Modelling occurrence and abundance of species when detection is imperfect

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Relationships between species abundance and occupancy are of considerable interest in metapopulation biology and in macroecology. Such relationships may be described concisely using probability models that characterize variation in abundance of a species. However, estimation of the parameters of these models in most ecological problems is impaired by imperfect detection. When organisms are detected imperfectly, observed counts are biased estimates of true abundance, and this induces bias in stated occupancy or occurrence probability. In this paper we consider a class of models that enable estimation of abundance/occupancy relationships from counts of organisms that result from surveys in which detection is imperfect. Under such models, parameter estimation and inference are based on conventional likelihood methods. We provide an application of these models to geographically extensive breeding bird survey data in which alternative models of abundance are considered that include factors that influence variation in abundance and detectability. Using these models, we produce estimates of abundance and occupancy maps that honor important sources of spatial variation in avian abundance and provide clearly interpretable characterizations of abundance and occupancy adjusted for imperfect detection.

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With the introduction of the metapopulation concept (Levins 1969, Hanski 1999), considerable theoretical and practical attention has been focused on patch occupancy and related metapopulation concepts. Patch occupancy has replaced abundance as the state variable of interest in many animal population studies. At least in part, this is because many interesting ecological phenomena are naturally expressed in terms of occupancy metrics or related quantities (e.g. species range) but also because occurrence is simpler to quantify in many problems. Interest in patch occupancy, at least in a population monitoring context, is often motivated by its likely relationship to abundance. That is, site occupancy is believed to be an informative index to population status.

A recent paper by He and Gaston (2003) focused on general phenomenological models for both the relationship between occupancy and abundance (Wright 1991, Hanski et al. 1993) and the relationship between the mean and variance of abundance over space (Taylor 1961). They combined the two general models into a single model and stated: "the unification of the two general ecological patterns of variance/mean and occupancy/abundance implied by the model is novel and has not apparently been reported and investigated before" (He and Gaston 2003: 366). Then, using several data sets, they estimate one of these two general relationships and used the resulting parameters to predict the other relationship in order to provide evidence that these two relationships "are just different expressions of the same phenomenon" (He and Gaston 2003: 367).

In the present paper, we offer two suggestions for modeling and investigating the relationships discussed

by He and Gaston (2003). The first suggestion is that it is useful to view these relationships not through the combination of two phenomenological models but as a natural consequence of the fact that all three quantities of interest, abundance, occupancy, and variance in abundance, are completely specified by the species abundance distribution. Most commonly used discrete probability models needed to describe such distributions impose structural relationships between variance and mean. In addition, abundance and occupancy are expressed as parameters, quantiles, or other functions of the parameters of such distributions. Thus, the relationships emphasized by He and Gaston (2003) emerge directly from species abundance distributions.

For example, we recently elaborated on the fundamental relationship between occupancy and abundance (Royle and Nichols 2003). Specifically, let N_i be the abundances of a species in a set of disjoint regions (or spatial locations) $i = 1, 2, \ldots, R$. If the N_i are viewed as realizations of a random variable with density $g(N; \theta)$, then occurrence probability (patch occupancy, denoted by ψ) is simply $\Pr(N > 0; \theta)$. Thus, a characterization of the abundance distribution, yields a characterization of occurrence probability. Obviously, quantiles of g may be expressed in terms of the parameters θ (i.e. mean and variance) as discussed at length by He and Gaston (2003). For example, if N is Poisson, then

$$\psi \equiv 1 - g(0; \lambda) = 1 - e^{-\lambda} \tag{1}$$

If N is negative binomial with mean μ and over-dispersion parameter k, then

$$\psi \equiv 1 - g(0; \mu, k) = 1 - \left(1 + \frac{\mu}{k}\right)^{-k} \tag{2}$$

Although the focus of our paper was on occupancy and abundance, structural mean/variance relationships are imposed by consideration of any particular abundance distribution. Importantly, inference about the precise linkage between mean/variance and abundance/occupancy from observational data is therefore a model selection problem (see Application).

Our second suggestion for the study of these relationships involves the recognition that species are virtually never detected with certainty. Thus, while detection of a species at a location may be unambiguous, failure to detect the species may be a consequence of either true absence of the species or presence, but failure to detect (Bayley and Peterson 2001, Kéry 2002, MacKenzie et al. 2002, 2003, Moilanen 2002, Royle and Nichols 2003, Tyre et al. 2003, Gu and Swihart 2004). Thus we recommend direct incorporation of detection probability parameters into any attempts to draw inferences about abundance and occupancy and the true underlying parameters of interest. This is important because factors that influence detectability may vary spatially and temporally, and thus variation in observed counts cannot be attributed solely to variation in abundance. Importantly, occurrence probability will be under-stated when simple counts are regarded as true abundance. Although He and Gaston (2003) noted the importance of detectability, they estimated relationships between occurrence and abundance assuming that abundance is observable without error. We note in passing that most of the evidence for the two general relationships emphasized and combined by He and Gaston (2003) also failed to use the inference methods (Seber 1982, Williams et al. 2002) needed to deal with the fundamental reality that perfect detection is seldom encountered in field sampling of animal populations.

Recognizing that occupancy is not generally detected with certainty, Bayley and Peterson (2001), MacKenzie et al. (2002, 2003) describe an approach for estimating occupancy from detection/non-detection data, but without considering the relationship between occupancy and abundance. Royle and Nichols (2003) extended this work by exploiting the relationship between heterogeneity in detection probability and variable abundance in order to estimate the abundance distribution and occupancy from simple detection/non-detection data. Royle (2004a) elaborated on an extension of this approach to modeling abundance from counts that are assumed to have a binomial sampling distribution. Under these models, it is possible to estimate abundance distribution parameters, and hence occupancy, when detection probability is less than 1.

In this paper we elaborate on these two suggestions by considering inference about the relationship among occupancy, abundance and variance in abundance in the case where organisms are imperfectly detected (detection probability < 1). Drawing on a considerable body of recent work that deals with estimation and modeling in the presence of imperfect detection, we describe a theory for statistical inference about mean/variance−occupancy/abundance phenomena in the presence of imperfect detection of organisms. This theory incorporates the basic structnral elements that were the focus of He and Gaston (2003), and includes inference procedures based on observable qnantities as elaborated by Kéry (2002), MacKenzie et al. (2002, 2003), Royle and Nichols (2003), Tyre et al. (2003), Gu and Swihart (2004), and Royle (2004a).

In the following section we describe a common type of data structure that enables estimation of abundance/occupancy models in the presence of imperfect detection. In the next section we describe estimation of these models via maximum likelihood. An application to modeling abundance and occurrence of birds in the presence of imperfect detection is given in Application. We conclude with some general discussion and considerations for further development of these models.

Data structure and models

In the present development, we assume that animals are counted at R spatial locations ("sites") $i = 1, 2, \ldots, R$ such that the counts can be viewed as realizations of a binomial random variable with index N_i (local abundance) and detection probability p. Denote these counts as y_i, and let

$$y_i \sim Bin\,(N_i, p)$$

indicate that y_i has this binomial probability distribution. It is not possible to estimate or model variation in abundance free of detection probability without additional information. In many animal sampling problems, a simple way to acquire this additional information is to generate replicate counts (in time) under the conventional "closed population" assumption that no gains or losses occur over the duration of the replicate sampling. That is, let $y_{it}; t = 1, 2, \ldots, T$ be independent counts made at sites $i = 1, 2, \ldots, R$ so that

$$y_{it} \sim Bin\,(N_i, p); \quad t = 1, 2, \ldots, T$$

That local abundance, N_i, is constant for each replicate sample (t) at location i is the manifestation of the closure assumption.

For clarity, the binomial sampling model has been expressed with constant detection probability across sites and samples within sites. However, one may consider the general case where p varies spatially and temporally, perhaps in relation to measurable covariates. We provide such an example in Application.

Under this binomial sampling model, the joint likelihood of the data from all sites is the product binomial

$$L(\{N_i\}, p|\{y_{it}\}) = \prod_{i=1}^{R} \left\{ \prod_{t=1}^{T} Bin\,(y_{it}; N_i, p) \right\} \qquad (3)$$

containing the collection of abundance parameters $\{N_i\} = (N_1, N_2, \ldots, N_R)$ and detection probability p (and any parameters that describe variation in detection probability). Although this likelihood is not inherently intractable, practical considerations in many problems render it so. In particular, there are a large number of unknown "parameters", and often the observed counts at each site are relatively sparse owing to low densities of many animals relative to sample extent.

In part, this statement of the problem as a difficult estimation problem motivates the need for additional model structure. However, as noted in the Introduction, there is considerable ecological interest in models of abundance and occurrence. This interest provides a framework that facilitates meaningful inference in the context of counts observed with imperfect detection. In particular, specification of a model to describe variation in abundance among sites is, in effect, a prior distribution on the unobservable abundance parameters. This prior distribution is exploited to efficiently combine data

from these spatially referenced samples in order to yield estimates of model parameters that include both those of the abundance distribution, and those that describe the detection process.

Abundance models

Specification of a probability model for abundance, $q(N; \theta)$, is fundamental to the problem of conducting inference based on the sampling model given by Eq. 3. We note that He and Gaston (2003) elaborated in some detail on the abundance/occurrence relationships induced by such models, but neglected consideration of observational models of the sort specified in the preceding section. Subsequently, we provide a brief synopsis of abundance models before describing the integration of models for observational data with those of abundance.

The Poisson model is a natural candidate for describing animal abundance because it arises under the assumption that individuals are distributed completely at random. For this reason, it is a standard null model for the distribution of organisms in many ecological studies of plants and animals. Under the hypothesis that individuals are randomly distributed, aggregating over disjoint (sample) units of constant area yields that N_i has a Poisson distribution with mean λ. For units that are of varying area, $\lambda_i = A_i \lambda_0$ where A_i is the area of the ith unit.

In some problems, it may be important to admit the possibility that expected abundance varies spatially. There are two natural extensions of the Poisson model that accommodate this. First, if there exist covariates thought to influence abundance, then one might consider the log-linear model:

$$\log(\lambda_i) = b_0 + b_1 x_i \qquad (4)$$

where x_i is the value of some covariate at location i. Second, a general form of spatial variation in abundance is obtained by allowing λ to vary stochastically. For example, if λ_i has a Gamma distribution then N_i has a negative binomial distribution, which is the most common model for counts containing excess variation relative to the Poisson (White and Bennetts 1996). The negative binomial model with mean μ and over-dispersion parameter k yields the abundance/occupancy relationship given in the Introduction (Eq. 2). Factors that influence abundance may be incorporated into the negative binomial mean as in the Poisson case:

$$\log(\mu_i) = b_0 + b_1 x_i \qquad (5)$$

Extra-Poisson variation of the sort described by the negative binomial model might arise, for example, when abundance is related to unobserved covariates (i.e. that have been omitted from the model), or if individuals occur in clusters. Abundance models other than Poisson or negative binomial that allow for more flexibility

in modeling over-dispersion may also be considered (Bhattacharya and Holla 1965, Puig 2003). In practice, it may be desirable to formally choose among several plausible models of abundance given observational data because more complex (e.g. negative binomial) models may be unnecessary in some instances.

We emphasize that while the model development presented here has focused on describing variation in abundance, the linkage between abundance and occurrence is direct. In particular, regardless of the abundance model under consideration, occurrence probability can be related to parameters of that abundance model by evaluating the density at $N = 0$, corresponding to the event of non-occurrence. For example, under the Poisson and negative binomial models the occurrence probabilities are those given by Eq. 1 and 2, respectively. Consequently, given estimates of the abundance parameters (e.g. $\hat{\lambda}$ under the Poisson, or $\hat{\mu}$ and $\hat{k}$ under the negative binomial), one may thus obtain estimates of the probability of occurrence in addition to a characterization of abundance and the implied mean/variance relationship. In the following Section, we describe estimation of the parameters of these abundance/occurrence models by maximum likelihood when individuals are imperfectly detected.

Parameter estimation by maximum likelihood

The probability model $g(N; \theta)$ for the unobservable abundance parameters, $\{N_i\}$, in conjunction with the sampling model Eq. 3 yields what is often referred to as a hierarchical model (Link et al. 2002, Clark 2003, Wikle 2003). In this model, the abundance parameters are regarded as random effects for which the conventional treatment in classical statistics is to remove them from the likelihood by integration (Laird and Ware 1982). Estimation is then based on the marginal (or integrated) likelihood of the data which is a function of θ and, in the present context, parameters of the model which describes the detection process (nominally, p in Eq. 3).

Under the product binomial likelihood (Eq. 3) for the count data, the integrated likelihood is:

$$L(\theta, p | \{y_{it}\}) = \prod_{i=1}^{R} \left(\sum_{N_i=0}^{\infty} \left\{ \prod_{t=1}^{T} \text{Bin}(y_{it}; N_i, p) \right\} g(N_i; \theta) \right)$$

(6)

where $g(N_i; \theta)$ is the Poisson, negative binomial, or another suitable (discrete probability density) abundance model.

Although Eq. 6 does not simplify in a meaningful way, it can be maximized numerically using conventional methods that are available in many modern software packages. Results in the following section were obtained using the nlm optimizer in the free software package R (Ihaka and Gentleman 1996).

Maximizing Eq. 6 yields estimates of the parameters of interest (i.e. those describing abundance and occurrence). Furthermore, it is also possible to obtain estimates of the number of individuals that were susceptible to sampling (nominally, the "population size"), or even estimates of particular N_i's (local population size) using conventional methods of predicting random effects (Royle and Nichols 2003, Royle 2004a). However we expect there is little ecological interest in obtaining estimates of such small, localized populations in most cases.

Application

We consider willow tit (*Parus montanus*) data collected as part of the Swiss Breeding Bird Survey (Schmid et al. 2001, Kéry and Schmid 2004, Kéry et al. 2005). This species is a small (9–12 g) songbird that inhabits forests rich in standing dead logs. Data are counts of putative "territories" obtained from applying the territory mapping method (Bibby et al. 1992) at 239 sites (1 km quadrats) distributed in a systematic sample across Switzerland. Quadrats are sampled 3 times during the breeding season (15 April–15 July) along specific routes. The willow tit is a sedentary species and there are few movements within this period. Thus, abundance here is interpreted as the mean number of willow tit territories per 1 km^2.

Primary interest here focuses on estimating abundance and occurrence probability maps from these data. Importantly, spatial variation in abundance is fundamental to these objectives. In this regard, several possible variables affecting abundance were considered: (1) elevation, E (m); (2) percent forest cover, F; and (3) route length, L (km). The possibility of a quadratic elevation effect was also considered because we expect that the highest densities of many species occur at mid-elevations. Elevation and forest cover are natural candidates for describing avian abundance. On the other hand, route length is essentially related to effective sampling area. Because the sample route through each quadrat was not standardized, the population of territories susceptible to detection is liable to vary depending on route length.

These abundance covariates were modeled on the log-mean scale according to

$$\log(\lambda_i) = b_0 + b_1 E_i + b_2 E_i^2 + b_3 F_i + b_4 L_i$$

where λ_i is the Poisson mean, E_i, F_i and L_i are elevation, forest cover and route length for quadrat i, respectively, and b_0, b_1, b_2, b_3, b_4 are the parameters to be estimated. Analogous model structure was considered for the

negative binomial abundance model. Elevation (mean = 1177 m, SD = 646 m) and forest cover (mean = 38.24, SD = 25.77) were standardized to have mean 0 and standard deviation 1. Route length was log-transformed to preserve the desired area-scaling behavior of abundance as sample area is increased.

Likewise, detectability is believed to vary among surveys (conducted on different days during the breeding season) because nesting pairs are best detectable during territory establishment and more elusive during the incubation and early feeding stages. This suggests the potential for a nonlinear response of detection probability to date, and so we considered the possibility of a quadratic date effect. These potential effects on detection probability were modeled using a logit-linear model according to

$$\text{logit}\,(p_{it}) = a_0 + a_1 D_{it} + a_2 D_{it}^2$$

where D_{it} is the day on which observation t = (1, 2, 3) was made on quadrat i and a_0, a_1, a_2 are the detection parameters to be estimated.

We fit the integrated likelihood models under both Poisson and negative binomial distributions for abundance. Results for the top 5 models of each class, according to AIC (Burnham and Anderson 1998), are summarized in Table 1. We see that the negative binomial models are favored by AIC, with the most complex model (containing all of the effects) being slightly favored to those without either the quadratic sample day effect, or with no day effect.

The best negative binomial model was used to construct estimated abundance and occurrence probability (according to Eq. 2) maps. These are shown in Fig. 1 and 2, respectively. These maps show the strong relationship between willow tit abundance/occurrence and the distribution of forested mid-elevation areas in Switzerland. The willow tit is not common at lower elevations, probably because intensive forest use has eliminated a large part of standing dead trees and, obviously, it does not occur above the treeline. It reaches its maximum abundance, and probability of occurrence, at mid-elevations where forest use is much less intensive. The estimated optimal elevation for density occurs at

approximately 1446 m. This was obtained as $\text{elev}_{opt} = 0.898/2.159$ from the estimated quadratic response of abundance to elevation (Table 1), and then rescaled by the mean (1177 m) and standard deviation (646 m).

Discussion

In this paper we have demonstrated how to estimate abundance and occurrence probability models from avian count data that are biased by imperfect detection. These models represent an important generalization over the ideas suggested by He and Gaston (2003) because they enable estimation of abundance and occupancy in the presence of imperfect detection.

The detectability of individuals is an important consideration when inference is to be conducted about animal abundance because animals are seldom detected perfectly. Importantly, factors that influence abundance and detectability may vary spatially and temporally, and abundance itself influences the probability of detecting organisms. Consequently, we believe that inferences about abundance/occupancy relationships are of little practical utility when the detectability of organisms is disregarded and that it is crucial for ecologists to understand the importance of detectability when attempting to make inferences regarding abundance and occupancy relationships from observational data.

Detection is especially crucial when interest is focused on estimating and modeling occurrence, because observation of zero individuals can arise either because the species of interest was not present, or because it was present but not detected. More generally, the linkage between occurrence and abundance under any parametric model is directly influenced by the mean of the abundance model (e.g. λ in Eq. 1 or μ in Eq. 2). Thus, any bias in estimates of mean abundance (such as that due to non-detection) will yield biased estimates of occurrence probability. This bias cannot be resolved without consideration of detectability. The models used here permit unambiguous inference about the relationship between abundance and occupancy unconfounded by sampling covariation.

Table 1. Estimates of negative binomial and Poisson abundance model parameters and AIC for the willow tit territory count data.

Model	Abundance parameters						Detection parameters			AIC
	k	b0	for	el	el^2	len	a_0	day	Day^2	
NB	1.667	−1.750	0.773	2.159	−0.898	1.410	−0.814	−0.138	0.038	1048.5
NB	1.692	−1.703	0.772	2.130	−0.885	1.400	−0.773	−0.089	−	1049.3
NB	1.709	−1.659	0.783	2.076	−0.898	1.413	−0.866	−	−	1051.2
NB	1.781	0.428	0.855	2.084	−0.820	−	−0.809	−0.137	0.037	1052.9
NB	1.799	0.456	0.853	2.057	−0.807	−	−0.768	−0.090	−	1053.6
P	−	−1.779	0.636	2.363	−0.874	1.059	0.069	−0.189	0.074	1212.0
P	−	−1.714	0.629	2.322	−0.859	1.025	0.210	−0.095	−	1217.3
P	−	−1.712	0.633	2.289	−0.865	1.037	0.153	−	−	1218.9
P	−	−0.217	0.734	2.350	−0.807	−	0.124	−0.186	0.067	1232.7
P	−	−0.202	0.725	2.312	−0.793	−	0.243	−0.101	−	1236.6

Expected value of N(s) — quantile scale

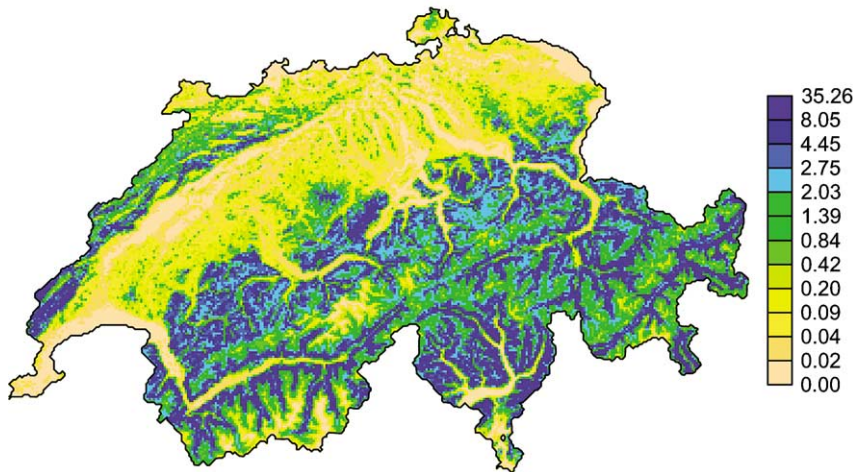|	
■	35.26
■	8.05
■	4.45
■	2.75
■	2.03
■	1.39
■	0.84
■	0.42
■	0.20
■	0.09
■	0.04
■	0.02
■	0.00

Fig. 1. Abundance map for the willow tit under the best fitting negative binomial model.

Here we applied a general class of abundance/occurrence models based on simple counts (Royle and Nichols 2003, Royle 2004a) to avian count data from the Swiss Breeding Bird Survey. In addition to parameters which describe variation in abundance of organisms (He and Gaston 2003), these models also contain parameters that describe variation in detection probability. Poisson and negative binomial models of abundance were considered. In each case, a number of covariates thought to influence abundance and detectability were considered. Based on AIC, the over-dispersed negative binomial model was favored over the Poisson model. The resulting estimated abundance and occurrence maps honor variations in landscape structure that influence bird abundance (e.g. forest cover, elevation) in addition to structure in the observed counts that is due to variation in detectability. Estimates based on our models represent an improvement over other attempts at estimating the relationship

between occurrence and abundance (He and Gaston 2003) because they account for general bias due to failing to detect all individuals and variations in detectability across time.

We have illustrated the use of simple count data for estimating abundance and occurrence but note that many other common sampling protocols (i.e. other than simple counts) can be employed, including some that do not require temporally replicated sampling. For example, double-observer (Nichols et al. 2000), temporal removal (Farnsworth et al. 2002) and distance sampling (Rosenstock et al. 2002) have all been used to estimate avian abundance in the presence of imperfect detection. Estimation of models of abundance and occurrence from such data has been elaborated on for these more general protocols by Royle et al. (2004) and Dorazio et al. (2004). Various more specialized cases have also been considered including use of only detection/non-detection

Pr(occurrence)

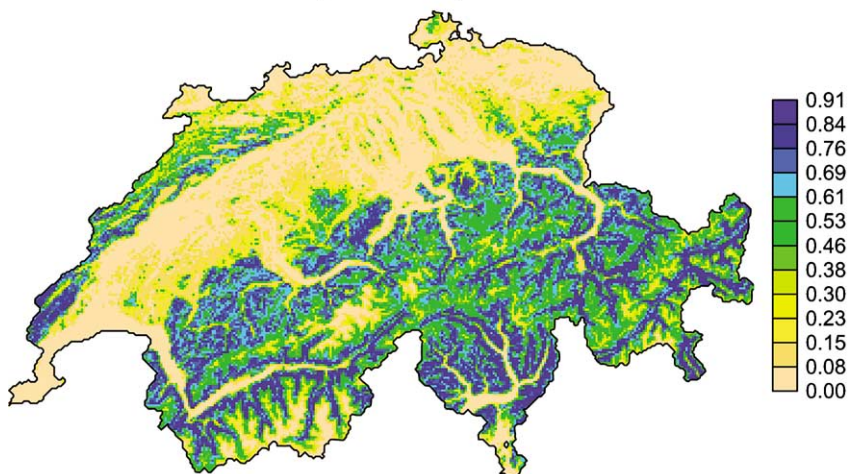|	
■	0.91
■	0.84
■	0.76
■	0.69
■	0.61
■	0.53
■	0.46
■	0.38
■	0.30
■	0.23
■	0.15
■	0.08
■	0.00

Fig. 2. Occurrence probability map for the willow tit under the best fitting negative binomial model.

data, (Royle and Nichols 2003) and ordinal abundance "index" data (Royle 2004b).

Finally, we believe that substantial generalization of the models applied here can be achieved by considering demographically open metapopulation systems involving local extinction and colonization processes. We note that such models have been developed for sampling that yields simple detection/non-detection data (MacKenzie et al. 2003), but not for more general data structures.

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