

Inference about density and temporary emigration in unmarked populations

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Abstract. Few species are distributed uniformly in space, and populations of mobile organisms are rarely closed with respect to movement, yet many models of density rely upon these assumptions. We present a hierarchical model allowing inference about the density of unmarked populations subject to temporary emigration and imperfect detection. The model can be fit to data collected using a variety of standard survey methods such as repeated point counts in which removal sampling, double-observer sampling, or distance sampling is used during each count. Simulation studies demonstrated that parameter estimators are unbiased when temporary emigration is either “completely random” or is determined by the size and location of home ranges relative to survey points. We also applied the model to repeated removal sampling data collected on Chestnut-sided Warblers (*Dendroica pensylvanica*) in the White Mountain National Forest, USA. The density estimate from our model, 1.09 birds/ha, was similar to an estimate of 1.11 birds/ha produced by an intensive spot-mapping effort. Our model is also applicable when processes other than temporary emigration affect the probability of being available for detection, such as in studies using cue counts. Functions to implement the model have been added to the R package *unmarked*.

Key words: Chestnut-sided Warbler; *Dendroica pensylvanica*; detection probability; hierarchical models; *N*-mixture model; population density; spot-mapping; temporary emigration; unmarked populations; White Mountain National Forest, USA.

INTRODUCTION

Estimating population density is a central objective of basic and applied ecological research because it enables population monitoring as well as the assessment of processes such as habitat selection and density dependence. Density is often estimated using count data from surveys of unmarked individuals because mark-recapture methods can be invasive or too expensive to employ over large areas. Unfortunately, such counts can be biased by several sources of measurement error. Imperfect detection probability is one source of measurement error, and many models have been developed to account for it (Borchers et al. 2002). However, these models almost universally assume geographic closure, i.e., no immigration or emigration during the survey period.

The geographic closure assumption is frequently violated when surveying mobile species because individuals enter and leave survey plots during the course of sampling, a process known as temporary emigration. Ignoring temporary emigration can bias density estimates because the probability of detection, given presence, and the probability of being present are confounded (Kendall et al. 1997, Nichols et al. 2009,

Riddle et al. 2010). In this case, the interpretation of abundance changes from the number of individuals per plot to the number of individuals that could potentially use the plot (i.e., the superpopulation size). The effective area surveyed (the area over which the superpopulation of individuals resides) is thus unknown, and density cannot be estimated.

In addition to estimating density, ecological research is often concerned with modeling spatial variation in density. Among the earliest models permitting simultaneous treatment of variation in density and detection probability were the multinomial and binomial *N*-mixture models (Royle 2004a, b), which have proven useful for estimating habitat-specific abundance and evaluating species' responses to management practices (Dodd and Dorazio 2004, Kéry et al. 2005, Chandler et al. 2009, Schlossberg et al. 2010). These models assume demographic and geographic closure, and thus are typically applied to data collected over short sampling periods during which it is safe to assume that mortality and recruitment do not occur. For mobile organisms, however, plots often will not be geographically closed.

In this paper we extend the *N*-mixture models to open populations where temporal dynamics are governed by a temporary emigration model similar to that of Kendall et al. (1997). Our model can be used to estimate superpopulation size, population density, the probability that an individual is present during a sampling

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period, and detection probability. We then assess the performance of the model by fitting it to simulated data as well as data collected on Chestnut-sided Warblers (*Dendroica pensylvanica*) in the White Mountain National Forest, USA.

MODEL DEVELOPMENT

State models

We consider a standard sampling design in which unmarked individuals are counted at $i = 1, 2, \dots, R$ sample units on $t = 1, 2, \dots, T$ occasions. For clarity, we suppose that sample units are circular, fixed-radius plots such as are commonly used in plot-based sampling (Borchers et al. 2002); however, other sample units could be considered. At each plot, we assume that the superpopulation size (M_i) can be regarded as an outcome of a discrete probability distribution such as the Poisson or negative binomial with mean λ , which may be a function of plot-specific covariates. This distribution is the first level of our hierarchical model, denoted $f(M_i|\lambda)$. We again note that M_i is the total number of individuals that could possibly be detected at plot i over the duration of sampling.

The second level of our state model describes the subset of the superpopulation present within a plot on a particular occasion, N_{it} . Following the “completely random” temporary emigration model of Kendall et al. (1997), we assume that each member of the superpopulation will be present within the survey plot with probability ϕ ; thus, $1 - \phi$ is the temporary emigration probability. We will refer to this level of our state model by $g(N_{it}|\phi, M_i)$, where g is the binomial probability mass function.

The completely random temporary emigration model is attractive because of its simplicity and statistical tractability and because variation in ϕ can be modeled as a function of plot- and survey-specific covariates; in many cases, however, heterogeneity in ϕ will exist due to variation in the size and location of home ranges relative to the survey plots (Efford 2004). This information cannot be known without auxiliary data, and such unmodeled heterogeneity could bias estimators obtained under our model. We therefore assessed the robustness of our model to the completely random assumption using simulation (see *Simulation study*).

Observation models

Let \mathbf{y}_{it} be a vector of counts made at plot i on occasion t that arise conditional on N_{it} and the probability of detection (p). One of the strengths of our model is the flexibility with which this observation model, $h(\mathbf{y}_{it}|p, N_{it})$, can be specified (where h is a probability mass function). Here, we adopt the requirement that \mathbf{y}_{it} can be regarded as either multinomial or binomial outcomes. Examples of protocols yielding multinomial outcomes include removal sampling, double-observer sampling, and distance sampling (for definitions, see Williams et al. 2002). Binomial outcomes could be obtained by dividing

each survey occasion into J subintervals during which independent counts are made.

Letting $f(M_i|\lambda)$ be Poisson and $h(\mathbf{y}_{it}|p, N_{it})$ be multinomial, our model can now be described as a three-level hierarchical model:

$$M_i \sim \text{Poisson}(\lambda)$$

$$N_{it} \sim \text{Binomial}(M_i, \phi)$$

$$\mathbf{y}_{it} \sim \text{Multinomial}(N_{it}, \boldsymbol{\pi}_{it})$$

where $\boldsymbol{\pi}_{it}$ is the vector of multinomial cell probabilities computed from a function of the detection probability p . For example, in a removal design with three passes, the probabilities of detecting an individual for the first time during each pass are $\boldsymbol{\pi} = \{p, (1-p)p, (1-p)^2p\}$, with the fourth cell probability being $\pi_0 = (1-p)^3$, the probability of not detecting an individual.

Integrated likelihood

Our model is essentially a generalization of the multinomial and binomial N -mixture models of Royle (2004a, b). For the multinomial case in which $T \equiv 1$ and observations \mathbf{y}_i are independent when conditioned on local population size N_i and p_{it} , the integrated likelihood of \mathbf{y}_i can be computed easily (Royle 2004a, Dorazio et al. 2005). For a multinomial vector with three observable frequencies, the integrated likelihood is

$$L(\lambda, p | \mathbf{y}_i) = \prod_{i=1}^R \left\{ \sum_{N_i=\mathbf{y}_i}^{\infty} \left(\frac{N_i!}{y_{i1}! y_{i2}! y_{i3}! y_{i0}!} \pi_1^{y_{i1}} \pi_2^{y_{i2}} \pi_3^{y_{i3}} \pi_0^{N_i - y_i} \right) \times f(N_i|\lambda) \right\} \quad (1)$$

$$\text{where } y_i = \sum_{j=1}^3 y_{ij}.$$

Royle (2004b) derived the analogous likelihood for the binomial observation model when $J \equiv 1$.

To accommodate temporary emigration and the additional latent variable M_i , we expand the integrated likelihood to

$$L(\lambda, \phi, p | \mathbf{y}_{it}) = \prod_i^R \left\{ \sum_{M_i=\max(\mathbf{y}_{it})}^{\infty} \left[\sum_{N_{it}=\mathbf{y}_{it}}^{M_i} \left(\frac{N_{it}!}{y_{it1}! y_{it2}! y_{it3}! y_{it0}!} \pi_1^{y_{it1}} \pi_2^{y_{it2}} \pi_3^{y_{it3}} \pi_0^{N_{it} - y_i} \right) \times g(N_{it}|M_i, \phi) \right] f(M_i|\lambda) \right\} \quad (2)$$

For model parameters to be identifiable, $T > 1$ is necessary.

Integrating out two latent variables can be computationally difficult, but fortunately Eq. 2 can be simplified to

$$L(\lambda, \phi, p | \mathbf{y}_{it}) = \prod_{i=1}^R \left\{ \sum_{M_i=\max(\mathbf{y}_{it})}^{\infty} \left(\frac{M_i!}{y_{i1}!y_{i2}!y_{i3}!y_{i0}!} \times (\phi\pi_1)^{y_{i1}} (\phi\pi_2)^{y_{i2}} (\phi\pi_3)^{y_{i3}} (\phi\pi_0)^{M_i-y_i} \right) f(M_i | \lambda) \right\} \quad (3)$$

as described by Royle and Dorazio (2008:164). We again emphasize that each of the three parameters λ , ϕ , and p can be modeled as a function of covariates. To facilitate parameter estimation via maximum likelihood, we added the function “gmultmix” to the R package *unmarked* (R Development Core Team 2010, I. Fiske and R. B. Chandler, *unpublished manuscript*).

Density estimation

Under temporary emigration, some members of the superpopulation will have activity centers outside of the plot; therefore, it would appear as though density (D) estimation would not be possible because the effective plot area (A_e) is unknown and larger than the actual plot area (A). However, because our model only assumes that plots are closed during the sampling occasion, not among sampling occasions, density can be estimated by

$$\hat{D} = \frac{\widehat{E[N_{it}]}}{A} = \frac{\hat{\lambda}\hat{\phi}}{A}. \quad (4)$$

APPLICATIONS

Simulation study

We investigated the bias and precision of parameter estimates using two simulation studies. First, we simulated data under the completely random temporary emigration model with a removal sampling observation process. We used the following specifications for each of 5000 simulations, $R = 100$ 50-m radius plots, $T = 3$, $M_i \sim \text{Poisson}(\lambda = 3.14)$, $N_{it} \sim \text{Binomial}(M_i, \phi = 0.5)$, and $p = 0.3$ such that $\mathbf{y}_{it} \sim \text{Multinomial}(N_{it}, \boldsymbol{\pi} = \{0.3, 0.21, 0.147\})$. Therefore, $E[N_{it}] = \lambda\phi = 1.57$ and $E[D] = (E[N_{it}])/A_e = 2$ individuals/ha.

Assuming that all individuals have the same ϕ may not be justified in some cases, as described previously. To assess the performance of our model when fit to data generated under a more biologically justified, spatially explicit scenario in which ϕ is affected by the size and location of home ranges, we simulated data under an alternative state model, and fit the misspecified constant ϕ model to the data. Specifically, we drew 800 home range centers from a binomial point process model within a 2-km² space, such that $D = 2$ individuals/ha. We sampled this population on $T = 3$ occasions using 100

plots of 50 m radius, spaced by 200 m. On each occasion, the individual locations were determined by a symmetric bivariate normal movement model with parameter σ . This parameter was assigned values of 0, 10, and 30 m, corresponding, respectively, to no movement and movement land low and higher levels. For each of 5000 simulated data sets, we fit our model and estimated density using the naive estimate of $D = \lambda/A$ as well as Eq. 4, which acknowledges temporary emigration. A graphical depiction of this simulation study is shown in Fig. 1. All models were fit in R using the *unmarked* package.

Results of our simulation studies demonstrate that parameter estimators are unbiased when fit to data simulated from the completely random temporary emigration state model (Table 1). Density estimators were also unbiased when applied to data from the spatially explicit, misspecified model that included the bivariate normal movement process (Table 2, Fig. 2). Even though our model does not estimate σ , the density estimators were unbiased for all three levels of σ considered (Fig. 2). This provides strong evidence that our model is robust to heterogeneity in ϕ due to movement and the juxtaposition of home ranges with sample locations. Finally, our results reveal how the bias associated with ignoring temporary emigration increases with σ (Fig. 2).

Analysis of Chestnut-sided Warbler data

As part of an assessment of forest management practices in the White Mountain National Forest (Chandler et al. 2009), we surveyed Chestnut-sided Warblers in 38 “wildlife openings” using point counts and spot-mapping during June and July 2004, which corresponded to the height of the breeding season in this region (see Plate 1). Wildlife openings are managed using prescribed fire or mechanical treatments to create early-successional habitat. Details of the study area can be found in Chandler et al. (2009). In each site, we conducted 10-min, 50-m radius point counts. Survey points were located in the center of each site, with the exception of two sites large enough for more than one survey point, in which we spaced points by 250 m. Each point was surveyed three times by one of two experienced observers between 05:30 and 10:30 hours on days with little wind and no precipitation. Observers recorded the distance to each bird (using laser range-finders) and time intervals ($(0-2]$, $(2-5]$, and $(5-10]$ min) in which the bird was detected. Our objective was to estimate the density of territorial males, so only birds detected by song were included in analyses.

For comparative purposes, we also estimated density using an intensive spot-mapping effort (Bibby et al. 2000). Spot-mapping is considered a reliable method to derive absolute densities with which to validate model-based methods of density estimation (Buckland 2006). Four observers surveyed each site a total of eight times, with each visit length standardized to 20 min/ha (Bibby et al. 2000). During each survey, observers recorded the

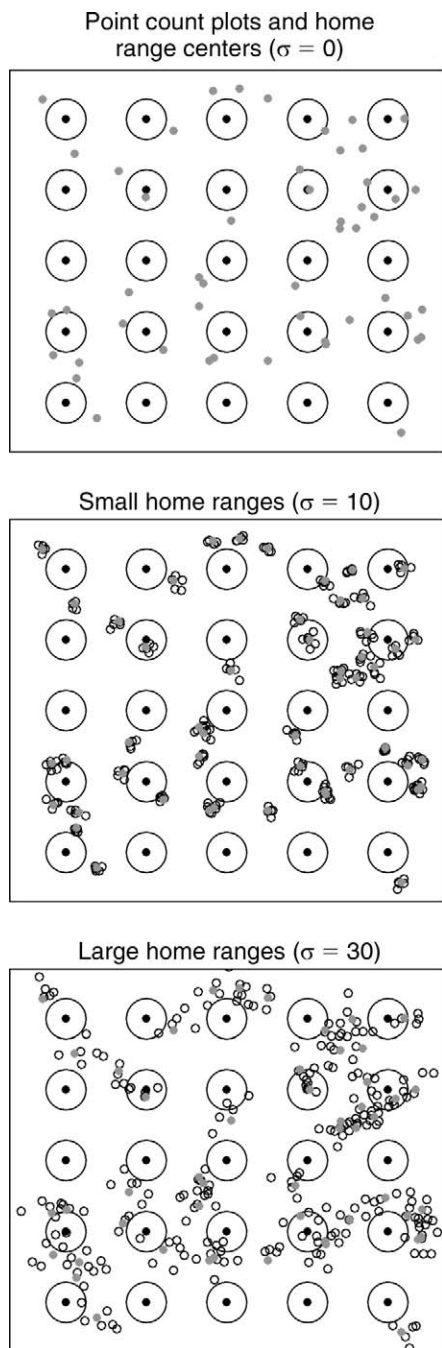


FIG. 1. Example simulations showing the state processes. Home range centers (gray) are distributed according to a binomial point process; small black dots represent the point at the center of each circular point count plot. The upper panel shows no movements ($\sigma = 0$); five movement events (open circles) are shown for small movements ($\sigma = 10$) and large movements ($\sigma = 30$). Survey plots ($n = 25$) are superimposed over the study area.

locations and movements of birds on 21.6×29.2 cm scaled digital orthophotographs, which were of a fine enough resolution to easily recognize patch boundaries and features such as trees and trails. Upon completion

of surveys, observers located and monitored nests. R. B. Chandler transposed the locations to transparency film for each species and each site. We identified territories as clusters of three or more locations and used countersinging to distinguish adjacent territories (Bibby et al. 2000). The small patch sizes, low bird abundances, structurally simple habitat, and knowledge of many of the nest locations made this a unique study system for determining the actual number of birds present.

We fit three different hierarchical models to the point count data: the temporary emigration model developed here, the multinomial N -mixture model of Royle (2004a) with a removal model observation process, and the binomial N -mixture model of Royle (2004b). We fit the multinomial N -mixture model to data from each of the three survey occasions independently. We accounted for the nonconstant time intervals by estimating the per-minute probability of detection. A primary objective of our study was to describe variation in abundance and detection parameters. For the abundance component of the models, we considered patch area, woody vegetation height, and the percent cover of woody vegetation as covariates. For detection probability, we considered time of day, date, observer, and vegetation height. For the temporary emigration model, we modeled ϕ as a function of patch area because birds in larger patches could move over larger areas. To identify the most parsimonious model, we used a forward model selection process in which we added covariates until no decrease in AIC was realized. We assessed model fit using a parametric bootstrapping approach (Kéry et al. 2005) in which we compared the observed sum of squared residuals to its expected sampling distribution based upon the fitted global model. All analyses were conducted in R using the add-on package *unmarked* (I. Fiske and R. B. Chandler, unpublished manuscript).

Model selection results are shown in the Appendix. There was no evidence of lack of fit based upon 500 parametric bootstrap simulations (all $P > 0.05$). Density estimates from the three models and from the intensive spot-mapping effort are shown in Fig. 3. With reference to the spot-mapping estimates, our new model outperformed the models ignoring temporary

TABLE 1. Results of 5000 simulations demonstrating that parameter estimates ($\hat{\theta}$) are unbiased when fit to data simulated under the "completely random" ϕ assumption.

Parameter (θ)	$\hat{\theta}^*$ quartiles			Coverage
	$q_{0.25}$	$q_{0.50}$	$q_{0.75}$	
$\lambda = 3.14$	2.80	3.13	3.57	0.95
$\phi = 0.50$	0.43	0.50	0.57	0.98
$p = 0.30$	0.27	0.30	0.33	0.95

Notes: Quartiles are the 25th, 50th, and 75th percentiles of the sampling distributions ($\hat{\theta}^*$). Coverage is the proportion of 95% confidence intervals including the true parameter value (θ); λ is the superpopulation size, ϕ is the probability of being present during the survey, and p is the detection probability.

TABLE 2. Simulation results from fitting the model to data generated using the misspecified model with heterogeneity in ϕ induced by a bivariate normal movement process.

Parameter (θ) by movement level	$\hat{\theta}^*$ quartiles		
	$q_{0.25}$	$q_{0.50}$	$q_{0.75}$
For $\sigma = 0$			
$\lambda = \text{—}$	1.49	1.58	1.66
$\phi = \text{—}$	0.95	1.00	1.00
$p = 0.30$	0.30	0.31	0.33
For $\sigma = 10$			
$\lambda = \text{—}$	1.97	2.09	2.22
$\phi = \text{—}$	0.71	0.75	0.81
$p = 0.30$	0.28	0.3	0.32
For $\sigma = 30$			
$\lambda = \text{—}$	3.54	4.03	4.66
$\phi = \text{—}$	0.33	0.39	0.45
$p = 0.30$	0.28	0.3	0.32

Notes: Five thousand simulations were conducted for each movement level ($\sigma = \{0, 10, 30\}$ corresponding to the values shown in Fig. 1), where σ is the movement parameter, λ is the superpopulation size, ϕ is the probability of being present during the survey, and p is the detection probability. Note that λ and ϕ were estimated, though not directly used to simulate the data (as indicated by the long dashes in column 1), but density was unbiased for all three movement levels (Fig. 2). Quartiles are the 25th, 50th, and 75th percentiles of the sampling distributions ($\hat{\theta}^*$).

emigration in terms of both precision and bias. The binomial N -mixture model appeared to overestimate density, whereas the multinomial N -mixture models underestimated density.

DISCUSSION

Our model builds upon previous efforts to estimate and model the density of organisms that cannot be detected perfectly and have not been individually marked. These models have been designed to explicitly account for sources of bias inherent to survey data; however, the assumptions of these models have been criticized (Bart et al. 2004, Efford and Dawson 2009, Simons et al. 2009). Geographic closure is among the most commonly cited assumption thought to be violated. Our model relaxes this assumption by allowing for temporary emigration and thus can be used to improve inference about spatial variation in density.

Simulation studies demonstrated that our model performs well under both the implicit completely random temporary emigration model and the misspecified spatially explicit temporary emigration model, in which ϕ is determined by the size and location of an individual's home range center relative to the survey point. The latter finding was surprising because our model does not include parameters related to these two unobserved covariates. The unbiasedness suggests that the misspecified model is reasonably well approximated by the constant ϕ model of random temporary emigration, because under the spatially explicit model,

$$E[N_{it}] = \sum_{i=1}^{i=M} \phi_i = M\bar{\phi}.$$

However, it can be shown that our variance estimator is under-dispersed relative to the variance of the spatially explicit model.

In addition to our simulation studies, we fit our model to Chestnut-sided Warbler count data collected under typical field conditions. The resulting density estimate, 1.09 birds/ha, was comparable to an estimate, 1.11 birds/ha, obtained using spot-mapping, suggesting that similar information can be obtained using far fewer resources than required by such labor-intensive

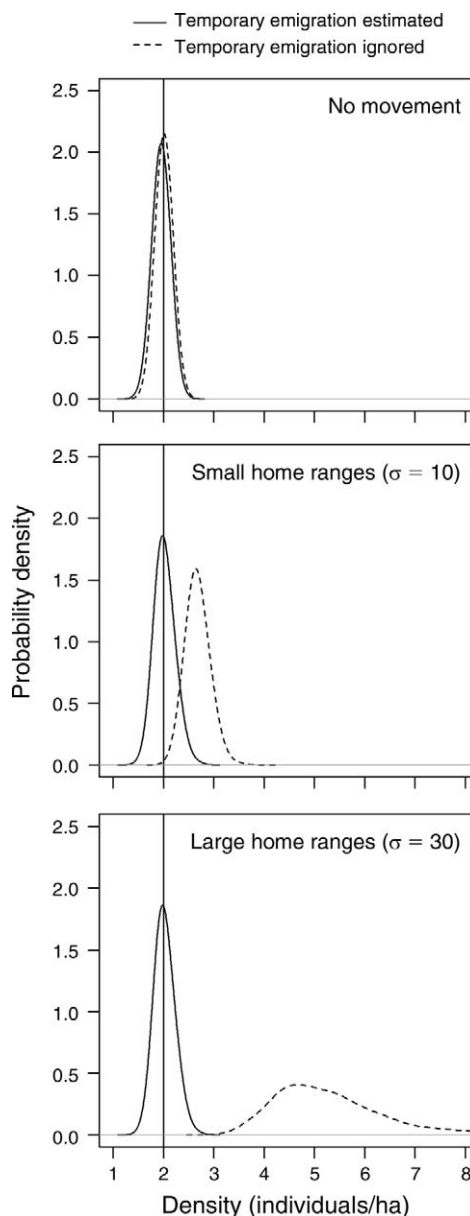


FIG. 2. Simulation results comparing density estimates when temporary emigration is ignored vs. estimated. Three different movement levels, corresponding to those in Fig. 1, are shown. The true density estimate (2 individuals/ha) is represented by the vertical line. The bias associated with ignoring temporary emigration increases with movement.



PLATE 1. Male Chestnut-sided Warbler, 22 May 2009, Snaggy Mountain Road, McHenry, Maryland, USA. Photo credit: Mikey Lutmerding.

field methods. Our results also highlight the bias that can arise from ignoring temporary emigration. For the binomial N -mixture model, this bias does not affect the superpopulation abundance estimate, and thus does not detract from the model's utility in many cases. Rather, temporary emigration induces upward bias in

the density estimate because the effective survey area is greater than the actual plot area. For the multinomial N -mixture models applied to each occasion separately, temporary emigration should not have strongly affected the density estimate because little movement is expected to occur during a 10-min period. That these density estimates appeared to be negatively biased suggests that some individuals were present but not available for detection. The development of models to address this form of availability bias is an area of ongoing research (Nichols et al. 2009, Riddle et al. 2010).

We have focused on study designs in which populations are only open with respect to movement, and ϕ is the probability of an individual being present during the survey. However, in other contexts ϕ may be interpreted differently. For example, when counting cues, such as whale blows, ϕ would be the probability that an individual produces a cue, and p would be the probability of detecting the cue. Alternatively, populations may be open to both movement and demographic processes, in which case our model would not be appropriate. Other options exist for such situations. Recently, Kéry et al. (2009) extended the binomial N -mixture model to estimate temporal trends in abundance. Dail and Madsen (*in press*) developed an open N -mixture model that includes recruitment and apparent survival parameters. These models are similar to ours in that the parameters are hierarchically structured, and variation at each level can be directly modeled as functions of covariates. They are also complementary

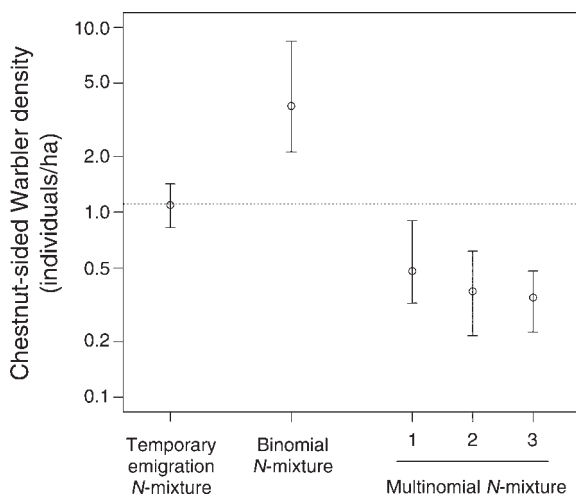


FIG. 3. Chestnut-sided Warbler (*Dendroica pensylvanica*) density estimates and 95% confidence intervals (note the log scale) from (1) the N -mixture model accounting for temporary emigration, (2) the binomial N -mixture model of Royle (2004b), and (3) the multinomial N -mixture model of Royle (2004a) applied to each survey occasion. A removal sampling observation model was used for (1) and (3). The horizontal dotted line is the spot-mapping estimate.

approaches for modeling different types of population dynamics.

Few species are distributed uniformly in space and rarely are populations geographically closed, yet these realities are often ignored when modeling abundance or density. Only recently developed spatially explicit capture–recapture models (Royle and Young 2008) can directly model spatial variation in density and movement, but these models require individual recognition, which may be expensive or invasive in practice. Our model provides an alternative way of estimating the density of mobile species with imperfect detection probability that have not been uniquely marked. Furthermore, many research projects already collect replicated count data using suitable protocols; thus, we expect that our model will be widely applicable in studies of spatial variation in density.

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APPENDIX

Parameter estimates and AIC values for models of Chestnut-sided Warblers abundance, temporary emigration, and detection probability (*Ecological Archives* E092-122-A1).

ERRATA

Richard B. Chandler has reported three errors in the paper by Chandler et al., published in the July 2011 issue (Chandler, R. B., J. A. Royle, and D. I. King. 2011. Inference about density and temporary emigration in unmarked populations. *Ecology* 92:1429–1435). First, the expression $J \equiv 1$ following Eq. 1 should be $T \equiv 1$.

Additionally, Eq 2 should be changed from

$$L(\lambda, \phi, p|\mathbf{y}_{it}) = \prod_i^R \left\{ \sum_{M_i=\max(\mathbf{y}_{it.})}^{\infty} \left[\sum_{N_{it}=y_{it.}}^{M_i} \left(\frac{N_{it}!}{y_{it1}!y_{it2}!y_{it3}!y_{it0}!} \pi_1^{y_{it1}} \pi_2^{y_{it2}} \pi_3^{y_{it3}} \pi_0^{N_{it}-y_{it.}} \right) g(N_{it}|M_i, \phi) \right] f(M_i|\lambda) \right\}$$

to

$$L(\lambda, \phi, p|\mathbf{y}) = \prod_{i=1}^R \left\{ \sum_{M_i=\max(\mathbf{y}_{it.})}^{\infty} \left(\prod_{t=1}^T \left[\sum_{N_{it}=y_{it.}}^{M_i} \frac{N_{it}!}{y_{it1}!y_{it2}!y_{it3}!y_{it0}!} \pi_1^{y_{it1}} \pi_2^{y_{it2}} \pi_3^{y_{it3}} \pi_0^{N_{it}-y_{it.}} g(N_{it}|M_i, \phi) \right] \right) f(M_i|\lambda) \right\}$$

Finally, Eq. 3 should be changed from

$$L(\lambda, \phi, p|\mathbf{y}_{it}) = \prod_{i=1}^R \left\{ \sum_{M_i=\max(\mathbf{y}_{it.})}^{\infty} \left(\frac{M_i!}{y_{i1}!y_{i2}!y_{i3}!y_{i0}!} (\phi\pi_1)^{y_{i1}} (\phi\pi_2)^{y_{i2}} (\phi\pi_3)^{y_{i3}} (\phi\pi_0)^{M_i-\mathbf{y}_{it.}} \right) f(M_i|\lambda) \right\}$$

to

$$L(\lambda, \phi, p|\mathbf{y}) = \prod_{i=1}^R \left\{ \sum_{M_i=\max(\mathbf{y}_{it.})}^{\infty} \left(\prod_{t=1}^T \frac{M_i!}{y_{it1}!y_{it2}!y_{it3}!y_{it0}!} (\phi\pi_1)^{y_{it1}} (\phi\pi_2)^{y_{it2}} (\phi\pi_3)^{y_{it3}} (\phi\pi_0)^{M_i-y_{it.}} \right) f(M_i|\lambda) \right\}$$

The authors thank Robert Dorazio for calling these mistakes to their attention.

Ian Carroll has reported an error in Eq. 3 of the article by Carroll et al. in the May 2011 issue (Carroll, I. T., B. J. Cardinale, and R. M. Nisbet. 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology* 92:1157–1165). The second overbar in the expression on the right-hand side of the equation should not extend over the “2” exponent. The corrected expression is as follows:

$$\text{RFD} = \exp \left[\left((\overline{\ln S})^2 - \overline{\ln S^2} \right)^{1/2} \right]$$