



ESTIMATING ABUNDANCE FROM BIRD COUNTS: BINOMIAL MIXTURE MODELS UNCOVER COMPLEX COVARIATE RELATIONSHIPS

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ABSTRACT.—Abundance estimation is central to avian ecology. For replicated counts, Royle (2004) developed a model to estimate abundance adjusted for detectability. Hitherto, it was unknown whether the same covariate was allowed to affect both abundance and detectability. This situation was disconcerting, because relationships between abundance and such covariates describing, for example, habitat, lie at the heart of ecology. I test this by simulation and provide additional guidelines on the model as well as code to fit it in a Bayesian mode of analysis. I simulated 1,000 data sets mimicking the Swiss breeding-bird survey “Monitoring Häufige Brutvögel” (three surveys in each of 268 quadrats). Elevation affected abundance negatively and detectability positively, resulting in a hump-shaped relationship between counts and elevation. I used WinBUGS to fit the model and estimate parameters, including quadrat-specific abundance and total abundance, across all 268 quadrats. For every parameter, the model recovered estimates that showed no indication of bias. The mean error in the estimated total population size across all quadrats was only 2%, whereas the summed maximum counts, a conventional abundance estimate, underestimated total population size by 43%. In contrast to maximum counts, the binomial mixture model revealed the true negative relationship between abundance and elevation. This model is a promising new alternative to capture–recapture or distance sampling methods to estimate bird abundance free of distorting effects of detectability. It has perhaps the fewest requirements, needing neither individual identification nor distance information to “convert” simple counts (“relative abundance”) into estimates of true abundance. It ought to be seriously considered in future bird-survey schemes. *Received 2 September 2006, accepted 17 June 2007.*

Key words: abundance estimation, Bayesian analysis, binomial mixture model, bird counts, monitoring, multi-site estimation, point counts, simple count data, WinBUGS.

Estimación de Abundancia a Partir de Conteos de Aves: Modelos Mixtos Binomiales Revelan Relaciones Covariadas Complejas

RESUMEN.—La estimación de la abundancia es un aspecto central en la ecología de aves. Royle (2004) desarrolló un modelo para estimar la abundancia ajustada por detectabilidad para conteos replicados. Hasta entonces, se desconocía si las mismas covariables podían afectar tanto a la abundancia como a la detectabilidad. Esta situación era desconcertante debido a que las relaciones entre la abundancia y covariables que describen, por ejemplo, el hábitat, son centrales en ecología. En este trabajo evalué esto mediante simulaciones y proveo directrices adicionales sobre el modelo y el código para ajustarlo a un modo de análisis Bayesiano. Simulé 1000 conjuntos de datos imitando el muestreo de aves reproductivas de Suiza “Monitoring Häufige Brutvögel” (tres muestreos en cada uno de 268 cuadrantes). La elevación afectó a la abundancia de forma negativa y a la detectabilidad de forma positiva, resultando en una relación en forma de joroba entre conteos y elevación. Utilicé WinBUGS para ajustar el modelo y estimar parámetros, incluyendo la abundancia específica para cada cuadrante y la abundancia total para los 268 cuadrantes. Para cada parámetro, el modelo generó estimados que no mostraron indicios de sesgo. El error promedio para el tamaño poblacional total fue sólo del 2%, mientras que la suma de los conteos máximos, un estimado de abundancia convencional, subestimó el tamaño de la población total en un 43%. De modo contrastante a los conteos máximos, el modelo mixto binomial reveló la relación negativa verdadera entre abundancia y elevación. Este nuevo modelo es una alternativa promisoría a los métodos de captura y recaptura o a los muestreos con distancias para estimar la abundancia de aves sin el efecto distorsionante de la detectabilidad. Este nuevo modelo tiene quizás el menor número de requerimientos, pues no necesita la identificación a nivel de individuo ni la información de distancia para “convertir” los conteos simples (“abundancia relativa”) en estimaciones de abundancia verdadera. El modelo debería ser considerado seriamente en los esquemas futuros de monitoreo de aves.

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TO A GOOD approximation, counting birds is the defining activity of a field ornithologist. Bird counts have produced the raw material for scientific studies in many branches of ecology, such as community dynamics (Boulinier et al. 1998), sexual selection (Doherty et al. 2003), population ecology (Sæther et al. 2006), and distribution (Guisan and Thuiller 2005). In addition, bird counts are among the most important organismic indicators in biodiversity monitoring programs, where the population sizes of selected species or guilds of species (e.g., farmland birds) are used as a measure of environmental health (e.g., Fewster et al. 2000, Gillings and Fuller 2001). Bird counts are also frequently used to measure the efficacy of nature-protection actions.

In practice, birds cannot be counted with certainty. Rather, their numbers must be estimated, because in nearly every instance some individuals will be missed. This follows from the fact that detection probability is rarely equal to 1. In an abundance context, detection probability is the probability that an individual present and exposed to sampling is actually detected and, therefore, appears in a count (Williams et al. 2002).

Many studies merely compare abundance over time (e.g., for estimating trends), regions (e.g., to identify range changes), or habitats (e.g., to detect high-density habitats for preserve selection). Ornithologists interested in comparative studies sometimes claim that only relative but not absolute abundance matters and that, consequently, it is unnecessary to estimate the fraction of birds counted (= detectability) (Anderson 2001, 2003; Engeman 2003). Simple counts are, therefore, widely used as indices of relative abundance by scientists claiming, believing, or at least hoping—perhaps after controlling for covariates (e.g., Link and Sauer 1998)—that the average detection probability is constant over dimensions of comparison such as time, regions, or habitats. The problems with this assumption have been shown repeatedly (e.g., Diefenbach et al. 2003, Selmi and Boulinier 2003, Kéry et al. 2005), perhaps nowhere so strikingly as in figure 1 of Link and Sauer (1998). Therefore, even when comparisons rather than absolute abundance are the focus of a study, it may be prudent to adjust for variation in detectability. This may help to avoid interpretation of patterns in counts that may reflect patterns in detectability rather than patterns in the underlying true abundance. One can adjust for detectability indirectly, by using covariates believed to reflect variation in detection probability (Link et al. 2006), or directly by estimating it, which will also result in an estimate of absolute abundance.

Bird abundance is usually estimated using distance sampling or some variant of capture–recapture sampling (Nichols et al. 2000, Farnsworth et al. 2002, Pollock et al. 2002). Both distance sampling and capture–recapture designs yield bird counts with some added information that enables true abundance to be estimated. With distance sampling, the added information is the distance of each bird counted from the transect or point of observation, whereas for all variants of capture–recapture (including removal) sampling, it is the unique identity of each counted bird. Very extensive literature exists on both designs, summarized in books by Buckland et al. (2001, 2004a) and Williams et al. (2002).

It was long believed that simple counts without information on identity or distance were useless for unbiased estimation of absolute abundance and that, therefore, their use in comparisons may be risky, owing to the possible distortions induced by patterns

in detectability (e.g., Burnham 1981; Anderson 2001, 2003; Rosenstock et al. 2002). For spatially and temporally replicated counts in a closed population, Royle (2004) developed a binomial mixture model for estimation of abundance that adjusts for detectability. Replicated counts are commonly used in bird surveys, whereby a large number of sites are each surveyed multiple times within an interval in which the population is effectively closed (e.g., within a breeding season). Royle's (2004) binomial mixture model thus appears to be promising for estimating abundance from animal-survey data and has performed well in first applications (Kéry et al. 2005, Royle et al. 2005). Covariates can be introduced for both abundance and detectability to test for the presence of such relationships and to improve the precision of the estimates.

However, hitherto it was unknown whether Royle's (2004) binomial mixture model was able to separate the effects of the same covariate acting on both abundance and detectability. Inability to do so might severely compromise the model's usefulness, because such covariates are likely to occur in many practical situations. For instance, habitat could influence both bird density and detectability. My aims here are (1) to test whether the binomial mixture model can actually elucidate effects of the same covariate on abundance and detectability, (2) to draw attention to this potentially very useful model, and (3) to provide code for fitting the model in a Bayesian mode of analysis using the free software R (R Development Core Team 2005) and WinBUGS (Spiegelhalter et al. 2003).

METHODS

Generation of data.—I simulated data to mimic the design of the Swiss breeding-bird survey “Monitoring Häufige Brutvögel” (MHB), a program conducted annually since 1999 by the Swiss Ornithological Institute (Kéry and Schmid 2004, Kéry et al. 2005). In the MHB, a systematic random sample of 268 quadrats, each 1 km², is surveyed three times using territory-mapping (Bibby et al. 1992) during each breeding season (15 April–15 July) in Switzerland along a quadrat-specific, irregular transect route averaging 5 km. About 20% of quadrats above 2,000 m in elevation are surveyed only twice, but I did not consider this feature here. For each species and year, a data set thus consists of the counts c_{ij} for 268 quadrats (indexed i) and three temporal replicates (indexed j).

Poisson-dispersed counts were simulated assuming that a single covariate had opposing effects on abundance and detection probability. Specifically, a negative relationship was assumed on the log scale between abundance (λ) and mean quadrat elevation: $\log(\lambda) = \alpha_1 + \beta_1 * \text{elevation}$, with $\alpha_1 = 2$ and $\beta_1 = -0.5$. Similarly, a positive relationship was assumed on the logistic scale between detection probability (p) and mean quadrat elevation: $\text{logit}(p) = \alpha_2 + \beta_2 * \text{elevation}$, with $\alpha_2 = 1$ and $\beta_2 = 2$. For computational reasons, I rescaled elevation by subtracting the mean and dividing by the standard deviation. Under this model specification, the relationships between elevation, abundance, and detectability partly cancel themselves out in the expected counts. Such a pattern may be attributable to effects of the habitat: A species depending on woodland may have greatest densities at lower elevations with greater forest cover, but may be more easily detectable at higher elevations with sparser forests. However, the details of the genesis of such complex relationships between one covariate and abundance

and detection probability, respectively, do not really matter for the purpose of the present study. I assumed that such covariates likely exist and wanted to know whether the parameters describing their relationship with abundance and detection probability are identifiable under the model.

The mixture model for counts.—Let N_i be the local abundance for quadrat i . Assuming a closed population, successive counts c_{ij} in quadrat i are considered binomial random variables with index N_i and detection probability p_{ij} , index j being for repeated surveys. Thus, the model for the replicate observations (the “observation model”) for the counts at site i is the product-binomial

$$g(c_i | N_i, p) = \prod_j \text{Bin}(c_{ij} | N_i, p)$$

Without loss of generality, I have considered here the case where p is constant but recognize that, in most applications, covariates thought to influence p will be available. It is useful to note that the information about detection probability p comes from the “similarity” of the repeated counts. Indeed, a moment estimator for p is given by the mean Pearson correlation coefficient among the counts.

The model as specified so far contains one abundance “parameter” for each quadrat. The N_i values can be regarded as random effects with (local abundance) distribution $f(N_i; \theta)$, and estimation and inference then focuses on the parameter(s) θ . A natural assumption about N_i values is that they follow a Poisson distribution with mean λ (Royle et al. 2005). The Poisson distribution is the customary description of a random spatial point pattern. In the frequent case where landscape covariates explain some variation in abundance, λ can be considered site-specific, such that

$$\log(\lambda_i) = \alpha + \sum_{k=1}^K \beta_k x_{ik}$$

where x_{ik} is the value of the k th covariate at site i . A natural generalization is to consider N_i to be negative binomial random variables, in which case f is parameterized by an overdispersion parameter in addition to the mean. Alternatively, extra-Poisson variation in λ can be expressed as an additive normal random effect for $\log(\lambda)$. In either case, models that include covariates can again be entertained.

Detection probability can vary in response to covariates as well. To allow for this, a linear logistic relationship can be considered:

$$\text{logit}(p_{ij}) = \alpha + \beta x_{ij}$$

here shown for a single covariate x_{ij} (e.g., survey duration or some measure of weather).

Regardless of the abundance model considered, estimation of abundance and detection probability parameters can be based on the integrated likelihood, a standard approach for estimation and inference in classical random-effects models (e.g., Laird and Ware 1982). Details can be found in Royle (2004), Kéry et al. (2005), and Royle et al. (2005). Alternatively, the model yields easily to Bayesian

analysis by Markov-chain Monte Carlo (MCMC) methods described briefly below.

Fitting the model.—I fitted the model in a Bayesian mode of analysis. Compared with the maximum-likelihood analysis (see R code in Kéry et al. 2005), Bayesian inference via MCMC results in remarkably more-parsimonious code (Royle and Dorazio 2006). The MCMC approach uses iterative samples from a simulated Markov chain to approximate features such as the mean and the dispersion of complex joint probability distributions of the parameters in a statistical model. A certain number of initial values of the chain must be discarded as not representative of the stationary distribution (so-called “burn-in”). After that, summaries such as mean and standard deviation can be used as point estimates and standard errors for the parameters of the model. The fitting of statistical models using MCMC has been made possible to many biologists mainly through the development of the popular free software WinBUGS. Link et al. (2002) give an accessible introduction to Bayesian inference, MCMC, and WinBUGS for biologists. More general information about Bayesian statistical inference using MCMC can be found in Brooks (2003) and Gelman et al. (2004).

I ran an initial analysis of one simulated data set in WinBUGS with 100,000 iterations to assess the number of iterations required to reach convergence. Visual inspection of the sampled chains for α , β_1 , α_2 , β_2 , and N_{total} suggested that convergence had been reached after ~250 iterations. Running multiple chains with different initial values yielded the same conclusion. Therefore, to be conservative, the first 1,000 iterations in the main simulation were discarded as burn-in. Thereafter, I used every fifth of 10,000 iterations to reduce autocorrelation among repeated iterations; such thinning results in a smaller but more information-dense sample of the posterior distribution. As a result, I used 2,000 iterations for inference about parameters. For all analyses, I used conventional vague priors for the parameters, so that all values of α , β_1 , α_2 , and β_2 were distributed as normal (mean = 0, variance = 10,000; also see Appendix).

I used R to generate 1,000 replicate data sets containing 268 sites with 3 replicated counts each and analyzed them using WinBUGS, version 1.4, executed in batch mode using the R add-on library R2WinBUGS (Sturtz et al. 2005). This took 72 h on a Pentium M 1.6-GHz processor with 1 GB RAM. The Appendix gives an R function to simulate and analyze the data under the Royle (2004) model using WinBUGS.

RESULTS

Features of the generated data.—In the simulated data, mean territory density per square kilometer declined from 17 at 200 m elevation to 3 at 2,700 m (Fig. 1A). Conversely, detection probability increased from 0.09 to 0.99 across the same elevational gradient (Fig. 1B). Adding Poisson sampling variation (i.e., going from Fig. 1A to 1C) did not change the pattern in abundance. However, the counts, which were much lower than the actual abundance, showed a quadratic effect of elevation, with highest “apparent abundance” at medium elevations (Fig. 1D–F). Hence, the effect of elevation on detection probability completely distorts its relationship with abundance.

Recovery of generating parameters.—The binomial mixture model succeeded in recovering the parameters for the relationships

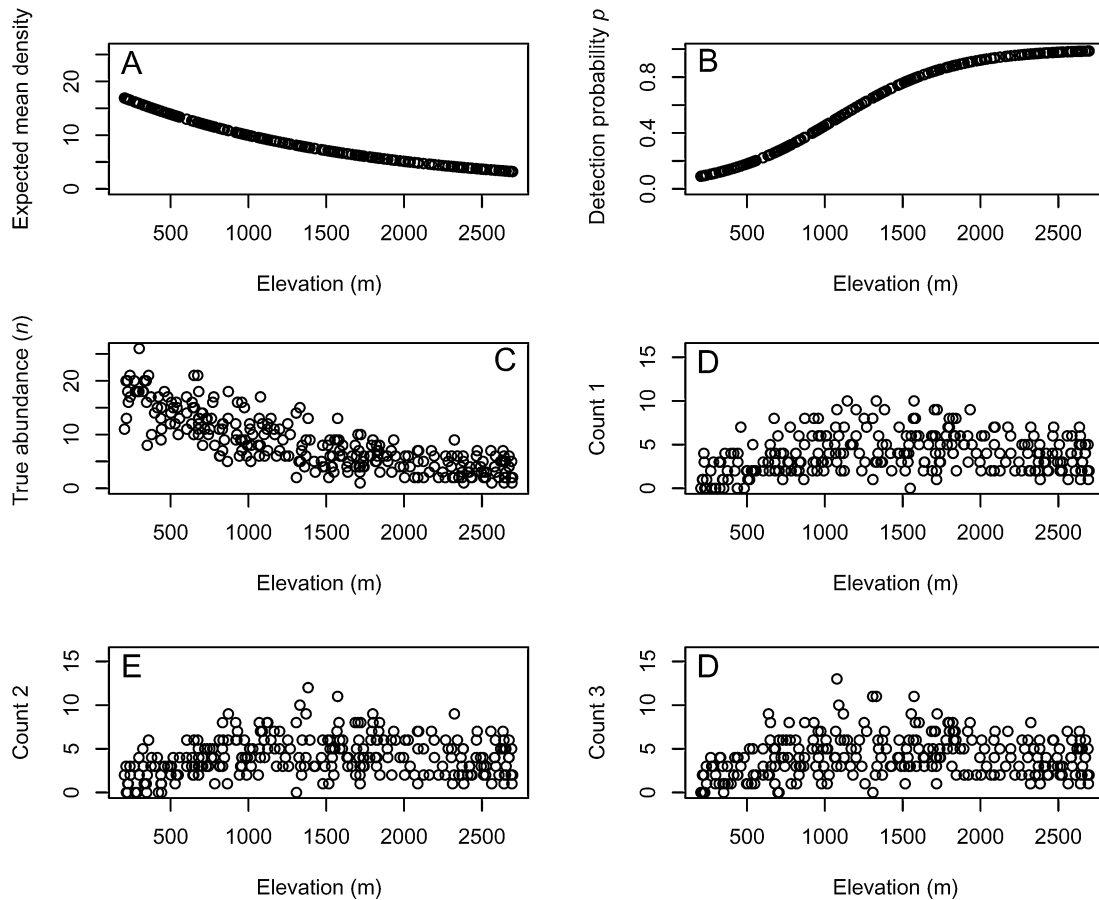


FIG. 1. Features of a single simulated data set. (A) Mean density (e.g., number of territories) declines with increasing elevation. (B) Detection probability p (e.g., of a territory) increases with elevation. (C) True abundance N is the realized true number of territories in each 1-km² sample quadrat. Panels D–F depict the counts from surveys 1–3 in relation to elevation. Note that A and B will be virtually identical for each of the 1,000 simulated data sets, but the remainder will differ somewhat owing to the Poisson (in abundance) and binomial (in the counts) sampling errors.

between elevation and both abundance and detection probability. Parameter estimates showed no indication of bias with respect to the generating parameters (Fig. 2). Mean estimates (\pm SD) for the relationship with abundance were 2.005 ± 0.049 for α_1 and -0.507 ± 0.059 for β_1 (Fig. 2A, B; remember that true values are 2.0 and -0.5). Mean estimates for the relationship with detection probability were 0.994 ± 0.098 for α_2 and 2.010 ± 0.084 for β_2 (Fig. 2C, D; true values 1 and 2).

The model also succeeded well in estimating total population size across all 268 quadrats. The total population in the 1,000 generated data sets ranged from 2,115 to 2,398 (mean = 2,239). The total population estimated under the binomial mixture model ranged from 1,865 to 2,957 (mean = 2,274). Expressing estimation error as the absolute difference between the true and the estimated total population size for each of the 1,000 simulated data sets yielded a mean estimation error of 35, a mere 1.6% in relation to the true values. The sum of the maximum counts in each quadrat, a conventional estimate of total population size, in the 1,000 simulated data sets ranged from 1,186 to 1,387

(mean = 1,284), and the mean error in this estimate was -955 , or 42.7% of the true value. Therefore, not accounting for detection probability resulted in a greatly underestimated population size with a mean estimation error $27\times$ ($42.7/1.6$) greater than under the binomial mixture model (although this, of course, depends on the values chosen for detection probability). The average detection probability over all 268 quadrats and 1,000 simulated data sets was 0.57.

I used a single, randomly selected data set among those generated to illustrate the patterns in the estimates of local population size in the 268 quadrats. Estimates under the binomial mixture model showed no indication of bias with respect to the generating parameters. By contrast, the maximum count was severely biased low for larger population sizes (Fig. 3). Particularly attractive in the binomial mixture model is the fact that its estimates reveal the true negative relationship between abundance and elevation. By contrast, using the maximum count as an estimate of relative abundance wrongly identifies a quadratic relationship with maximum abundance at medium elevations (Fig. 4).

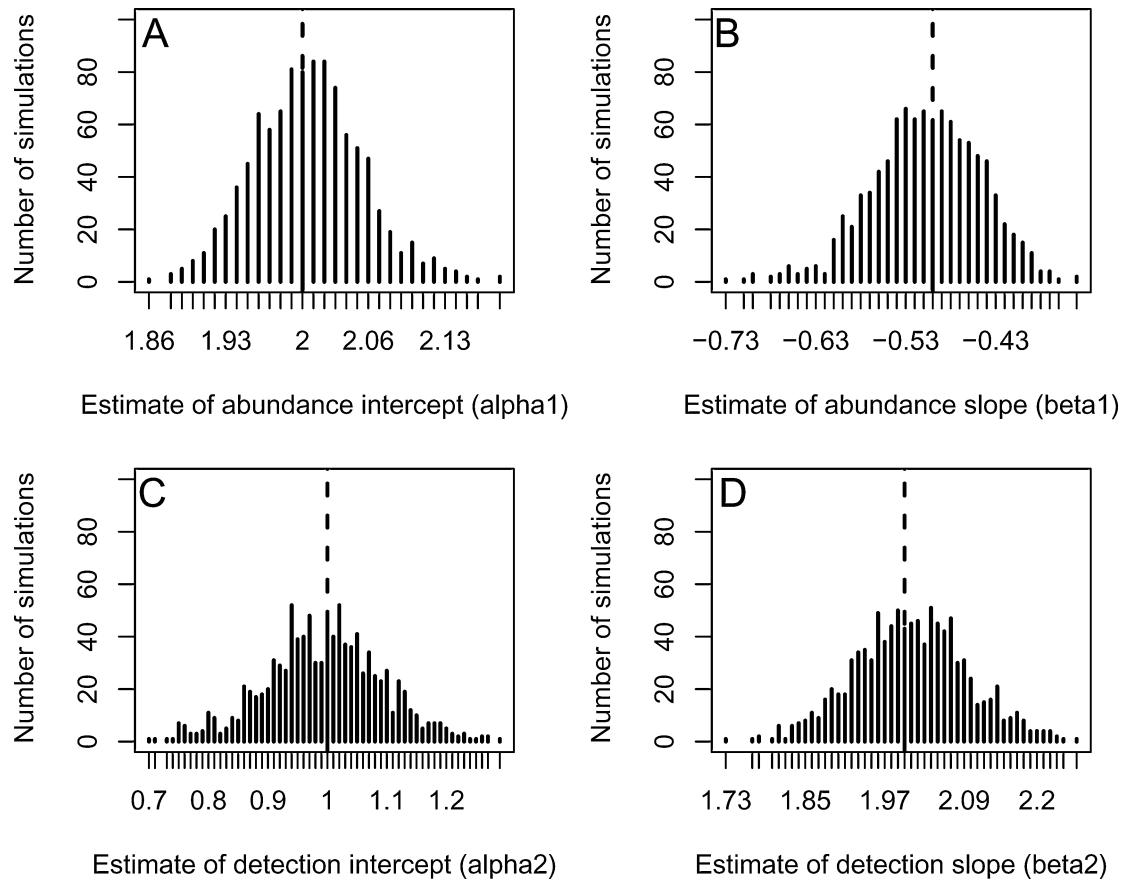


FIG. 2. Distribution of parameter estimates from 1,000 simulations. Dashed vertical line indicates the true parameter value; α_1 and β_1 are for abundance and α_2 and β_2 for detection probability. Note that here, the unit is a single parameter estimate from each of the total 1,000 simulations.

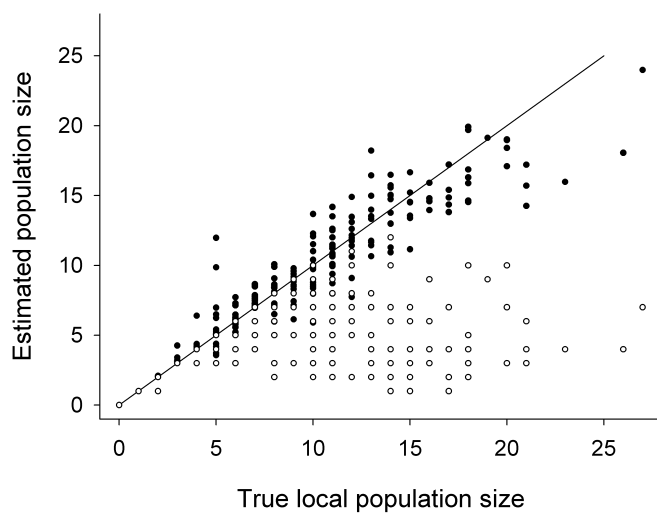


FIG. 3. Comparison of the estimates of local population size at each of 268 quadrats in a single simulated data set. Filled dots indicate mean posterior estimates under the mixture model, and open dots indicate maximum count. Line indicates the points where $y = x$.

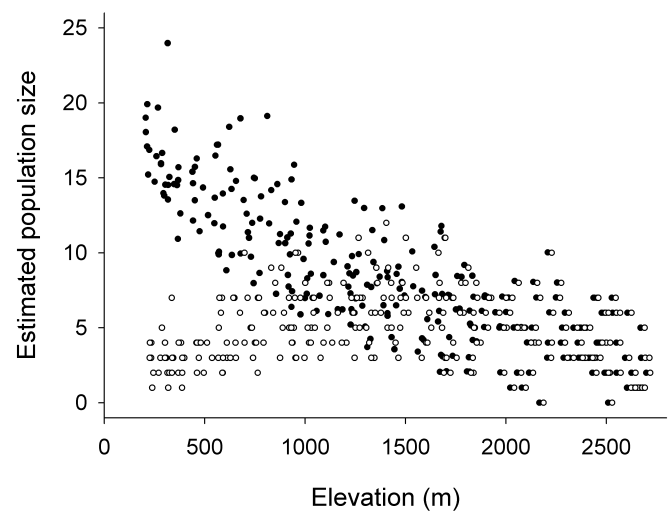


FIG. 4. Comparison of the perceived relationship between abundance and elevation. Filled dots indicate mean posterior estimates under the mixture model, and open dots indicate maximum count. The latter were translated 20 m along the elevation axis to improve visibility.

DISCUSSION

Advantages of the binomial mixture model for simple counts.—The motivating question for this study was whether the binomial mixture model (Royle 2004) was able to tease apart complex covariate relationships or, equivalently, whether the parameters of this relationship are identifiable under this model. The answer to these questions is yes, which is very encouraging, because Royle's (2004) model combines several attractive features. It provides estimates of abundance adjusted for variation in detectability. This confers protection from wrongly concluding that some pattern is present in true abundance when, in reality, this is just a pattern in detection probability. In addition, for many applications, estimates of true abundance are required (e.g., to assess the vulnerability of populations to extinction, predation, or harvesting). Simple counts or indices of "relative abundance" are then not sufficient.

The binomial mixture model results in efficient use of all abundance information. By integrating locally sparse data from many sites, it yields estimates of abundance where, perhaps, small local sample sizes might have prevented this with previously available estimation methods. One approach to the problem of small sample size is to pool data, but this would preclude the use of covariates. In mixture models, the data remain disaggregated and the fitting of covariates remains possible (see Royle et al. 2004).

When a model contains covariates on abundance, the function describing this relationship can be mapped to produce a true-abundance map; see Royle et al. (2005) for one example. Such maps may look superficially similar to relative-density maps familiar to ornithologists from many second-generation bird atlases (e.g., Gibbons et al. 1993, Schmid et al. 1998). The big difference is that they show true abundance adjusted for any patterns in detection probability.

W. A. Link (pers. comm.) emphasized that the point of the present study—that abundance and detection in the Royle (2004) model are always separately identifiable—can be proven analytically, because site-specific replication solves the problem. He pointed out the following. Suppose that no structure on N and p is specified and that all one has are three replicate counts at a single site. Given the binomial assumption, N and p are estimable using moment estimators (Royle 2004). Including spatial replication and imposing the additional covariate structure enhances the capacity for estimating model parameters. Hence, the present study is an illustration of a general principle, rather than a stand-alone simulation study.

Practical application of the binomial mixture model.—The excellent performance of the model in the simple simulation exercise presented here needs to be moderated by consideration of several issues relevant to its application in practice. I discuss five here: (1) the assumption of a closed population, (2) the selection of covariates and of a particular functional form for the covariate relationships, (3) the choice of an adequate mixture distribution for the unobserved abundance parameters, (4) goodness of fit, and (5) the consequences of using Bayesian inference.

Only for a closed population do repeated counts follow a binomial distribution with constant index N_i . If the model is applied to data from an open population, serious bias may result. Hence, the temporal scale of a study must be adapted to the scale of the

temporal dynamics of the bird population under study. The more dynamic a population in terms of births, deaths, or movement, the more closely spaced surveys are required to meet the closure assumption. Alternatively, counts made during a period when a population was not closed could be discarded—which, in practice, would introduce missing values in the data. This poses no greater problem for the binomial mixture model than for any other statistical model. For instance, counts of a migrant species conducted before most of the population had arrived could simply be changed into missing values and the model fit to the remainder of the data (provided there is still more than one count per site).

In practice, we will rarely know what discrete or continuous covariates affect abundance and detection probability, or what functional form these relationships may have. Multiple reasonable models that differ in these respects will then have to be fitted to the data, and statistical tests or model selection criteria—such as Akaike's Information Criterion (AIC) or, in a Bayesian mode, the deviance information criterion (DIC; Spiegelhalter et al. 2002)—applied to pick the "right" covariates, interactions, and functional forms (Royle 2004, Kéry et al. 2005). However, "null" models with constant average abundance and constant detection probability may also be entertained and have performed well (Kéry et al. 2005).

Royle's (2004) model requires specification of a weak stochastic relationship among site-specific abundance parameters, N_i , in the form of a parametric distribution. Although the Poisson distribution is a natural first choice for count data, cases could exist where additional spatial variability in abundance must be addressed in the model to ensure an unbiased estimator. The simplest remedy may be to use covariates to explain such extra-Poisson variation. Alternatively, as explained above, more clumped distributions for abundance are available (e.g., the negative binomial), and, in a frequentist mode of analysis, AIC (Royle 2004, Kéry et al. 2005) or goodness-of-fit statistics can be used as a criterion for selecting among them. Inference based on several or even all models considered would also be possible, by computing weighted parameter estimates with weights proportional to the support of the respective models (Buckland et al. 1997). One special case where a homogeneous Poisson process is an inadequate model for the latent abundance parameters is where the spatial replicates have unequal area. This known component of variation in abundance is easily handled by introducing $\ln(\text{area})$ as an offset into the linear predictor for the Poisson parameter λ (McCullagh and Nelder 1989), thereby making expected density per unit area, rather than the numbers of birds, log-linearly dependent on covariate x .

By using a model-selection criterion such as AIC or DIC, one implicitly assumes that at least one of the models compared fits the observed data adequately. For models fit by maximum likelihood, conventional deviance statistics (Royle 2004) or bootstrap techniques (Dixon et al. 1998) can be used. In a Bayesian analysis, Bayesian p -values can be used to assess fit (Gelman et al. 2004).

Bayesian inference using MCMC has many advantages, and I believe that a typical biologist will feel more comfortable fitting a reasonably complex model by using WinBUGS than by numerically maximizing the likelihood for the same model. However, dangers are inherent in this approach. For instance, convergence must be carefully examined when using Bayesian inference by

MCMC. Still, inspecting chains by eye, running multiple chains from widely dispersed starting points, and formal convergence diagnostics (Gelman et al. 2004) make this perhaps not more difficult than assessment of convergence in the classical numerical optimization of a likelihood. In the present study, I fit a fairly simple model to a rather modest data set, and convergence was rapidly reached.

Some possible extensions.—Occupancy is another state variable increasingly used in biological surveys and usually estimated from detection–nondetection data (MacKenzie et al. 2006). It is important to note the functional relationship between abundance and occupancy (Royle and Nichols 2003). Occupancy probability equals the probability that abundance is greater than zero; hence, any model of abundance is, directly, also an occupancy model (see Royle et al. 2005). Under the Poisson model, occupancy probability (ψ) is given by $\psi = 1 - \exp(-\lambda)$. Thus, for my simulated data, the relationship between occupancy and elevation is described by $\psi = 1 - \exp[-(2 - 0.5 \cdot \text{elevation})]$.

The principal goal of many bird surveys is to detect trends in abundance. When data are available for several years, introducing a linear trend into the binomial mixture model is straightforward. For example, abundance N in quadrat i and year t could be written as $N_{it} \sim \text{Pois}(\lambda_{it})$, with $\log(\lambda_{it}) = \alpha + \beta \cdot T$, where λ_{it} is the expected abundance in quadrat i in year t , T a covariate representing time, and α and β the intercept and slope parameters of the log-linear trend.

One exciting new avenue in the analysis of animal populations is the combination of several kinds of data in a single population model (Besbeas et al. 2002, Brooks et al. 2004, Buckland et al. 2004b). This enables some parameters to be estimated that are not identifiable when each data set is analyzed in isolation and, furthermore, yields estimates with greater precision for those parameters than can be estimated in each data set separately. Typically, ring-recovery and perhaps other types of data have been combined with simple-count survey data (Besbeas et al. 2002, Brooks et al. 2004). Using a binomial mixture model for the replicated counts as one component of such an integrated population model would yield estimates of true abundance, and of true population trajectories, that are free of any potentially distorting effects of detection probability.

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APPENDIX. R code to simulate data suitable for the counts N -mixture model of Royle (2004) and to analyze it in WinBUGS from R.

This is an R function that writes out the BUGS model code and then calls WinBUGS to fit that model. To run the model, one copies the function into an R session and executes it thus:

```
sim.rep <- Nmix.fn(11000,1000,5)
```

Note that the R2WinBUGS package must be installed in R. `debug = FALSE` can be changed to `debug = TRUE` so that WinBUGS stays open after completing analysis of one data set and can be used to produce summaries or compute autocorrelation functions. The path of the WinBUGS program must be given in the `bugs.directory` argument of the `bugs` function.

```
Nmix.fn<-function(ni=11000,nb=1000,nt=5){
  # ni: number of iterations
  # nb: burn-in length
  # nt: thinning rate
  # Default settings yield 2k iterations for inference

  # Generate the data
  T <- 3                                # Number of temporal replicates
  R <- 268                              # Number of spatial replicates
  ele <- runif(R, 200, 2700)            # Quadrat elevation 200 - 2700
  eles <- as.vector(scale(ele))         # Elevation standardised

  alpha1 <- 2                           # Model for true abundance N
  beta1 <- -0.5
  lambda <- exp(alpha1+beta1*eles)      # Abundance negative function of eles
  N <- rpois(R, lambda)
  trueNtot <- sum(N[])                  # Add up the true total N

  alpha2 <- 1                           # Model for detection probability p
  beta2 <- 2
  p <- 1 / (1 + exp(-(alpha2+beta2*eles))) # p positive function of eles
  y <- matrix(NA,nrow=R,ncol=T)
  for(i in 1:R){
    y[i,] <- rbinom(3,N[i],p[i])        # Generate the counts
  }

  # Analyse the max. count as a simplistic approximation of N
  Cmax <- apply(y,1,max)
  obsCtot <- sum(Cmax[])

  library("R2WinBUGS")                  # Load R2WinBUGS package
  sink("mlin.txt")
  cat("
model {
  alpha1 ~ dnorm(0, 0.0001)             # Note conventional vague priors
  beta1 ~ dnorm(0, 0.0001)
  alpha2 ~ dnorm(0, 0.0001)
  beta2 ~ dnorm(0, 0.0001)
  for (i in 1:R) {
    log(lambda[i]) <- alpha1+beta1*eles[i]
    N[i] ~ dpois(lambda[i])

    for (j in 1:T) {
      linpred[i,j] <- alpha2+beta2*eles[i]
      p[i,j] <- 1 / (1 + exp(-linpred[i,j]))
      y[i,j] ~ dbin(p[i,j], N[i])
    }
  }
}
```

```
Ntot <- sum(N[]) # Total abundance across quadrats
}
",fill=TRUE)
sink()

Nst <- apply(y,1,max)+1 # Starting values for N
data <- list("R","T","Y","eles")
inits <- function(){
list(alpha1=0, beta1=0, alpha2=0, beta2=0, N=Nst)}
parameters <- c("alpha1","beta1", "alpha2", "beta2", "Ntot")
out <- bugs (data, inits, parameters, "mlin.txt", n.thin=nt,n.chains=1,n.burnin=nb,
n.iter=ni, debug = FALSE,bugs.directory = "c:/Program Files/WinBUGS14/")

# Package simulated data, obsCtot, Ntot
and MCMC results
output <- list(ele = ele, eles = eles,
lambda = lambda, N = N, p = p, y = y,
obsCtot= obsCtot, trueNtot=trueNtot,
out=out) return(output)

}
```