimators based on obtaining an estimate of π_0 from the conditional likelihood

$$f(\mathbf{y}|\mathbf{N},\mathbf{p}) = \frac{y_{..}!}{y_{.1}! y_{.2}! y_{.3}!} \left(\frac{\pi_1}{1-\pi_0} \right)^{y_{.1}} \left(\frac{\pi_2}{1-\pi_0} \right)^{y_{.2}} \left(\frac{\pi_3}{1-\pi_0} \right)^{y_{.3}} \quad (4)$$

The likelihood given by (4) is motivated by noting that the sufficient statistic for N_i is $y_{i.}$, and so by conditioning on $y_{i.}$, N_i is removed from the problem. Estimators based on the conditional likelihood (4) and the "unconditional" likelihood (3) are asymptotically

equivalent (Sanathanan, 1972), and both specifications are commonly used in practice.

For the common parameterizations of π_k (under the sampling protocols described previously), it is clear that the aggregated counts are sufficient statistics for those model parameters contained in π_k , and hence use of aggregated counts can be justified under likelihood (4) if interest is focused on estimating detection probability parameters. Estimation of N_{total} is then based on the assertion that $y_{..} = \sum_i y_{i.}$ is *Binomial* ($N_{total}, 1-\pi_0$). While this may be true, it should be noted that it was not $y_{..}$ that was conditioned on in order to obtain Eq. (4), but rather $y_{i.}$. The neglected likelihood component is

$$\prod_i \frac{N_i!}{y_{i.}!(N_i - y_{i.})!} \pi_0^{y_{i.}} (1-\pi_0)^{N_i - y_{i.}}$$

Once again, there is no way to reformulate this in terms of N_{total} without additional model structure on N_i (e.g., if N_i has a Poisson distribution).

The metapopulation view

A more appealing and general solution to the problem of spatial replication can be achieved by regarding the collection of local populations as a metapopulation (Levins, 1969; Hanski & Gilpin, 1977). For the present purposes, a useful operational definition of metapopulation is simply "a population of (local) populations indexed by space". Interest in the study of metapopulation biology has exploded in recent years both in terms of theoretical development and applications of metapopulation concepts to many taxa. Patch occupancy, local extinction and local colonization are all metapopulation characteristics of some theoretical and practical interest.

In the present context, that of demographically closed systems during the time of sampling, the local population trait in question is *size*, but in general (open systems) local population mortality and recruitment events are also of interest, the metapopulation summaries being local extinction and colonization probabilities, respectively. Note that mortality at the local population level is the aggregate of individual mortality and emigration processes, and recruitment at the local population level is the aggregate of individual recruitment and immigration processes. The relationship between local population processes and several important metapopulation parameters are given in table 1.

Note that demographic closure *during sampling* is not inconsistent with metapopulation theory which requires that populations mix *across time* to some extent. In a demographically closed system, I view local population size as being a more general description of patch occupancy. The event that a patch is occupied is equivalent to the event that $N_i > 0$, and patch occupancy is $Pr(N > 0)$ for a collection of homogeneous patches. In general, $Pr(N > 0)$ is a function of density, and the variation in local population sizes as described shortly.

Table 1. Summary of metapopulation concepts.

Tabla 1. Resumen de conceptos metapoblacionales.

Time scale	Closure status	Local population attribute	Metapopulation parameter
Within year	Closed local pops.	Occurrence	Patch occupancy
		Size	Density
Across years	Open local pops.	Mortality	Extinction probability
		Recruitment	Colonization probability

Extinction and colonization events are also intimately linked to local abundance (among other things). Thus, models of variation in abundance are of more relevance than simply as a characterization of abundance *per se*.

Probabilistic characterization of metapopulations

It is natural to express the notion of a metapopulation probabilistically, by imposing a probability distribution on abundance. This is expressed by

$$N_i \sim g(N|\theta)$$

where " \sim " is read "is distributed as" and $g(N|\theta)$ is some discrete probability density. The local populations may be independent, or not, but considerable simplicity arises when they are independent. Practically, independence means that individuals cannot occur in more than one local population (i.e., the N_i 's do not overlap). The generality that this probability characterization permits is that θ may be allowed to vary spatially in a number of ways, any discrete probability density may be considered for $g(N|\theta)$.

The main practical benefit of this metapopulation view is that the metapopulation structure serves as a framework for combining a large number of spatially referenced count data surveys. In essence, this model is a *prior distribution* on abundance. More generally, I believe that the structure of the metapopulation is of fundamental interest. That is, the goal of many (if not most) studies of avian abundance can be formulated in terms of the metapopulation distribution or its summaries such as $E[N]$ (density), covariate effects (on density), etc.

The simplest example of a metapopulation model is that resulting from a uniform distribution of individuals across the landscape. Then, aggregating occurrence events into non-overlapping sample areas yields $N_i \sim \text{Poisson}(\lambda)$.

This seems a natural choice for describing variation in abundance because it arises under a homogeneous Poisson point process, the standard null distribution for the spatial arrangement of organisms. Moreover, it is also an assumption that underlies many common animal sampling methods (e.g.,

distance sampling). More importantly, there is an obvious and simple extension to accommodate a *non-uniform* distribution of individuals. One can consider that λ varies spatially, for example:

$$N_i \sim \text{Poisson}(\lambda_i)$$

where $\log(\lambda_i) = b_0 + b_1 x_{i1}$ where x_{i1} is the value of some covariate at site i . Several further extensions are also obvious. One is to allow for excess Poisson variation by inclusion of a random effect, ϵ_p , as:

$$\log(\lambda_i) = b_0 + \epsilon_i$$

where $\epsilon_i \sim \text{Normal}(0, \sigma^2)$. Alternatively, a more natural model of over-dispersion for N_i is the negative binomial distribution

$$N_i \sim \text{NegBin}(\mu, a)$$

with variance $\mu + \mu^2/a$. In any spatial sampling problem, it is natural to consider the possibility that the spatial process is correlated. That is, that there exists latent structure beyond any covariates that are contained in the model. Royle et al. (2004b) consider a model in which the log-linear model for the mean contains a spatially indexed random effect that is (spatially) correlated. Such structure may be appealing in many animal abundance modeling problems where it is likely that habitat affinities are only known imprecisely, or there is limited ability to quantify the relevant habitat components.

Open systems

The focus of this paper is on modeling and estimation of abundance in demographically closed systems. The linkage between local abundance and patch occupancy in closed systems has been mentioned previously. However, similar relationships between other metapopulation attributes and abundance can also be made. For example, local colonization probability is $\Pr(N_{t+1} > 0 | N_t = 0)$ and local extinction probability is $\Pr(N_{t+1} = 0 | N_t > 0)$. In fact, one can characterize $\Pr(N_{t+1} | N_t)$ in general, for each discrete state N_p , which represents an important generalization over the current treatments of the problem that characterize occurrence as being the binary event that $N > 0$, extinction as

the event that $N_{t+1} = 0 \mid N_t > 0$ and colonization as the event that $N_{t+1} > 0 \mid N_t = 0$. Under this coarse characterization of metapopulation dynamics, there is no consideration of density dependent mechanisms, and variation in abundance leads to heterogeneity in detection probability (Royle & Nichols, 2003) which must then be modeled indirectly. These issues are beyond the scope of this paper.

Estimation and inference

The metapopulation description of local abundance as a random (spatial) process seems a natural way to describe spatially referenced populations and may be appealing to many ecologists. However, local abundance is never observed, instead being informed by survey data according to one of the many possible sampling protocols described in "Notation and preliminaries" section (among others). Thus, it is necessary to incorporate this metapopulation model into a framework that is amenable to estimation and inference from data.

The metapopulation model is essentially a "random effects" distribution for local abundance, N_i . The classical approach to handling random effects (e.g., Laird & Ware, 1982) is to base inference on the marginal likelihood of the data, having removed the random effects from the likelihood by integration. In the multinomial sampling problems considered here, the integrated likelihood of \mathbf{y}_i is:

$$f(\mathbf{y}_i \mid \mathbf{p}, \theta) = \sum_{N_i=0}^{\infty} \left(\frac{N_i!}{y_{i1}! y_{i2}! y_{i3}! y_{i0}!} \pi_1^{y_{i1}} \pi_2^{y_{i2}} \pi_3^{y_{i3}} \pi_0^{N_i - y_i} \right) g(N_i \mid \theta)$$

Integrated likelihood has been considered under similar models by Royle & Nichols (2003), Dorazio et al. (2004), Royle (2004b) and Royle et al. (2004).

The Poisson distribution seems to be the *de facto* standard for the distribution $g(M \mid \theta)$ as it can be used to justify analysis based on the aggregated counts, and its motivation as a random distribution of individuals in space (a homogeneous point process) is appealing. Subsequently, I will focus on the Poisson case. In this case, the integrated likelihood is:

$$L(\{\mathbf{y}_i; i = 1, 2, \dots, R\} \mid \mathbf{p}, \lambda) = \prod_{i=1}^R \left\{ \sum_{N_i=0}^{\infty} \left(\frac{N_i!}{y_{i1}! y_{i2}! y_{i3}! y_{i0}!} \pi_1^{y_{i1}} \pi_2^{y_{i2}} \pi_3^{y_{i3}} \pi_0^{N_i - y_i} \right) g(N_i \mid \lambda) \right\}$$

where π_k are functions of p (depending on the sampling protocol used). This does have a closed form that is more amenable to computation. In particular,

$$L(\{\mathbf{y}_i; i = 1, 2, \dots, R\} \mid \mathbf{p}, \lambda) = \prod_i \prod_k \frac{e^{-\lambda \pi_k} (\lambda \pi_k)^{y_{ik}}}{y_{ik}!} \quad (5)$$

This is just the product of (independent) Poisson random variables. Maximization of (5) yields esti-

mates of λ or any covariate effects on abundance, and detection probability parameters. The fact that λ appears as a product with each π_k in Eq. (5) may lead one to question identifiability of model parameters. However, the π_k are not freely varying parameters, but instead are constrained by the sampling protocol to depend on a smaller set of detection probability parameters. One can easily write down consistent moment estimators for λ and detection probability parameters from Eq. (5) under the common sampling protocols.

It is a simple matter to maximize Eq. (5) numerically using conventional methods found in many popular software packages. For example, the free software package **R** (Ihaka & Gentleman, 1996) was used in the analyses of "Applications" section (routines are available from the author upon request).

A natural alternative to integrated likelihood for fitting random effects models is to adopt a Bayesian view and focus on characterizing the posterior distribution of the model unknowns conditional on the data using common Markov chain Monte Carlo (MCMC) methods. While this is straightforward in the present problem, I neglect those details here. While there are considerable philosophical differences between the two approaches, I believe that the main practical difference has to do with estimating the random effects (or summaries of them) and characterizing uncertainty in those estimates. This is discussed in the following section. In more complex models, such as when additional random effects are considered in a model for λ_p , estimation by integrated likelihood becomes difficult and so adopting a Bayesian formulation of the problem might become necessary (see Royle et al., 2004b).

Estimating abundance and related quantities

The MLE of λ , $\hat{\lambda}$, is an estimate of the *prior* mean abundance at a site. Or, in the case where λ_i varies (e.g., covariates), one obtains $\hat{\lambda}_i$ as a function of abundance covariates. To estimate N_{total} note that, under the Poisson assumption on N_p , $N_{total} \sim \text{Poisson}(R\lambda)$ and so

$$\hat{N}_{total} = R \hat{\lambda}$$

where $\hat{\lambda}$ is the MLE from the integrated likelihood.

Generally, interest may not be in the estimated prior means, but rather in estimating the realized abundance either for the collection of sample locations, or aggregated in some manner (over some spatial domain, or a collection of sample sites). For this, the classical method of estimating random effects is referred to as *Best Unbiased Prediction* (BUP). That is,

$$\hat{N}_i = E[N_i \mid \mathbf{y}_i, \lambda]$$

where $\hat{\lambda}$ is used in place of λ . This is a simple calculation (see Royle, 2004a for an example).

The Bayesian treatment of the problem is more general in the sense that variation in $\hat{\lambda}$ is directly considered. For example, the Bayes estimator of N_i is the posterior mean:

$$\hat{N}_i^* = E[N_i | \mathbf{y}_i].$$

In effect, the dependence on λ has been removed by integration. Consequently, one could expect \hat{N}_i^* to be more variable than \hat{N}_i in practical sample sizes.

Estimates of patch occupancy, say ψ , can also be obtained from these random effects models. For example, under the Poisson model for N_i , $\psi = 1 - e^{-\lambda}$.

Goodness-of-fit and model selection

One convenient implication of the closed form likelihood given by Eq. (5) is that one can use conventional deviance statistics for Poisson data to assess goodness-of-fit (see Dorazio et al. [2005] and Royle et al. [2004a] for examples). Under negative binomial models, or when the likelihood is not multinomial, bootstrap procedures appear to be necessary (Dorazio et al., 2005; Royle, 2004b; Dodd & Dorazio, in press). Model selection based on integrated likelihood may be carried out using AIC (Burnham & Anderson, 1998) regardless of the form of the likelihood.

Applications

The modeling framework presented here can be easily applied to any of the common bird sampling protocols described previously. To illustrate, we consider application to data collected using conventional point count data, and also data collected according to temporal removal protocol. A comprehensive analysis of a large-scale capture-recapture data set is considered by Royle et al. (2004b) and an application to distance sampling data is given by Royle et al. (2004a). Dodd & Dorazio (in press) provide a comprehensive integrated-likelihood analysis of frog count data collected according a point counting protocol.

Point counts

Point counts are often considered to be of marginal value to statisticians with an interest in conventional modeling of marked animal data because there is a widespread misperception that information on abundance cannot be disentangled from detection probability. Royle (2004) showed that if point counts are spatially and temporally replicated within a demographically closed system, then the integrated likelihood methods described in "Estimation and inference" section can be used to effectively model both detection and abundance effects.

An important distinction between the point count protocol and the others considered previously is that temporal replication is necessary to estimate detection from simple point counts. This is because given simple binomial counts, y_i , with index N_i and probability p , where N_i are independent random variables from $g(N| \theta)$, p appears as a product with the location parameter of g in the integrated likelihood. For example, in the Poisson case with mean λ , the marginal distribution (the integrated likelihood) of y_i is Poisson with mean $p\lambda$. Royle et al. (unpublished report) gave a heuristic explanation to demonstrate that additional information from spatial and temporal replication is available. In particular, a moment estimator for p is simply the correlation between counts made in successive sample periods. i.e.,

$$\tilde{p} = \text{Corr}(y_{i1}, y_{i2}) \quad (6)$$

for counts made at two sampling occasions. Then, $\hat{\lambda}$ is \bar{y}/\tilde{p} .

More formally, the integrated likelihood under the replicated point count protocol is

$$f(\mathbf{y}|p, \theta) = \prod_i \left\{ \sum_{N_i=0}^{\infty} \left\{ \prod_t \frac{N_i}{(N_i - y_{it})!} p^{y_{it}} (1-p)^{N_i - y_{it}} \right\} g(N_i | \theta) \right\} \quad (7)$$

p can vary as a function of covariates, and even temporally, but we neglect that generality here. Note that Eq. (7) does not close, contrary to the multinomial likelihood case that yields Eq. (5).

Data considered here are a subset of those analyzed by Royle (2004a) consisting of replicated point counts at 50 stops along a North American Breeding Bird Survey route. The point counts were replicated 11 times within approximately a one month period during the breeding season. Here, we consider only the first two counts for all 50 stops. Poisson and negative binomial models were considered for abundance. Under the Poisson model, the moment estimates of p and λ were also computed (\tilde{p} and $\hat{\lambda}$ based on Eq.(6)). For comparison, an abundance index being the mean (across sites) of the maximum count (over the two samples) was also computed. The 4 species considered are: Ovenbird (*Seiurus aurocapillus*), Hermit thrush (*Catharus guttatus*) Woodthrush (*Hylocichla mustelina*) and American robin (*Turdus migratorius*). Results of the model fitting are given in table 2, along with AIC scores (Burnham & Anderson, 1998).

Generally, the overdispersed negative binomial appears favored (except for the Hermit thrush). Estimated mean abundance differs considerably from that reported by Royle (2004) based on analysis of all 11 replicates. This is consistent with lack of closure over the longer time period or higher rates of temporary emigration which is why I have restricted attention to the first two replicate observations here.

The main purpose of this example is to demonstrate that it is feasible to estimate abundance

Table 2. MLEs and AIC for Poisson and negative binomial hierarchical models fitted to the avian point count data: $\tilde{\rho}$ and $\tilde{\lambda}$ are the Poisson moment estimates.

Tabla 2. Estimaciones de los parámetros de máxima verosimilitud (MLE) y criterio de información de Akaike (AIC) para modelos Poisson y modelos jerárquicos binomiales negativos ajustados a los datos de recuentos puntuales: $\tilde{\rho}$ y $\tilde{\lambda}$ son las estimaciones del momento de Poisson.

Species	Index	Poisson				Negative binomial				
		$\tilde{\rho}$	$\tilde{\lambda}$	$\hat{\rho}$	$\hat{\lambda}$	AIC	$\hat{\rho}$	$\hat{\mu}$	$\hat{\alpha}$	AIC
Ovenbird	0.96	0.53	1.25	0.43	1.53	215.68	0.33	2.01	1.69	213.70
Hermit thrush	0.10	0.55	0.13	0.55	0.13	47.82	0.55	0.13	inf	49.82
Woodthrush	0.52	0.60	0.63	0.58	0.65	150.59	0.53	0.72	0.78	147.44
Am. Robin	1.12	0.46	1.65	0.38	2.02	241.73	0.17	4.53	1.21	235.16

from simple point counts while controlling for (i.e., modeling) detection probability. In point count sampling, there is some advantage to reducing the time interval between counts to the extent possible in order to minimize temporary emigration which leads to some complication interpreting $\hat{\lambda}$ as density (applicable to a known area). Thus, consecutive counts (e.g., consecutive three minute point counts) may be the best strategy for implementing the point count estimator.

Removal counts

Next we consider avian point count data collected in Frederick County, Maryland. The data were collected at 70 locations within a large forest tract, according to a conventional removal sampling protocol (Farnsworth et al., 2002) with four sample intervals of length three minutes. The main objective was to evaluate the effect of two habitat covariates: understory foliage cover (UFC) and the basal area of large trees (BA). See Royle et al. (2004) for further description and an alternative analysis of some of these data.

We focus here on data for the Ovenbird (*Seiurus aurocapillus*). The data for each sample point are $y_i = (y_{i1}, y_{i2}, y_{i3}, y_{i4})$ where y_{ik} is the number of males first seen in interval k . For this illustration, we assume that detection probability, p , is constant so that the multinomial cell probabilities are:

$$\begin{aligned} \pi_1 &= p \\ \pi_2 &= (1 - p)p \\ \pi_3 &= (1 - p)^2 p \\ \pi_4 &= (1 - p)^3 p \end{aligned}$$

Several covariates were collected that are thought to influence p (e.g., time of day) and a more complete analysis of these data is in progress. Here, we consider only the habitat effects on abundance. That reasonable covariates on both detection and abundance can be identified is important

motivation for considering the mixture models elaborated on in "Estimation and inference" section. Removal data from several sites are shown in table 3, highlighting the typical small sample data sets that arise from local scale bird counting.

Models were fit using the Poisson metapopulation model assuming that

$$N_i \sim \text{Poisson}(\lambda_i)$$

where

$$\log(\lambda_i) = b_0 + b_1 \text{UFC}_i + b_2 \text{BA}_i$$

Results for several models are summarized in table 4, including AIC scores for evaluating the relative merits of each model.

For example, under the constant model $\hat{\lambda} = 1.138$ (SE = 0.093), or 1.138 male ovenbirds per point count sample. Point counts in this study were of radius 100 m, so one could interpret this as density if so inclined. More importantly, the habitat effects appear important so that density changes as a function of UFC and BA. There is a large positive effect of UFC and negative effect of BA. Because ovenbirds are ground nesters, and therefore would benefit from protection afforded by understory foliage, these results appear sensible. Also, the fact that the model containing both effects was not favored is not unexpected because UFC and BA are negatively correlated. These results are broadly consistent with those reported by Royle et al. (2004a) obtained using a distance sampling protocol (data were collected in a manner consistent with multiple protocols).

Conclusions

In this paper I have considered the problem of modeling spatially replicated avian count data that are collected according to many common sam-

Table 3: Ovenbird removal data (number first seen in four consecutive intervals).

Tabla 3. Datos de extracción del tordo mejicano (primer número observado en cuatro intervalos consecutivos).

	t = 1	t = 2	t = 3	t = 4
point 34	0	0	0	0
point 35	0	0	0	0
point 36	2	0	1	0
point 37	1	0	0	0
point 38	0	1	0	0
point 39	1	1	0	0
point 40	1	0	0	0
point 41	2	1	0	0
point 42	0	1	0	0
point 43	1	2	0	0
point 44	0	0	0	1
point 45	1	0	1	0

pling protocols. These include methods that yield a multinomial sampling distribution including conventional capture–recapture methods, multiple observer sampling, temporary removal and even simple point counts. One important statistical consideration is that data are frequently sparse (low counts and many zeros), owing to generally low densities of most breeding birds, and small sample areas. In addition, the likelihood under spatial replication may contain a large number of abundance parameters (N_i for each sample location) that render it intractable using conventional methods.

Conventional methods of analyzing bird count data often focus on estimating total abundance

over the collection of sample locations. Under this limited treatment of the problem, variation at the level of the sample location is, in effect, averaged out. Covariates cannot be considered, and one must consider spatial scale in deciding how to aggregate data. Importantly, aggregation may only be justifiable under certain spatial homogeneity assumptions. For example, if local abundance (at the level of the sample locations) is assumed to be Poisson with constant mean, then aggregation can be justified. However, this may not be a reasonable assumption in many problems.

Alternatively, the spatial attribution of the data is an important consideration in many studies, and can be exploited to develop more general models for describing abundance. For example, the goal of many studies is to estimate abundance covariate effects. And, factors that influence detectability may also vary among sample locations. Explicitly acknowledging spatial variation in local abundance facilitates investigation of these possibilities.

The solution to the problem of modeling spatially replicated data proposed here is to view local abundance as a random process. Then, attention can be focused on developing a model for the variation in local abundance free of detection probability considerations. This is appealing in the context of familiar metapopulation ideas that seek to characterize the structure among spatially referenced (local) populations that constitute the metapopulation. Taken together, the data model (the multinomial likelihood) and metapopulation model define a simple hierarchical model for which formal and rigorous methods of analysis are possible. For example, one can estimate parameters and conduct inference based on the integrated likelihood (having removed the random effects by integration). Alternatively, Bayesian analysis based on the posterior distribution is relatively straightforward.

The generality of the proposed modeling strategy is appealing. Mean abundance (λ under the Poisson model) may be parameterized in terms of additional parameters that describe variation in the Poisson mean (and hence abundance), and

Table 4: Results of models fit to ovenbird counts obtained under a temporary removal protocol.

Tabla 4. Resultados de los modelos ajustados a los recuentos del tordo mejicano obtenidos con arreglo a un protocolo de extracción temporal.

Model	p	b_0	UFC	BA	AIC
Constant	0.572	0.130			303.86
+ UFC	0.572	0.113	1.859		303.32
+ BA	0.572	0.106		-0.829	302.35
+ UFC + BA	0.572	0.102	1.042	-0.643	303.72

there is no need even to restrict attention to a Poisson random effects distribution. Such generality is easily dealt with formally within the context of the hierarchical model specification.

Two brief examples were given to demonstrate how a classical analysis of such models might proceed. The first example made use of simple point counts (replicated temporally) and considered a simple constant detection model and both Poisson and negative binomial models for local abundance. In the second example, data collected according to a removal sampling protocol were considered. In that example, habitat covariates were considered as possible effects on local abundance.

Extension to demographically open systems

Considerable generality can be achieved by considering extensions of hierarchical abundance models to systems that are demographically open, such as might occur if sampling is conducted during the breeding season in multiple years. There are several interesting "open population" situations that may be considered: (1) Many monitoring programs that generate counts in multiple years may not yield information on individual animals across years. This is common of most "point counting" surveys. In this situation, a simple metapopulation model structure such as $N_{i,t} \sim \text{Poi}(\lambda_t N_{i,t-1})$ may be useful for integrating data across years. Moreover, they facilitate a characterization of metapopulation dynamics that represents a generalization over methods considered by, for example, MacKenzie et al. (2003) that are based on detection/non-detection data; (2) A common lack of closure is due to the phenomenon of "temporary emigration". In this case, let M_i be the size of some super-population located at sample location i . Let $N_{i,t} \sim \text{Bin}(M_i, \phi)$ be the number of individuals available for sampling during occasion t at site i . Finally, let $\mathbf{y}_{i,t}$ be the multinomial data with index $N_{i,t}$ collected according to one of the standard sampling protocols. Note that $N_{i,t}$ may be removed by integration so that, marginally, $\mathbf{y}_{i,t}$; $t = 1, 2, \dots$ are multinomial random variables with index M_i and cell probabilities $\phi \pi_k$. Consequently, the joint likelihood of the data is a product *multinomial*, similar to that described in "Point counts" section. However, here the temporal replication, combined with some protocol other than simple point counts, allows estimation of the additional parameter ϕ , which is 1 minus the *temporary emigration* probability; (3) The third type of open scenario is that in which there exists encounter information on individual animals across years such as that arising from sampling based on networks of mist net stations. In this case, N_t must be decomposed into a survival component and a recruitment component where the survival component is $\text{Bin}(N_{t-1}, \phi_s)$ and the recruitment component is $\text{Poi}(N_{t-1}, \lambda_t)$. Note that individual encounter information is directly informative about ϕ whereas a spatial model for abundance is informative about

the *total* of the survival and recruitment processes. It stands to reason that such models will yield improved estimates of (local) survival and recruitment parameters.

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