

Models for Estimating Abundance from Repeated Counts of an Open Metapopulation

D. Dail* and L. Madsen**

Department of Statistics, Oregon State University, Corvallis, Oregon 97331, U.S.A.

*email: daild@science.oregonstate.edu

**email: madsenl@onid.orst.edu

SUMMARY. Using only spatially and temporally replicated point counts, Royle (2004b, *Biometrics* **60**, 108–115) developed an N -mixture model to estimate the abundance of an animal population when individual animal detection probability is unknown. One assumption inherent in this model is that the animal populations at each sampled location are closed with respect to migration, births, and deaths throughout the study. In the past this has been verified solely by biological arguments related to the study design as no statistical verification was available. In this article, we propose a generalization of the N -mixture model that can be used to formally test the closure assumption. Additionally, when applied to an open metapopulation, the generalized model provides estimates of population dynamics parameters and yields abundance estimates that account for imperfect detection probability and do not require the closure assumption. A simulation study shows these abundance estimates are less biased than the abundance estimate obtained from the original N -mixture model. The proposed model is then applied to two data sets of avian point counts. The first example demonstrates the closure test on a single-season study of Mallards (*Anas platyrhynchos*), and the second uses the proposed model to estimate the population dynamics parameters and yearly abundance of American robins (*Turdus migratorius*) from a multi-year study.

KEY WORDS: Avian point counts; Breeding bird survey; Closure test; N -mixture models; Population dynamics estimation; Spatially replicated counts.

1. Introduction

Ecological research depends on the knowledge of animal abundance and how abundance is changing over space and time (Krebs, 2001). For many species, however, an accurate measure of abundance is difficult to obtain because some animals present in the study area may go undetected (Thompson, 1992). Instead of accounting for this, some monitoring programs use the observed counts as a proxy for true population size. This comes with the implicit assumption that either detection probability is perfect (if interest is in abundance), or the detection probability is constant on average across time (if interest is in trend in abundance). It has been shown for many species that analyzing raw counts without accounting for detection probability leads to bias in abundance and trend estimates (see, e.g., Kéry, Royle, and Schmid, 2005; Wenger and Freeman, 2008).

Sampling protocols that have been developed to simultaneously estimate detection probability and abundance include capture–recapture (Pollock et al., 1990), removal (Farnsworth et al., 2002), distance (Buckland et al., 2001), and multiple observer sampling (Nichols, Hines, Sauer, et al., 2000). In addition to the total number of observed animals, each protocol calls for the collection of auxiliary information used to estimate detection (or capture) probability, p , independently of abundance, N . For instance, in multiple observer sampling,

a list of observers that detected the presence of each animal is recorded, and this is used to estimate p . However, the cost and effort required to collect information beyond the observed counts is often prohibitive. In addition, if the site-specific population sizes are small, it may be difficult to collect enough data to adequately estimate p , and subsequently estimate N (Royle and Nichols, 2003).

An alternative protocol is to collect point counts in surveys replicated over space and time, where the total area is divided into R distinct sites that are independently surveyed on T sampling occasions. This provides enough information for p to be estimated, and to simultaneously estimate the sum of the abundances at all sampled sites, referred to here as “total abundance.” For each site ($i = 1, \dots, R$) and sampling occasion ($t = 1, \dots, T$), only the total observed count, n_{it} , is recorded, giving a matrix of observed point counts, denoted $\{n_{it}\}$. This is the sampling protocol used by many large-scale monitoring programs, such as the North American Breeding Bird Study (BBS), Great Backyard Bird Count, and the North American Amphibian Monitoring Program. A subset of data arising from one such study, annual point counts for the American robin (*Turdus migratorius*) along a BBS route in Oregon, is given in Table 1.

Several models have been proposed to estimate total abundance from repeated point counts as in Table 1 (e.g., Olkin

Table 1

Yearly point count data for the American robin from the first five stops (sites) along a BBS route in Oregon. This is a subset of the entire data set, which consists of 50 sites.

	Sampling occasion (year)					
	2003	2004	2005	2006	2007	2008
Site 1	3	5	3	2	2	2
Site 2	2	1	2	3	2	1
Site 3	1	3	1	2	1	2
Site 4	2	3	2	1	2	1
Site 5	2	4	2	2	1	1

Petkau, and Zidek, 1981; Carroll and Lombard, 1985). The model Royle (2004b) proposes (hereafter the “Royle model”) has been shown to have the best performance of these, especially in the presence of sparse counts (Royle, Nichols, and Kéry, 2005; Kéry, 2008).

Inherent in the Royle model, as in all the proposed models, is the assumption that each site has a closed population: the population at each site cannot experience births, deaths, or migration, and so remains constant throughout the entire course of the study. This assumption applies to the populations of animals whose home ranges overlap the sampled sites (i.e., the site superpopulations), so movement of individual animals is allowed as long as site superpopulations remain constant (Nichols, Thomas, and Conn, 2008). Therefore, the Royle model accommodates temporary emigration at sampled sites, because the superpopulations are unaffected. Because it is biologically justifiable to assume population closure when sampling is replicated only during a period of known animal inactivity, such as a bird monitoring study during one breeding season, the Royle model is useful in many settings.

We refer to the overall population (i.e., the metapopulation) as “open” when there are additions or deletions in the site superpopulations. Parameters governing the rate of these changes are referred to as “population dynamics parameters.” Until now there has been no method to use the observed point count data to test the closure assumption, and no method to analyze point counts when the closure assumption is invalid. This is important because the closure assumption has been shown to be violated in some cases where closure seems justified biologically, such as a single breeding season (Rota et al., 2009), and is clearly invalid in annual count studies such as the one presented in Table 1. Furthermore, applying the Royle model when the closure assumption is invalid leads to large bias in estimated total abundance, as shown in Section 4.

We develop a class of models (hereafter the “generalized model”) that generalizes the Royle model and does not assume population closure. Comparing the generalized model to the Royle model results in a formal test of the closure assumption, which can be used either as an aid in model selection or simply to verify the appropriateness of the Royle model. For populations that are found to be open, the generalized model provides an estimate of the population dynamics parameters, as well as estimates of the total abundance during each sampling period.

Royle’s N -mixture model is briefly described in Section 2. In Section 3, we describe the proposed generalized model, the closure test, and open population dynamics and abundance estimation. A simulation study to evaluate the performance of the proposed model is presented in Section 4. Two applications involving avian point counts are presented in Section 5.

2. Royle’s Model for Spatially Replicated Counts

In the study design considered here, detected animals are counted at $\{i = 1, \dots, R\}$ spatially distinct sites during $\{t = 1, \dots, T\}$ sampling occasions. Animal detections in a site are assumed independent, and all animals present on a site i at any time t , denoted N_{it} , are assumed to have the same detection (or capture) probability, denoted p_{it} . For clarity, p_{it} will be expressed here as a constant across all sites and through time, although in general p may vary spatially and temporally, possibly in relation with measurable covariates. This generalization is explored in Sections 4 and 5.

Therefore, conditional on p and N_{it} , the observed count n_{it} is a binomial random variable $n_{it} \sim \text{Bin}(N_{it}, p)$. The R sites are assumed to be spatially independent, so the joint likelihood is

$$L(\{N_{it}\}, p | \{n_{it}\}) = \prod_{i=1}^R \left\{ \prod_{t=1}^T \text{Bin}(n_{it}; N_{it}, p) \right\}, \quad (1)$$

where $\text{Bin}(n_{it}; N_{it}, p)$ is the binomial likelihood. This has $RT + 1$ unknown parameters: the RT abundance parameters $\{N_{it}\}$ and the detection probability parameter, p . The primary interest here is in estimating the total abundance at some time t , denoted $N_{.t}$. Additionally, estimates of the site-specific population sizes at any time t , N_{it} , may be of interest. The grand total abundance, $N_{..}$, could also be important, as it may represent the total volume of animal migration through a series of stopover sites. Obtaining an estimate of the trend in population size for a particular site i and time t , $\Phi_i = N_{it}/N_{it-1}$, although not the focus in this article, could be desired when the population is found to be open.

Royle’s (2004b) proposal for estimating $N_{.t}$ from (1) begins with the assumption of closed populations at every site, $N_{i1} = N_{i2} = \dots = N_{iT} = N_i$ for $i = 1, 2, \dots, R$. Then we have $n_{it} \sim \text{Bin}(N_i, p)$ and the number of unknown parameters in (1) is reduced to $R + 1$. The N_i are regarded as random effects, assumed to be independent random variables with some prior distribution $f(N_i; \theta)$, and then integrated from the joint likelihood. This results in an integrated likelihood that depends only on p and (possibly vector valued) θ :

$$L(p, \theta | \{n_{it}\}) = \prod_{i=1}^R \left\{ \sum_{N_i = \max_t n_{it}}^{\infty} \left(\prod_{t=1}^T \text{Bin}(n_{it}; N_i, p) \right) f(N_i; \theta) \right\}. \quad (2)$$

Although (2) does not simplify to a closed form, maximum likelihood estimates (MLEs) for θ and p can be obtained

using conventional methods of maximization. The summation over N_i is restricted to a large (but finite) bound K , chosen large enough to have negligible impact on MLEs found using (2).

We consider Poisson and negative binomial densities for $f(N_i; \theta)$ in this article, although any positive discrete distribution could be used. The Poisson model arises from assuming individuals are distributed in space completely at random and independently, whereas the negative binomial model allows for extra variation. Both models can be parameterized to have mean λ , with overdispersion parameter α for the negative binomial. The estimate for total abundance is then $\hat{N}_{..} = \hat{N}_t = R\hat{\lambda}$. Additional spatial variation can be modeled by including site-specific covariates thought to influence abundance: $\log(\lambda_i) = \beta_0 + \beta_1 x_{i1} + \dots + \beta_r x_{ir}$, where $x_{ij}; j = 1, \dots, r$ are the r covariates recorded for site i . In the same way site- and time-specific covariates thought to influence detection probability p can be included using a generalized linear model with the logit link.

The Royle model can be applied to an open population if the population experiences known periods of closure (called primary periods), during which multiple samples are obtained (pp. 4–7 of Royle and Dorazio, 2008; Kéry et al., 2009). This is the situation referred to as “robust design” in the literature for capture–recapture models (Pollock, 1982) and site occupancy applications (MacKenzie et al., 2003). Although these robust design models do not require the assumption that populations are closed for the entire duration of the study, population closure assumptions are still required within each primary period.

It is technically possible to use the Royle model when the population closure assumption is invalid, but the resulting estimate of total abundance will generally be highly biased, as demonstrated in Section 4. The same is true for violations of the primary period closure assumptions required in robust design models. This bias results from the models interpreting changes in observed counts as detections or nondetections rather than changes in population abundance. The fluctuations in observed counts arising from changes in abundance therefore lead to a low estimate of p and increased estimate of N .

The proposed model described in the following section provides a formal test of the closure assumption of the Royle model. It also provides estimates of the population dynamics parameters and total abundance that are valid for open populations without a robust design.

3. Generalized N -Mixture Model

With counts of the observed animals at R sites and on T different sampling occasions, we assume sites are independent and individual animal detections are independent, giving the likelihood in equation (1). However, the generalized model does not require the population closure assumption. Instead, we have

$$L(p, \theta | \{n_{it}\}, \{N_{it}\}) = \prod_{i=1}^R \left\{ \left(\prod_{t=1}^T \text{Bin}(n_{it}; N_{it}, p) \right) f(\{N_{i1}, N_{i2}, \dots, N_{iT}\}; \theta) \right\}$$

for some joint probability mass function f that depends on (possibly vector valued) θ .

The population abundances $\{N_{it}\}$ are regarded as random effects and integrated from the likelihood, as in Section 2. This gives

$$L(p, \theta | \{n_{it}\}) = \prod_{i=1}^R \left\{ \sum_{N_{i1}=n_{i1}}^{\infty} \dots \sum_{N_{iT}=n_{iT}}^{\infty} \left(\prod_{t=1}^T \text{Bin}(n_{it}; N_{it}, p) \right) \times f(\{N_{i1}, N_{i2}, \dots, N_{iT}\}; \theta) \right\}. \quad (3)$$

Estimation using (3) is greatly simplified by assuming $\{N_{it}\}$ has the Markov property. Together with the assumption of site independence, this implies that for any site i and sampling occasion $t \geq 2$, N_{it} depends only on N_{it-1} . Note that this is less restrictive than either assuming that site abundances across time are equal, or that site abundances at time $t + 1$ are independent of site abundances at time t .

With the Markov assumption, we have

$$f(\{N_{i1}, \dots, N_{iT}\}; \theta) = f(N_{i1}; \theta) \prod_{t=2}^T f(N_{it}; N_{it-1}, \theta). \quad (4)$$

Because $f(N_{i1}; \theta)$ can be interpreted as the initial spatial distribution of animals to sites, the same choices are available as were described for $f(N_i; \theta)$ in Section 2. Again, we restrict our attention to the Poisson and negative binomial models, noting that other possibilities could be considered.

Using the migration decomposition approach of Nichols, Hines, Lebreton, et al. (2000) and Royle (2004a), we model $f(N_{it}; N_{it-1}, \theta)$ as the density of the sum of two random variables, S_{it} and G_{it} . S_{it} denotes animals in site i at time t who survived in that site since time $t - 1$, and G_{it} denotes gains at site i since time $t - 1$. With ω representing the survival probability and γ the arrival rate, we have

$$\begin{aligned} S_{it} | N_{it-1} &\sim \text{Bin}(N_{it-1}, \omega) \\ G_{it} | N_{it-1} &\sim \text{Poisson}\{\gamma(N_{it-1})\}, \end{aligned} \quad (5)$$

where $\gamma(N_{it-1})$ represents the fact that γ may depend on the level of N_{it-1} . Additional spatial variation can be accommodated by using a negative binomial model or including site-specific covariates for γ , as described for λ in Section 2. Note that because individual animal identities are not recorded, no distinction is possible between either deaths and emigrants for the animals departing, or between births and immigrants for new arrivals.

For clarity here we assume S_{it} and G_{it} are independent, although a dependent structure can be accommodated (as discussed in Section 6.1). Then we can find the one-step transition probability from state $N_{it-1} = j$ to state $N_{it} = k$, denoted P_{jk} , using the discrete convolution:

$$P_{jk} = \sum_{c=0}^{\min\{j, k\}} \text{Bin}(c; j, \omega) \cdot \text{Pois}\{k - c; \gamma(j)\}. \quad (6)$$

Combining (6) with a Poisson prior for $f(N_{i1}; \theta)$ fully specifies $f(\{N_{i1}, \dots, N_{iT}\})$ and leads to the following integrated likelihood, valid without the closed population assumption:

$$\begin{aligned}
L(p, \lambda, \gamma, \omega | \{n_{it}\}) \\
= \prod_{i=1}^R \left[\sum_{N_{i1}=n_{i1}}^{\infty} \cdots \sum_{N_{iT}=n_{iT}}^{\infty} \left\{ \left(\prod_{t=1}^T \text{Bin}(n_{it}; N_{it}, p) \right) \right. \right. \\
\left. \left. \times \frac{e^{-\lambda} \lambda^{N_{i1}}}{N_{i1}!} \cdot \prod_{t=2}^T P_{N_{it-1}, N_{it}} \right\} \right]. \quad (7)
\end{aligned}$$

Although (7) does not simplify to a closed form, the Markov assumption allows for a rearrangement of terms that greatly reduces the computational burden of calculating likelihoods, demonstrated in Web Appendix A. Conventional numerical optimization techniques will then yield the MLEs $\{\hat{\lambda}, \hat{p}, \hat{\gamma}, \hat{\omega}\}$.

In practice a large, but finite, value K must be set for the infinite sums over N_{it} , as is the case for equation (2). Again, the impact of this choice can be evaluated using various values of K . The minimum appropriate choice of K depends on the largest observed count, so analysis of a study with large observed counts will require using a large value for K . In the examples of Section 5, $K = 200$ was used.

3.1 Closure Test

Royle's likelihood in equation (2) is a specific case of the generalized likelihood in equation (7) with $\omega = 1$ and $\gamma = 0$, demonstrated in Web Appendix B. This nested structure between the two models can be used to test the closure assumption.

The asymptotic test provided by Self and Liang (1987) can be used to formally test $\{H_0: \gamma = 0, \omega = 1\}$ versus $\{H_1: 0 \leq \gamma, 0 \leq \omega \leq 1\}$ (Dominicus et al., 2006), where the asymptotic validity depends only on the number of sampled sites R being large. Let Λ denote the ratio of the likelihood (7) maximized under H_0 to the likelihood maximized under H_1 . The likelihood ratio test statistic is then $-2\log(\Lambda)$. Under the standard regularity conditions, under H_0 this test statistic asymptotically approaches a χ^2_2 distribution. However, the regularity conditions are not met, as H_0 has parameters on the boundary of the parameter space.

Instead, under H_0 the test statistic asymptotically approaches a mixture of χ^2_0 , χ^2_1 , and χ^2_2 distributions with mixing probabilities $0.5 - \delta$, 0.5 , and δ , respectively. Typically δ is determined using a calculation involving the Fisher information matrix, denoted \mathbf{I} , partitioned into four blocks $\mathbf{I}_{\psi\psi}$, $\mathbf{I}_{\psi\eta}$, $\mathbf{I}_{\eta\psi}$, and $\mathbf{I}_{\eta\eta}$, where $\psi = (\gamma, \omega)$ and $\eta = (\lambda, p)$. Then, with $\tilde{\mathbf{I}} = \mathbf{I}_{\psi\psi} - \mathbf{I}_{\psi\eta} \mathbf{I}_{\eta\eta}^{-1} \mathbf{I}_{\eta\psi}$, we have $\delta = \cos^{-1}\{\tilde{I}_{12}/\sqrt{\tilde{I}_{11}\tilde{I}_{22}}\}/2\pi$. However, because the Fisher information matrix \mathbf{I} is not available for the likelihood in equation (7), we advise using the observed information matrix to calculate δ (see, e.g., Efron and Hinkley, 1978), although an alternative may be to approximate the distribution of the test statistic by simulating data sets under H_0 (Rota et al., 2009).

When the Royle and generalized models are not nested, as when covariates for detection probability are included in the Royle model but not in the generalized model or different priors are used for $f(N_{i1})$, a formal test is no longer available. Instead, model comparisons must be made informally, such as with Akaike information criterion (AIC) values from competing models (Burnham and Anderson, 2002). The simulations in Section 4 use AIC comparison to compare nonnested mod-

els, and the examples in Section 5 demonstrate the likelihood ratio test for nested models.

3.2 Model Extensions

Because γ can depend on N_{it-1} , as in $\log(\gamma) = \varphi_0 + \varphi_1 \log(N_{it-1})$, classical population dynamics models can be embedded within the generalized model. This is obtained by setting $\varphi_1 = 1$ in the previous equation, giving $G_{it} | N_{it-1} \sim \text{Poisson}(\gamma^* N_{it-1})$, where $\gamma^* = e^{\varphi_0}$. This is referred to here as the ‘‘autoregressive’’ model. Note that γ^* measures the strength of dependence on the abundance (or density) of the previous time period.

A model where γ does not depend on N_{it-1} can be obtained by setting $\varphi_1 = 0$, and this is referred to here as the ‘‘constant’’ generalized model. If neither model is preferred by AIC selection, the model with φ_1 unrestricted should be considered as well. Other models for G_{it} are possible, such as allowing $\log(\gamma)$ to vary across sites or over time according to some measured covariates. The same is true regarding covariates for $\log(\omega)$. Choosing among competing models is accomplished with standard model selection procedures (see, e.g., Burnham and Anderson, 2002).

Additionally, it may be desirable to construct a model with a dependent structure between γ and ω . One such structure already investigated is the Royle model, where $\gamma = 0$ and $\omega = 1$, but others are available as well. For example, $\gamma = (1 - \omega)\lambda$ forces $\Phi = 1$, so the trend is always 1 (i.e., abundances are constant) but animal movement is possible. The two extremes of this model are where $\omega = 1$, which gives the Royle model, and $\omega = 0$, which gives the ‘‘reshuffle’’ model. The reshuffle model represents a population of animals that are entirely redistributed to sites each sampling period, independently of where each animal was in previous periods. Although this may not make sense biologically, it demonstrates the range of population dynamics accessible to the proposed generalized model.

3.3 Estimating Abundance

There are two approaches to estimating total abundance with the MLEs from (7). First, in cases where site-specific abundances are not of direct interest, area expansion can be used to obtain abundance estimates. This is the technique Royle (2004b) uses to estimate total abundance, leading to the equation $\hat{N} = R\hat{\lambda}$. For an open population, we can recursively estimate the total abundance on any sampling occasion, using $\hat{\lambda}$ in combination with the estimated population dynamics parameters:

$$\begin{aligned}
\hat{N}_{\cdot 1} &= R\hat{\lambda} \\
\hat{N}_t &= \hat{\omega}\hat{N}_{t-1} + R\hat{\gamma}. \quad (8)
\end{aligned}$$

The total abundance of the sampled areas at time t , $N_{\cdot t}$, can be expressed explicitly for both the constant and autoregressive generalized models:

$$\hat{N}_{\cdot t} = \begin{cases} R\hat{\lambda}\hat{\omega}^{t-1} + \frac{R\hat{\gamma}(1 - \hat{\omega}^{t-1})}{1 - \hat{\omega}}, & \text{if } G_{it} \sim \text{Poisson}(\gamma) \\ R\hat{\lambda}(\hat{\omega} + e^{\hat{\varphi}_0})^{t-1}, & \text{if } G_{it} \sim \text{Poisson}(e^{\varphi_0} N_{it-1}). \end{cases}$$

Estimates of the trend in abundance, Φ , are obtained for each model by dividing \hat{N}_t by \hat{N}_{t-1} . This gives:

$$\hat{\Phi} = \begin{cases} \hat{\omega} + \frac{\hat{\gamma}}{\lambda}, & \text{if } G_{it} \sim \text{Poisson}(\gamma) \\ \hat{\omega} + e^{\varphi_0}, & \text{if } G_{it} \sim \text{Poisson}(e^{\varphi_0} N_{it-1}). \end{cases} \quad (9)$$

As in Royle (2004b), the approximate asymptotic variances of these estimates can be calculated either with the inverse Hessian evaluated at the MLE and the multivariate delta method (Lehmann, 1999), or by parametric bootstrap techniques (Dixon, 2002).

Second, an estimate of p can be combined with the observed counts to form an estimate for N_{it} for any site i and sampling occasion t . Following from the binomial assumption on n_{it} , we have:

$$\hat{N}_{it} = \frac{n_{it}}{\hat{p}}, \quad (10)$$

where \hat{p} is obtained from equation (7). However, equation (10) implies $\hat{N}_{it} = 0$ whenever $n_{it} = 0$, regardless of \hat{p} . An alternative estimate can be found with Bayes' Theorem. If we use the improper prior $f(N_{it}) \propto 1$, we have:

$$\Pr(N_{it} = k | n_{it}, p) = \binom{k}{n_{it}} p^{n_{it}+1} (1-p)^{k-n_{it}}.$$

We use the estimate \hat{p} in place of p , adopting the “plug-in” empirical Bayes procedure. The mean of this distribution is an estimate for N_{it} , appropriate even when $n_{it} = 0$:

$$\mathbb{E}[N_{it} | n_{it}, \hat{p}] = \frac{n_{it}}{\hat{p}} + \frac{1 - \hat{p}}{\hat{p}}. \quad (11)$$

Other (more informative) priors for N_{it} can be used instead, but may these may not yield an estimator available in closed form as desired here. Furthermore, it should be noted that estimating abundances using (10) or (11) is only appropriate for the proposed generalized model, because under the assumption of population closure site abundances are constant through time.

3.4 Nonconstant Sampling Periods

With the closed population assumption removed, the time interval between sampling occasions becomes important, because the likelihood model for observed counts must reflect additional opportunity for movement in cases where longer amounts of time separate two sampling occasions. Assuming sampling times are known, we define the vector of the time increments between successive sampling occasions at each site i as $\Delta_i = \{\Delta_{i2}, \dots, \Delta_{iT}\}$, with Δ_{it} representing lapsed time between sampling occasions t and $t-1$ at site i . In particular, if we sample each site at regular intervals through time, $\Delta_{it} = 1$ for all i and t .

We let \mathbf{P} denote the matrix of the one-step transition probabilities, P_{jk} , for $0 \leq j, k \leq K$, defined in (6). Then the matrix of Δ_{it} -step transition probabilities, $\mathbf{P}^{(\Delta_{it})}$, is found using the Chapman–Kolmogorov equation $\mathbf{P}^{(\Delta_{it})} = \mathbf{P}^{\Delta_{it}}$ (Ross, 2006). That is, $\Pr(N_{it} = k | N_{it-\Delta_{it}} = j)$ is the P_{jk} cell of \mathbf{P} (matrix-) multiplied by itself Δ_{it} times. Then, the Δ_{it} -step probabilities $P_{N_{it-1}, N_{it}}^{(\Delta_{it})}$ can be included in (7).

3.5 Robust Design

Although the robust design is not required by the proposed model, it is readily incorporated in the generalized likelihood

in equation (7). Within each of the $t = 1, \dots, T$ primary periods, we suppose each site is surveyed J_t times, where each site is assumed closed to migration within a primary period but not across primary periods.

Imposing the constraints $\gamma = 0$ and $\omega = 1$ for all surveys conducted within a primary period, $J_t \geq 2$, and leaving γ and ω unconstrained when $J_t = 1$, gives

$$\begin{aligned} L(p, \lambda, \gamma, \omega | \{n_{ijt}\}) \\ = \prod_{i=1}^R \left[\sum_{N_{i1}=\max_{j1} n_{ij1}}^{\infty} \dots \sum_{N_{iT}=\max_{jT} n_{ijT}}^{\infty} \right. \\ \left. \left\{ \left(\prod_{t=1}^T \prod_{j_t=1}^{J_t} \text{Bin}(n_{ijt}; N_{it}, p) \right) \right. \right. \\ \left. \left. \times \frac{e^{-\lambda} \lambda^{N_{i1}}}{N_{i1}!} \cdot \prod_{t=2}^T P_{N_{it-1}, N_{it}} \right\} \right]. \quad (12) \end{aligned}$$

The usefulness of the robust design is somewhat diminished for the survey protocols considered here as compared to the benefit offered to capture–recapture studies. In capture–recapture studies, the robust design is used to estimate abundance within periods and survival rates between periods (Pollock, 1982). Although these can both be estimated from the likelihood given in equation (7) even if only one sample is obtained for each primary period (i.e., $J_t = 1$ for all $t = 1, \dots, T$), using a robust design should offer improvement in terms of both accuracy and precision.

4. Simulation Study

A simulation study was conducted to determine the ability of the proposed generalized N -mixture model to detect population dynamics and estimate abundance in an open population, yet avoid falsely detecting dynamics when the population is closed. Data were simulated with population dynamics parameter values of $\gamma = \{0, 1, 2\}$ and $\omega = \{1, 0.8, 0.5\}$. The combination of $\gamma = 0$ with $\omega = 1$ represents population closure, where the Royle model is appropriate, whereas the other combinations represent open populations.

Additionally, data were generated with population dynamics taking a form different than expected by the generalized model. In these scenarios only the trend was specified instead of specifying survival and entering rates, with Φ taking the value of either 0.75 or 1.2. Site abundances were then determined for each sampling occasion ($t > 2$) by multiplying the previous site abundance by Φ and rounding the result to the nearest whole number.

The site and period combinations $(R, T) = (20, 5)$ or $(R, T) = (100, 10)$ were used with Poisson site-specific initial abundances having $\lambda = 2$ or $\lambda = 5$. Binomial data were then generated with either $p = 0.25$ or $p = 0.50$, giving 8 different settings for each population dynamics scenario.

Although the Royle model is not typically fit to simulated data of an open population, it was done in this study to facilitate an examination of the rate at which the generalized model detects the population dynamics. Additionally, abundance estimates obtained from the Royle model provide a baseline for comparison with the abundance estimates

obtained from the generalized model. To accommodate the large variation in observed counts at each site in the presence of an open population, the Royle model was allowed to have p vary either linearly or as a factor.

In order to establish lower limits on the performance of the generalized model, only the constant model with no covariates for p was considered as an open population model. This restriction made it easier for a Royle model to have a lower AIC score than the open population model, so it was therefore more difficult for the generalized model to detect the population dynamics.

Both Poisson and negative binomial priors for $f(N_{i1})$ were used for every model, giving six models considered for the Royle model and eight for the generalized model. AIC score was used to select the best generalized model and the best Royle model, because the competing models are not fully nested. Although models within two AIC units fit the data similarly well on the grounds of parsimony (Burnham and Anderson, 2002), for simplicity here only the models with the lowest AIC scores were chosen for evaluation.

For each scenario, the fraction of generalized models selecting a model that included population dynamics was recorded, and estimates of \hat{N}_T were compared between the Royle model and the generalized model. The models were fit using the optim procedure in the software package R (R Development Core Team, 2009). The numerical solution appeared stable in all cases.

4.1 Simulation Results

Simulation results for $(R, T) = (100, 10)$ are summarized in Table 2; Web Table 1 presents results for $(R, T) = (20, 5)$. Results for scenarios with population dynamics in a form other than expected by the generalized model are given in Web Tables 2 and 3.

These results indicate that if the population is closed, the generalized model falsely detects population dynamics at a very low rate (<0.01). This is true in all closed population scenarios considered here, regardless of R and T .

Additionally, although the generalized model had a much higher rate of detecting population dynamics in the open population scenarios with $(R, T) = (100, 10)$ than the open population scenarios with $(R, T) = (20, 5)$, in each of these scenarios its estimates of total abundance were less biased and had lower RMSE than the corresponding estimates of total abundance from the Royle model. For one case typical of $(R = 100, T = 10)$, with $\lambda = 2$ and $p = 0.50$, the centered sampling distributions of \hat{N}_{10} for both models are shown in Figure 1. Density plots are of the bias $\hat{N}_{10} - N_{10}$ for each model, so zero on the x -axis represents no discrepancy between \hat{N}_{10} and the actual value of N_{10} .

This result does not detract from the Royle model, because the Royle model would not typically be fit to data from an open population. Rather, it demonstrates the benefit of using the generalized model in conjunction with the Royle model.

As shown in Web Table 2, the generalized model detected population dynamics at very low rates for all four scenarios constructed with migration of a form other than expected, even with $(R, T) = (100, 10)$. To further investigate this, the generated data sets from these four scenarios were reanalyzed with the autoregressive generalized model allowed as an

additional candidate; results are displayed in Web Table 3. Allowing the autoregressive model as a candidate gave the generalized model a much improved rate of detecting population dynamics for the two scenarios with $(R, T) = (100, 10)$. Although the detection rates are unchanged for $(R, T) = (20, 5)$, they compare with the detection rates displayed in Web Table 1.

5. Applications Using Avian Point Counts

The proposed generalized model has potential use in two areas: first, it provides a test of the closure assumption in data settings where the Royle model would typically be applied; and second, the generalized model can be used to analyze point count data when the closure assumption is invalid, such as when sampling is replicated for multiple years or the closure test gives evidence of within-season dynamics. The following examples provide illustrations of both potential uses.

5.1 Test of the Closure Assumption

Kéry et al. (2005) use the Royle model to analyze one season (2002) of point count data collected by the Switzerland national monitoring program for breeding bird species. This monitoring program collects bird count data at more than 250 1-km² quadrats distributed in a grid across Switzerland, with each quadrat surveyed up to three times annually during the breeding season (April 1 through June 30). For more details regarding the sampling protocol see Kéry et al. (2005).

Point counts of Mallards (*Anas platyrhynchos*), as well as several site-specific and sampling occasion-specific covariates, are provided by Kéry et al. (2005). The best-fitting Royle model has a negative binomial prior for $f(N_{i1})$, includes elevation and percentage forest cover as covariates for the negative binomial mean, and includes sampling date (linear) as a covariate for detection probability.

Inferences made using this model, such as an estimate of total Mallard abundance and associations between the measured covariates and abundance, depend on the population closure assumption. Because the data come from only one breeding season the population closure assumption is biologically justifiable. However, the generalized model can be used to verify this assumption statistically with a formal test, which will strengthen conclusions obtained using the Royle model.

It is convenient to reformulate the closure test described in Section 3.1 to be in terms of the length of a primary period, with the null model having a primary period length longer than the study duration, and the alternative model having some specified shorter primary period length. Although it may be appropriate to repeat the closure test several times using different primary period durations, here we will only test the hypothesis that the primary period lasts all summer against the alternative that a primary period lasts 30 days. Choosing 30 days as the alternative is suitable because it results in a robust design with $T = 3$ and some sites having up to three observations in a primary period. This ensures all parameters of the generalized model will be identifiable and improves the resulting estimates (see the discussion in Section 6.2). In general, although the use of a shorter primary period length under the alternative hypothesis (e.g., 1 day) can expose animal movement in more detail, this

Table 2

Summaries of the sampling distribution of abundance estimates using the generalized (“Gen”) and Royle models based on 1000 simulated data sets with $R = 100$ sites and $T = 10$ sampling occasions. The population dynamics are defined by γ and ω . The Royle model assumes a closed population with $\omega = 1$ and $\gamma = 0$, and so is included here only for a baseline comparison. q_1 , q_2 , and q_3 are the first, second, and third quartiles of $\hat{N}_{\cdot 10} - N_{\cdot 10}$. RMSE is root mean square error for each model. Coverage is the fraction of 95% “asymptotic” confidence intervals that contained the true value of $N_{\cdot 10}$. Open is the fraction of generalized models that, via AIC model selection, preferred an open population model over one of the Royle models.

γ	ω	λ	p	Model	$\hat{N}_{\cdot 10} - N_{\cdot 10}$			RMSE	Coverage	Open
					q_1	q_2	q_3			
0	1	2	0.25	Gen	−10.20	0.90	13.51	19.92	0.978	0.006
				Royle	−10.11	0.90	13.53	19.56	0.983	
0	1	5	0.25	Gen	−10.89	0.06	13.08	18.59	0.996	0.001
				Royle	−10.89	0.06	13.08	18.47	0.997	
0	1	2	0.50	Gen	−2.95	0.45	4.01	5.27	0.999	0.004
				Royle	−2.95	0.48	4.03	5.28	0.999	
0	1	5	0.50	Gen	−31.17	0.26	40.70	56.87	0.959	0.004
				Royle	−30.94	0.61	41.45	57.12	0.961	
1	0.8	5	0.25	Gen	−70.54	2.91	243.55	345.66	0.698	0.746
				Royle	415.77	563.60	753.04	723.57	0.054	
1	0.8	2	0.50	Gen	−31.70	−1.00	34.14	50.97	0.962	1.000
				Royle	323.10	388.01	471.66	433.42	0.001	
1	0.5	5	0.25	Gen	−41.60	1.61	52.78	89.99	0.907	0.995
				Royle	1018.82	1425.82	2182.29	50, 225.47	0.537	
1	0.5	2	0.50	Gen	−37.02	−2.72	37.46	407.07	0.928	0.986
				Royle	805.33	993.79	1239.60	3100.75	0.034	
2	0.8	5	0.25	Gen	−117.16	14.05	168.19	416.57	0.898	0.945
				Royle	583.72	839.41	1144.05	4983.73	0.408	
2	0.8	2	0.50	Gen	−57.74	2.13	60.06	95.08	0.960	1.000
				Royle	507.98	622.51	786.66	726.55	0.001	
2	0.5	5	0.25	Gen	−51.93	283.97	2961.98	2891.50	0.794	0.503
				Royle	1408.50	2087.26	3365.92	3798.62	0.505	
2	0.5	2	0.50	Gen	−46.81	16.80	134.39	959.54	0.823	0.864
				Royle	1415.68	1745.64	2183.26	35, 077.78	0.038	

shortened primary period length will increase the number of unobserved primary periods at each site, reducing model performance.

Using the same covariates for λ and p as included in the best-fitting Royle model, the best-fitting generalized model (the “constant” model) only provides an increase in maximized likelihood of 0.56. The p -value from the likelihood ratio test is 0.29, so there is no evidence against closure in this study. Therefore, the closure test provides statistical backing for the ecological arguments for closure, strengthening the conclusions made using the Royle model.

R code and a tutorial for fitting the generalized model to these data and performing the closure test are provided in the Web Appendix.

5.2 Open Population Dynamics and Abundance Estimation

The North American BBS is a large-scale monitoring program that oversees the point count surveying of breeding birds along > 4000 routes throughout the United States and Canada. Each route has 50 stops (sites) spread one-half mile apart where an observer records the number of each species detected. For general background on the BBS, see Robbins, Bystrak, and Geissler (1986). Royle (2004b) applies the Royle model to data from a 1991 study where a set of BBS routes were surveyed multiple times within the same breeding season.

For these data the population closure assumption is biologically justifiable.

However, most BBS routes are surveyed only once per year. In this example, we consider point count data for the American robin (*Turdus migratorius*) along a BBS route in Oregon collected once per year from 2003 through 2008. Data for the first 5 of the 50 sites along this route are given in Table 1. Because of the sampling protocol, the assumptions that sites are independent and that n_{it} for sample location $i = 1, 2, \dots, 50$ and year $t = 1, 2, \dots, T$ are Binomial(N_{it}, p) seem plausible.

The generalized models considered as candidates in this analysis are the constant, autoregressive, and reshuffle models described in Section 3.2. The Royle model is also included as a candidate as protection against selecting an over-fit model, because it provides a reduced model to compare the constant and autoregressive models against.

Poisson and negative binomial priors for the initial spatial distribution $f(N_{i1})$ are fit for each of the four candidate models. Additionally, sampling year is used as a possible covariate for detection probability, included in the model either as a linear term or as a factor.

AIC comparison is used to select the subset of models that provide the best fit for the data, using the general rule that models with $\Delta AIC < 2$ fit a data set similarly well on the grounds of parsimony (Burnham and Anderson, 2002). Total abundance estimates for models within two AIC points

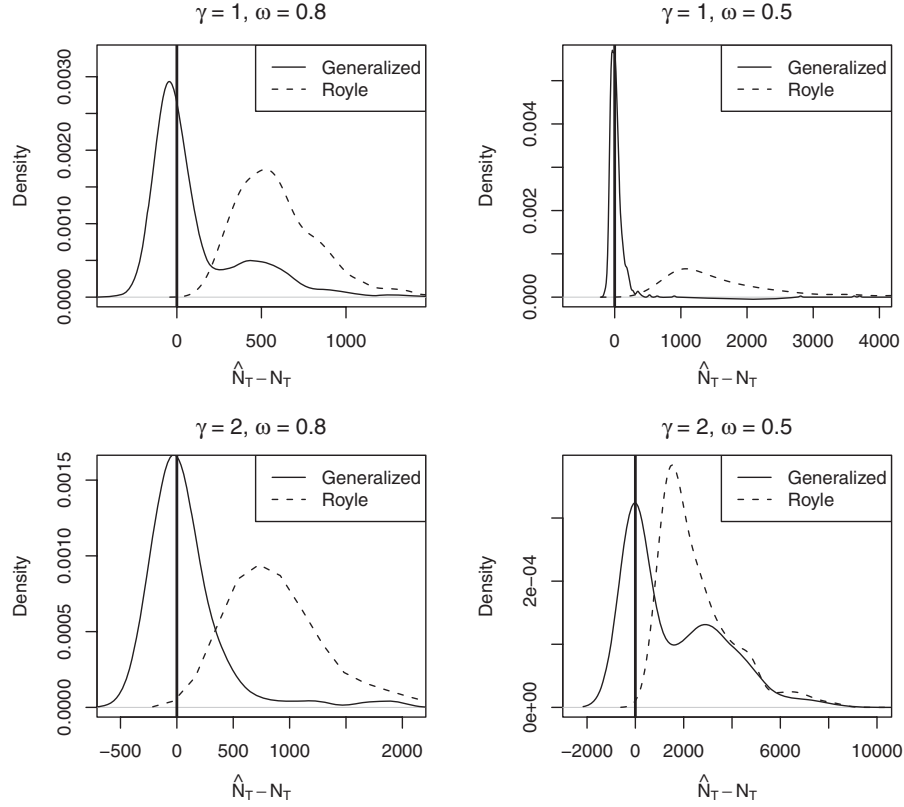


Figure 1. Centered sampling distributions ($\hat{N}_{10} - N_{10}$) for the generalized model and the Royle (2004b) model when $\lambda = 2$, $p = 0.50$, $R = 100$, $T = 10$. ω is the binomial survival probability and γ is the Poisson recruitment rate.

Table 3

Estimated yearly route abundance of American robins from one route of the BBS using different migration models. p covariate describes the use of sampling year as a covariate for detection probability, and is one of Intercept, Linear, or Factor. $f(N_{i1})$ is the prior distribution for initial site abundances, ΔAIC is the difference in AIC points between each model and the lowest AIC score observed, and \hat{N}_t is estimated route abundance during sampling of year t , with $t = 1$ representing calendar year 2003. Results are included here only for models with $\Delta AIC < 2$.

Model	$f(N_{i1})$	p covariate	ΔAIC	\hat{N}_1	\hat{N}_2	\hat{N}_3	\hat{N}_4	\hat{N}_5	\hat{N}_6
Constant	Pois	Intercept	0	115.3	105.1	97.9	92.8	89.3	86.8
Constant	Pois	Linear	0.81	157.1	97.9	69.0	55.0	48.1	44.8
Royle	Pois	Linear	0.91	192.5	192.5	192.5	192.5	192.5	192.5
Royle	Pois	Intercept	1.28	198.4	198.4	198.4	198.4	198.4	198.4
Constant	NB	Intercept	1.96	117.0	106.6	99.2	94.0	90.4	87.9

of the lowest observed AIC score are displayed in Table 3, with estimates for all 24 models considered included in Web Table 4.

The parametric bootstrap procedure (Dixon, 2002) gave no evidence of lack of fit (p -value 0.84) for the model with the lowest AIC score, the constant generalized model with Poisson prior and constant p .

Although multi-model inference using model averaging would be appropriate here (Buckland, Burnham, and Augustin, 1997), the best-fitting individual model can be obtained using formal tests. The closure test provides convincing evidence against the Royle models, giving a p -value of 0.003

for the “intercept” p model and a p -value of 0.008 for the linear p model. Then, with a p -value of 0.12, there is no evidence including sampling year as a linear term is necessary for the constant generalized model. Finally, with a p -value > 0.3 , there is no evidence of overdispersion in the Poisson prior for the constant migration model (case 5, Self and Liang, 1987).

Therefore, the best model is the constant generalized model that includes no covariates for p and a Poisson prior for $f(N_{i1})$. This model gives estimates of the population dynamics parameters to be $\hat{\gamma} = 0.48$ and $\hat{\omega} = 0.70$, with asymptotic 95% confidence intervals of (0.21, 1.14) and (0.32, 0.92), respectively.

6. Discussion

There are two advantages provided by the generalized model. First, it can be used to test the closure assumption of the Royle model. There are many studies that consist of sampling populations of animals during only one breeding season, when the closure assumption is biologically justified. The generalized model allows this assumption to be formally tested, strengthening conclusions made using the Royle model. Additionally, as the population closure assumption has been found to be violated in some studies of short duration (Rota et al., 2009), having a closure test will guard against incorrectly applying the Royle model to an open population.

Second, the generalized model provides an estimate of the population dynamics parameters when applied to an open population. These are then used to estimate of the total abundance (aggregated over all sampled sites) during any primary sampling period, as well as the linear trend in total abundance over time. These estimates are more appropriate than using the raw counts because the generalized model accounts for imperfect detection probability.

6.1 Other Model Assumptions

There are assumptions inherent in the generalized model that warrant investigation: site independence, the parametric form of the population dynamics, the independence of S_{it} and G_{it} , and that no animal was mistakenly counted as two.

First, sites may not be independent, especially if sites are adjacent (such as in a grid) because animals leaving one site will enter another site by necessity. One way to model this dependence may be to include the abundance at surrounding sites, weighted by distance, as a covariate for γ or ω . An alternative is to use Bayesian hierarchical modeling and the spatial dependence models developed by Royle et al. (2007). However, incorporating these models has proved difficult, so this remains an area of active research.

Second, the number of animals surviving and staying at a site will not be a binomial random variable if clusters of animals survive or emigrate together. Royle (2008) gives a framework for modeling the effect of cluster size in wildlife surveys, which relaxes the binomial assumption, and it may be possible to apply these models to the setting considered here. However, these models require auxiliary information beyond the observed counts, such as distance sampling or double-observer sampling, so extending this framework to include the generalized model is an open research question.

Third, although we assumed in this article that S_{it} is independent of G_{it} , this is not necessary. Instead, the dependence could be modeling by allowing $G_{it} | S_{it} = s$ to be a Poisson random variable with rate $\gamma = se^{\varphi_0}$. Then, P_{jk} takes the following form:

$$P_{jk} = \sum_{c=0}^{\min(j,k)} \text{Bin}(c; j, \omega) \cdot \text{Pois}(k - c; ce^{\varphi_0}).$$

Because $\hat{S}_{it} = \hat{\omega} \hat{N}_{it-1}$, estimates of abundance can be obtained using the recursive definitions

$$\begin{aligned} \hat{N}_1 &= R\hat{\lambda} \\ \hat{N}_t &= \hat{\omega} \hat{N}_{t-1} + R\hat{\omega} e^{\varphi_0} \hat{N}_{t-1}. \end{aligned}$$

The only difference between these and the recursive definitions for the autoregressive model in Section 3.3 is the $\hat{\omega}$ in $R\hat{\omega} e^{\varphi_0} \hat{N}_{t-1}$.

And finally, because the generalized model requires point counts be collected on each sampling occasion, it assumes that no animal was counted multiple times on any one sampling occasion. To address this, a goal of future research is to formulate the generalized model to allow instead for the collection of presence-absence (or detection nondetection) data. Despite collecting less information in each sampling effort, more samples can typically be obtained with the collection of presence-absence data than with point counts because it takes less effort to observe the presence of any animals on a site than it takes to count all the animals detected. Additionally, the possibility of double counting an animal is removed because counts are not even collected.

6.2 Discussion of Simulation Results

Results of the simulation study suggest that the generalized model falsely detects population dynamics at a very low rate, and that the rate at which it detects population dynamics in an open population is related to the number of observations, both R and T . When the generalized model was able to detect the population dynamics of an open population, the resulting abundance estimates have median and mode close to the correct values, and are only slightly biased despite the general skewness of \hat{N}_t .

The study also demonstrates that the generalized model is able to detect population dynamics in the form of a simple linear trend, even though this is different than the forms expected by either the constant or the autoregressive models. This is important because populations with more complicated dynamics will also have a large linear component (Urquhart, Overton, and Birkes, 1993). Although the more complicated dynamics present in these populations will go undiscovered by the generalized model, the generalized model will at least be able to detect the linear component. This could then be used as an indicator for further study to more accurately model the population dynamics. A more extensive simulation study is necessary to determine the exact relationship between the population dynamics detection rate with the value of the linear trend in abundance.

Informal explorations (via simulation) were performed to investigate the effects of increasing or decreasing R and T . These suggest that the slight bias in the abundance estimates decreases as R increases beyond 100, while increasing T beyond 10 seems to have little effect. Also, in an effort to address the identifiability of model parameters with small T , we found that when many sites are considered ($R = 100$), equation (7) has a unique maximum value when $T \geq 3$, but not when $T = 2$. This makes sense intuitively, because observations during the first primary period would be used to estimate λ , and then it would take two more primary periods to estimate p as well as both population dynamics parameters. Using the robust design will improve parameter estimates, and this is recommended for samples with $T = 3$.

Further simulation studies investigating the generalized model are warranted. Future studies should seek to assess the power of the formal test between the models; the ability of the generalized model to estimate population dynamics when

combined with the formal test; the performance of the generalized model in small T settings; and the ability of the generalized model to differentiate different population dynamics through the use of the constant, autoregressive, and reshuffle models.

6.3 Discussion of the Applications

The generalized model was used to statistically verify the population closure assumption for the analysis of Mallard point count data covering one breeding season. Though this test was introduced in Section 3.1 as being a test of the population dynamics parameters, it was convenient here to reformulate it to be a test of primary period length. Testing the alternative of 30 days gave a p -value of 0.29, which supports the conclusions reached using the Royle model as there is no evidence of population dynamics. Other alternative primary lengths could be tested to further support the conclusions of the Royle model.

Next, the generalized model was used to estimate the population dynamics and abundance of American robins using point count data replicated at 50 sites over 6 years. The population closure assumption is suspected to be invalid due to the extended time frame of the study, and this was confirmed as the generalized model with constant γ was found to best fit the data. This model was then used to estimate the population dynamics from only point counts, with $\hat{\gamma} = 0.48$ and $\hat{\omega} = 0.70$. This combination gives some evidence that total abundance of American robins at these sites gradually decreased throughout the study, illustrated by the estimates of total abundance decreasing each year from 115.3 in 2003 to 86.8 in 2008.

7. Supplementary Materials

Web Appendices and Tables referenced in Sections 3 and 4, as well as R code for analyzing the Mallard data in Section 5.2 and a tutorial for fitting the generalized model, are available under the Paper Information link at the *Biometrics* website <http://www.biometrics.tibs.org>.

ACKNOWLEDGEMENTS

We thank David Birkes, the associate editor, and two anonymous referees for their many helpful comments and suggestions, which greatly improved our article. We also thank David Zucker for his suggestion to use the likelihood ratio test described in Section 3.1

REFERENCES

- Buckland, S. T., Burnham, K. P., and Augustin, N. H. (1997). Model selection: An integral part of inference. *Biometrics* **53**, 613–618.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., and Thomas, L. (2001). *Introduction to Distance Sampling*. New York: Oxford University Press.
- Burnham, K. P. and Anderson, D. R. (2002). *Model Selection and Inference—A Practical Information-Theoretic Approach*, 2nd edition. New York: Springer-Verlag.
- Carroll, R. J. and Lombard, F. (1985). A note on N estimators for the binomial distribution. *Journal of the American Statistical Association* **80**, 423–426.
- Dixon, P. M. (2002). Bootstrap resampling. *Encyclopedia of Environmental Metrics* **1**, 212–220.
- Dominicus, A., Skrandal, A., Gjessing, H., Pedersen, N., and Palmgren, J. (2006). Likelihood ratio tests in behavioral genetics: Problems and solutions. *Behavior Genetics* **36**, 331–340.
- Efron, B. and Hinkley, D. V. (1978). Assessing the accuracy of the maximum likelihood estimator: Observed versus expected Fisher information. *Biometrika* **65**, 457–482.
- Farnsworth, G. L., Pollock, K. H., Nichols, J. D., Simons, T. R., Hines, J. E., and Sauer, J. R. (2002). A removal model for estimating detection probabilities from point-count surveys. *Auk* **119**, 414–425.
- Kéry, M. (2008). Estimating abundance from bird counts: Binomial mixture models uncover complex covariate relationships. *Auk* **125**, 336–345.
- Kéry, M., Royle, J. A., and Schmid, H. (2005). Modeling avian abundance from replicated counts using binomial mixture models. *Ecological Applications* **15**, 1450–1461.
- Kéry, M., Dorazio, R. M., Soldaat, L., van Strien, A., Zuiderwijk, A., and Royle, J. A. (2009). Trend estimation in populations with imperfect detection. *Journal of Applied Ecology* **46**, 1163–1172.
- Krebs, C. J. (2001). *Ecology: The Experimental Analysis of Distribution and Abundance*. Boston: Addison Wesley.
- Lehmann, E. L. (1999). *Elements of Large Sample Theory*, 2nd edition. New York: Springer.
- MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., and Franklin, A. B. (2003). Estimating site occupancy, colonization and local extinction probabilities when a species is not detected with certainty. *Ecology* **84**, 2200–2207.
- Nichols, J. D., Hines, J. E., Lebreton, J. D., Pradel, R. (2000). Estimation of contributions to population growth: A reverse-time capture-recapture approach. *Ecology* **81**, 3362–3376.
- Nichols, J. D., Hines, J. E., Sauer, J. R., Fallon, F. W., Fallon, J. E., and Heglund, P. J. (2000). A double-observer approach for estimating detection probability and abundance from point counts. *Auk* **117**, 393–408.
- Nichols, J. D., Thomas, L., and Conn, P. B. (2008). Inferences about landbird abundance from count data: Recent advances and future directions. *Journal of Environmental and Ecological Statistics* **3**, 201–236.
- Olkin, I., Petkau, A. J., and Zidek, J. V. (1981). A comparison of N estimators for the binomial distribution. *Journal of the American Statistical Association* **76**, 637–642.
- Pollock, K. H. (1982). A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* **46**, 757–760.
- Pollock, K. H., Nichols, J. D., Brownie, C., and Hines, J. E. (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs* **107**, 3–97.
- R Development Core Team (2009). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0.
- Robbins, C. S., Bystrak, D. A., and Geissler, P. H. (1986). *The Breeding Bird Survey: Its First Fifteen Years (1965–1979)*, Volume 157. Washington, DC: USDOI, Fish and Wildlife Service Resource Publication.
- Ross, S. M. (2006). *Probability Models*, 9th edition. Orlando, Florida: Academic Press.
- Rota, C. T., Fletcher, R. J., Jr., Dorazio, R. M., and Betts, M. G. (2009). Occupancy estimation and the closure assumption. *Journal of Applied Ecology* **46**, 1173–1181.
- Royle, J. A. (2004a). Generalized estimators of avian abundance from count survey data. *Animal Biodiversity and Conservation* **27**, 375–386.

- Royle, J. A. (2004b). N-mixture models for estimating population size from spatially replicated counts. *Biometrics* **60**, 108–115.
- Royle, J. A. (2008). Hierarchical modeling of cluster size in wildlife surveys. *Journal of Agricultural, Biological, and Environmental Statistics* **13**, 23–36.
- Royle, J. and Dorazio, R. (2008). *Hierarchical Modeling and Inference in Ecology*. Amsterdam: Academic Press.
- Royle, J. A. and Nichols, J. D. (2003). Estimating abundance from repeated presence-absence data or point counts. *Ecology* **84**, 777–790.
- Royle, J. A., Nichols, J. D., and Kéry, M. (2005). Modelling occurrence and abundance of species when detection is imperfect. *Oikos* **110**, 353–359.
- Royle, J. A., Kéry, M., Gautier, R., and Schmid, H. (2007). Hierarchical spatial models of abundance and occurrence from imperfect survey data. *Ecological Monographs* **77**, 465–481.
- Self, S. G. and Liang, K.-Y. (1987). Asymptotic properties of maximum likelihood estimators and likelihood ratio tests under nonstandard conditions. *Journal of the American Statistical Association* **82**, 605–610.
- Thompson, S. K. (1992). *Sampling*. New York: John Wiley.
- Urquhart, N. S., Overton, W. S., and Birkes, D. S. (1993). Comparing sampling designs for monitoring ecological status and trends: Impact of temporal patterns. In *Statistics for the Environment*, V. Barnett and K. F. Turkman (eds), 71–85. London: John Wiley.
- Wenger, S. J. and Freeman, M. C. (2008). Estimating species occurrence, abundance, and detection probability using zero-inflated distributions. *Ecology* **89**, 2953–2959.

Received January 2010. Revised April 2010.
Accepted May 2010.