

Spatially Explicit Maximum Likelihood Methods for Capture–Recapture Studies

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SUMMARY. Live-trapping capture–recapture studies of animal populations with fixed trap locations inevitably have a spatial component: animals close to traps are more likely to be caught than those far away. This is not addressed in conventional closed-population estimates of abundance and without the spatial component, rigorous estimates of density cannot be obtained. We propose new, flexible capture–recapture models that use the capture locations to estimate animal locations and spatially referenced capture probability. The models are likelihood-based and hence allow use of Akaike’s information criterion or other likelihood-based methods of model selection. Density is an explicit parameter, and the evaluation of its dependence on spatial or temporal covariates is therefore straightforward. Additional (nonspatial) variation in capture probability may be modeled as in conventional capture–recapture. The method is tested by simulation, using a model in which capture probability depends only on location relative to traps. Point estimators are found to be unbiased and standard error estimators almost unbiased. The method is used to estimate the density of Red-eyed Vireos (*Vireo olivaceus*) from mist-netting data from the Patuxent Research Refuge, Maryland, U.S.A. Estimates agree well with those from an existing spatially explicit method based on inverse prediction. A variety of additional spatially explicit models are fitted; these include models with temporal stratification, behavioral response, and heterogeneous animal home ranges.

KEY WORDS: Capture–recapture; Closed population; Hazard rate; Heterogeneity; Poisson process; Population density; Spatially explicit.

1. Introduction

Terrestrial wildlife populations and sampling methods have spatial structure: individuals typically range over some area, and sampling usually involves detection or capture effort at specific locations. Capture–recapture sampling is a widely used method of estimating population size, but the spatial nature of capture–recapture data is usually neglected in analysis. This article addresses that issue.

We consider the common situation in which a biological population extends indefinitely in two dimensions beyond the immediate vicinity of the traps. The biological parameter of interest is the density of the population sampled at the traps. Conventional capture–recapture methods estimate an ill-defined population size N_{traps} , which in these circumstances is not a parameter of direct biological interest, although it is often used as a surrogate for density. Estimates of animal density from \hat{N}_{traps} depend conventionally on the effective trapping area (ETA). This is assumed to be the area within some distance W of the traps. Most methods for determining W

are ad hoc, and the precise definition of the ETA remains uncertain (Otis et al., 1978; Jett and Nichols, 1987; Efford, Dawson, and Robbins, 2004). This reduces the reliability of density estimates constructed from N_{traps} .

Efford (2004) proposed an alternative formulation that avoided ETA by treating observations with a known trap layout as a function of density and a two-parameter capture function. The three parameters can be estimated jointly by simulation and inverse prediction (Brown, 1982), using conventional capture–recapture statistics as predictors (Efford et al., 2004). Despite some success, this method of estimation is limited with respect to model selection and the inclusion of covariates.

We develop likelihood-based methods for spatial capture–recapture data. These share some features with the simulation-based methods of Efford et al. (2004), and may also be used to estimate density without the conventional concept of ETA, but in many respects they are more flexible and

more general. Our models can be viewed as mixture models in which the mixture is over the distribution of animal locations. Estimators are based on the marginal distribution obtained by integrating the joint likelihood over the distribution of the unobserved locations. A variety of mixture models for capture probability exist in the capture–recapture literature (Burnham, 1972; Pledger, 2000; Dorazio and Royle, 2003). The key difference between our model and existing likelihood-based capture–recapture models is that ours takes explicit account of the spatial nature of the sampling process.

We give our notation in Section 2 and develop the basic likelihood model in Section 3. Section 4 deals with implementation issues, and Section 5 with interval estimation. In Section 6, we deal with the range of models accommodated by our formulation, including models with observable covariates. Results of a simulation study are given in Section 7. In Section 8, we apply our methods to estimate the density of a bird population.

2. Key Notation

We consider a trapping study in which the underlying density of a closed population is to be estimated by placing K traps in a region containing animals having home ranges with fixed centers. Once an animal is caught in a trap it remains there until released. Traps are checked at regular intervals and trapped animals are released after being marked in such a way that their complete capture history is known. The period preceding each trap check is called a trapping occasion. We define “occasion” as an interval rather than an instantaneous sampling time as in conventional capture–recapture (Otis et al., 1978) to focus attention on the capture process over the interval. We assume, initially, that animals are equally at risk of being caught on every occasion. In Sections 6 and 8, we discuss models for more general scenarios.

The traps are left in place for S trapping occasions. The k th trap is located at Cartesian coordinates \mathbf{x}_k and the locations of the traps in the study is $\mathbf{x} = (\mathbf{x}_1, \dots, \mathbf{x}_K)$. The number of unique animals caught is n . \mathbf{X} is the location associated with the animal—this might be its home-range center, but it need not be. However, for ease of reference we refer to \mathbf{X} as the home-range center. See Figure 1.

Let $\omega_i = 1$ if animal i was captured on any of the S occasions and $\omega_i = 0$ otherwise. In addition, let $\omega_{is} = k$ if animal i was captured in trap k on occasion s ($s = 1, \dots, S$), and $\omega_{is} = 0$ otherwise. The history of capture locations for the i th animal is $\omega_i = (\omega_{i1}, \dots, \omega_{iS})$.

Let $p_{ks}(\mathbf{X}; \boldsymbol{\theta})$ be the probability that an animal with home-range center at \mathbf{X} is caught in trap k on occasion s , where $\boldsymbol{\theta}$ is the capture probability parameter vector. Let $p_{\cdot s}(\mathbf{X}; \boldsymbol{\theta})$ be the probability that it is caught in any one of the K traps on occasion s and $p(\mathbf{X}; \boldsymbol{\theta})$ be the probability that it is caught at all over the S capture occasions: $p(\mathbf{X}_i; \boldsymbol{\theta}) = \Pr(\omega_i = 1 \mid \mathbf{X}_i; \boldsymbol{\theta})$. We consider capture probability functional forms in Section 3.3.

3. Likelihood Formulation

3.1 The Likelihood

The likelihood, or equivalently here, the joint distribution of the number of animals captured n , and their capture histories $\omega_1, \dots, \omega_n$ can be written in terms of the marginal distribution of n and the conditional distribution of $\omega_1, \dots, \omega_n$, given

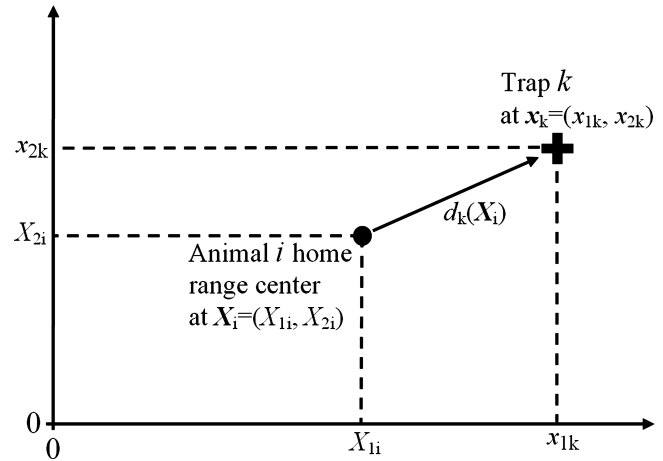


Figure 1. Notation for trap location, home-range center location and distance from center to trap: $d_k(\mathbf{X}_i)$ is the distance from the i th animal’s home range center at \mathbf{X}_i to the k th trap at \mathbf{x}_k .

n , as

$$L(\phi, \boldsymbol{\theta} \mid n, \omega_1, \dots, \omega_n) = \Pr(n \mid \phi, \boldsymbol{\theta}) \Pr(\omega_1, \dots, \omega_n \mid n, \boldsymbol{\theta}, \phi), \tag{1}$$

where $\boldsymbol{\theta}$ is the vector of capture function parameters and ϕ is a vector of parameters of the spatial point process governing animal density and distribution. We expand on the forms of $\Pr(n \mid \phi, \boldsymbol{\theta})$ and $\Pr(\omega_1, \dots, \omega_n \mid n, \boldsymbol{\theta}, \phi)$ below.

Suppose home-range centers occur independently in a plane according to an inhomogeneous Poisson process with rate parameter $D(\mathbf{X}; \phi)$, with associated parameter vector ϕ . Then assuming independent captures between animals, the marginal for n is Poisson with rate parameter $\lambda(\phi, \boldsymbol{\theta})$ that arises from integrating the Poisson process with the probability of being caught at least once: $\lambda(\phi, \boldsymbol{\theta}) = \int_{\mathcal{R}^2} D(\mathbf{X}; \phi) p(\mathbf{X}; \boldsymbol{\theta}) d\mathbf{X}$.

To enhance readability, we sometimes omit the parameter vectors as arguments in our development below. Assuming independent captures between captured animals, the conditional distribution for $\omega_1, \dots, \omega_n$, given n is $\Pr(\omega_1, \dots, \omega_n \mid n, \phi, \boldsymbol{\theta}) \equiv \Pr(\omega_1, \dots, \omega_n \mid \omega_1 > 0, \dots, \omega_n > 0, \phi, \boldsymbol{\theta}) = \binom{n}{n_1, \dots, n_C} \prod_{i=1}^n \Pr(\omega_i \mid \omega_i > 0, \phi, \boldsymbol{\theta})$, where n_1, \dots, n_C are the frequencies with which each of the C unique observed capture histories were observed, $\binom{n}{n_1, \dots, n_C}$ is the associated multinomial coefficient, and $\Pr(\omega_i \mid \omega_i > 0, \phi, \boldsymbol{\theta}) = \int_{\mathcal{R}^2} \Pr(\omega_i \mid \omega_i > 0, \boldsymbol{\theta}, \mathbf{X}) f(\mathbf{X} \mid \omega_i > 0, \phi, \boldsymbol{\theta}) d\mathbf{X}$ is the probability of observing capture history ω_i for individual i , given that it was captured.

We can express each of the terms inside the integral in terms of the capture probability function $p_{ks}(\mathbf{X}; \boldsymbol{\theta})$ and inhomogeneous Poisson process rate $D(\mathbf{X}; \phi)$. The probability of observing capture history ω_i for individual i , given that its home-range center is at \mathbf{X} , and that it was captured (omitting $\boldsymbol{\theta}$ for readability), is $\Pr(\omega_i \mid \omega_i > 0, \mathbf{X}) = p(\mathbf{X})^{-1} \prod_{s=1}^S \prod_{k=1}^K p_{ks}(\mathbf{X})^{\delta_k(\omega_{is})} [1 - p_{\cdot s}(\mathbf{X})]^{1 - \delta_{\cdot}(\omega_{is})}$, where $\delta_k(\omega_{is}) = 1$ if $\omega_{is} = k$ and is zero otherwise, $\delta_{\cdot}(\omega_{is}) = 1$ if $\delta_k(\omega_{is}) > 0$ for any $k = 1, \dots, K$ and is zero otherwise.

Assuming independence of capture between occasions, $p_s(\mathbf{X}) = 1 - \prod_{s=1}^S [1 - p_{\cdot s}(\mathbf{X})]$.

The second term in the integral, the conditional density of home-range centers given an animal is captured, can be expressed as follows:

$$\begin{aligned} f(\mathbf{X} \mid \omega_i > 0, \phi, \theta) &= \frac{D(\mathbf{X}; \phi) p_{\cdot}(\mathbf{X}; \theta)}{\int_{\mathcal{R}^2} D(\mathbf{X}; \phi) p_{\cdot}(\mathbf{X}; \theta) d\mathbf{X}} \\ &= \frac{D(\mathbf{X}; \phi) p_{\cdot}(\mathbf{X}; \theta)}{\lambda(\phi, \theta)}. \end{aligned}$$

The model parameters θ and ϕ can be estimated by maximizing the likelihood equation (1) with respect to them. Evaluating $D(\mathbf{X}; \phi)$ at the maximum likelihood estimate (MLE) $\hat{\phi}$ provides an estimate of the density surface. The mean value of $D(\mathbf{X}; \hat{\phi})$ over an area is the MLE of the mean animal density in the area, and the MLE of number of animals in the area is the integral $\hat{N} = \int D(\mathbf{X}; \hat{\phi}) d\mathbf{X}$.

3.2 Special Case: Homogeneous Poisson Density

When animal home-range centers occur according to a homogeneous Poisson process with rate parameter D , the likelihood function simplifies to

$$\begin{aligned} L(\theta, D) &= \frac{\{Da(\theta)\}^n \exp\{-Da(\theta)\}}{n!} \\ &\times \binom{n}{n_1, \dots, n_C} \prod_{i=1}^n \frac{\int \Pr(\omega_i \mid \mathbf{X}; \theta) d\mathbf{X}}{a(\theta)} \end{aligned} \quad (2)$$

where $\Pr(\omega_i \mid \mathbf{X}; \theta) = \prod_s \prod_k p_{ks}(\mathbf{X}; \theta)^{\delta_k(\omega_{is})} \{1 - p_{\cdot s}(\mathbf{X}; \theta)\}^{1 - \delta_k(\omega_{is})}$ and $a(\theta) = \int p_{\cdot}(\mathbf{X}; \theta) d\mathbf{X}$.

In this case, the parameters θ of the capture function (and hence capture probabilities for individual animals) can be estimated from the conditional likelihood, given that n animals were captured (i.e., from $L_n(\theta) = \prod_{i=1}^n \Pr(\omega_i \mid \mathbf{X}_i; \theta) / a(\theta)$) without estimating the parameter D . MLEs of θ from the conditional and full likelihood functions are equivalent (Sandland and Cormack, 1984). This allows for estimation of D using a Horvitz–Thompson-like estimator similar to that proposed by Huggins (1989) and Alho (1990). Having obtained the MLE $\hat{\theta}$ and hence $\hat{a} = a(\hat{\theta})$ from the conditional likelihood, D is estimated by $\hat{D} = n/\hat{a}$. More generally, when capture probability and a depend on other covariates z (see below), $\hat{D} = \sum_{i=1}^n \hat{a}(z_i)^{-1}$.

We note in passing that a likelihood similar to equation (1) for fixed animal abundance N in an arbitrary area can be constructed by formulating $\Pr(n \mid \phi, \theta)$ as $\Pr(n \mid \phi, \theta) = \binom{N}{n} p_c(\phi, \theta)^n (1 - p_c(\phi, \theta))^{N-n}$, where $p_c(\phi, \theta) = \int p_{\cdot}(\mathbf{X}; \theta) f(\mathbf{X}; \phi) d\mathbf{X}$, $f(\mathbf{X}; \phi) = D(\mathbf{X}; \phi) / \int D(\mathbf{X}; \phi) d\mathbf{X}$ and integration is over the arbitrary area. See Sandland and Cormack (1984) and Cormack and Jupp (1991) for discussion of Poisson versus multinomial likelihood functions for capture–recapture experiments.

3.3 Capture Probability Models

In this section, we consider the form of the capture probability function $p_{ks}(\mathbf{X}; \theta)$ and for brevity we omit the parameter θ . We consider only the case in which animals can only be caught

in one trap on any occasion. The probability of an animal with home-range center \mathbf{X} being caught on occasion s (during which animals are at risk of capture for a time T_s) is modeled using a competing risks survival model. A typical application of such models in survival analysis is one in which there are K possible causes of death, some more likely to cause death than others, but only one of which will ultimately be responsible for the death of an individual. The k th cause has associated with it a hazard function, $h_k(t)$ corresponding to the instantaneous probability of death due to cause k at time t . The causes “compete” to end the life of an individual.

In our context, “death” is capture, each trap is a different cause of “death” and “deaths” are reversed at the end of each trapping occasion when animals are released from traps. In addition, our hazard functions depend crucially on the distance $d_k(\mathbf{X})$ of the animal’s home range center from the trap, and given this distance, remain constant for the duration of each trapping occasion. We consider more general hazard functions in Sections 6 and 8. With this formulation, the probability of capture in any one of the K traps is

$$\begin{aligned} p_{\cdot s}(\mathbf{X}) &= 1 - \exp\left\{-T_s \sum_{k=1}^K h(d_k(\mathbf{X}))\right\}, \\ &= 1 - e^{-T_s h_{\cdot}(\mathbf{X})}, \end{aligned} \quad (3)$$

where $h_{\cdot}(\mathbf{X}) = \sum_{k=1}^K h(d_k(\mathbf{X}))$ is the total hazard of capture given \mathbf{X} , $h(d_k(\mathbf{X}))$ is the capture hazard function for trap k at distance $d_k(\mathbf{X})$ from \mathbf{X} (see Figure 1). We assume $T_s = 1$ for all s below, although the models are also applicable for cases in which T_s is different for different s . It follows that the probability of being caught in trap k on the occasion is $p_{ks}(\mathbf{X}) = \{1 - e^{-h_{\cdot}(\mathbf{X})}\} h(d_k(\mathbf{X})) / h_{\cdot}(\mathbf{X})$.

When there is only one trap present we refer to $p_{\cdot s}(\mathbf{X})$ as the “capture function” and denote it $p_s^1(\mathbf{X})$. This function is related to, but not the same as the animal’s home range (the wider the animal’s range, the wider the capture function) and its shape is determined by the hazard function, $h(d_k(\mathbf{X}))$. Although $d_k(\mathbf{X})$ is a scalar, this does not necessarily imply that home ranges are circularly symmetric: circular symmetry of $p_s^1(\mathbf{X})$ could just reflect our ignorance of the orientation of possibly asymmetric home ranges.

There is a wide variety of forms of hazard model that can be used for the capture function. (We omit subscript k in describing them in the remainder of this section.) One we consider is defined specifically to give a capture function with circular bivariate normal shape: $p_s^1(\mathbf{X}) = h_0 g(d(\mathbf{X}))$. Here $g(d(\mathbf{X})) = \exp\{-d(\mathbf{X})^2 / (2\sigma^2)\}$. The corresponding hazard function is $h(d(\mathbf{X})) = -\ln\{1 - h_0 g(d(\mathbf{X}))\}$. This is the form of capture function used by Efford (2004); it has a parameter vector $\theta = (h_0, \sigma)$. We also consider a second form of hazard function, with parameter vector $\theta = (h_0, \sigma, b)$, which is designed to give a capture function with the hazard-rate form of Hayes and Buckland (1983), but with intercept h_0 . This has a hazard function $h(d(\mathbf{X})) = -\ln(1 - h_0 [1 - \exp\{-(d(\mathbf{X})/\sigma)^{-b}\}])$. Proportional hazard functions of the following form may also be appropriate: $h(d(\mathbf{X})) = h_0 g(d(\mathbf{X}))$, where $g(0) = 1$.

4. Implementation Issues

4.1 Multiple Sets of Traps

In general, animals do not distribute themselves in space according to a homogeneous Poisson process. However, modeling density using a homogeneous Poisson process may be reasonable over small areas, particularly when multiple, randomly located sets of traps are used to infer density over a larger area. See Efford et al. (2005) for an example of this sort of design. With random location of trap sets, nonuniformities in expected density in the vicinity of sets will tend to average out, making the homogeneous Poisson model more reasonable across all sets.

Using the data pooled over sets, mean density and the parameters of the capture function can be estimated under the assumption of homogeneous Poisson home-range center distribution by maximization of equation (2).

4.2 Integration Limits and Numerical Issues

The likelihoods above have been formulated using integrals over the whole plane. Realistic capture functions decay to zero within a finite distance of home-range centers, or they decline to sufficiently close to zero that integration beyond some finite range has no effect on the estimates. In implementing the methods, integration is therefore over a finite area, A , chosen by the analyst. A may be defined to exclude (mask) parts of the plane in which home-range centers cannot lie, e.g., non-habitat such as roadways. The estimated density then applies to habitat areas only.

Estimation for this article used the Broydon–Fletcher–Goldfarb–Shanno (BFGS) minimization algorithm as implemented by Debord (2004). For minimization, parameters were transformed to a log scale (D , σ) or logit scale (h_0 , ψ) as needed to constrain them within feasible ranges. Reasonable starting values were needed to avoid floating point overflow; these were obtained for D , h_0 and σ by the method of Efford et al. (2004, Appendix).

4.3 Estimation of Home-Range Centers

Estimates of density model parameters ϕ can be used to estimate the probability density function (PDF) of animal home-range centers in area A as follows: $\hat{\pi}(\mathbf{X}) = \hat{D}(\mathbf{X}) / \int_A \hat{D}(\mathbf{X}) d\mathbf{X}$. Moreover, given the capture history ω_i of individual i , and an estimate of the capture function parameter vector θ , the probability density for the location of this individual's home-range center \mathbf{X} can be estimated as $\hat{f}(\mathbf{X}_i | \omega_i) = \hat{\Pr}(\omega_i | \mathbf{X}_i) \hat{\pi}(\mathbf{X}_i) / \int_A \hat{\Pr}(\omega_i | \mathbf{X}) \hat{\pi}(\mathbf{X}) d\mathbf{X}$. In the homogeneous Poisson case this reduces to $\hat{f}(\mathbf{X}_i | \omega_i) = \hat{\Pr}(\omega_i | \mathbf{X}_i) / \int_A \hat{\Pr}(\omega_i | \mathbf{X}) d\mathbf{X}$.

5. Interval Estimation

Profile likelihood confidence intervals for D can be constructed from the likelihood equation (1) or (2). Estimates of the asymptotic variances and covariances of parameters can be obtained directly from the inverse of the information matrix when either one of these likelihoods is maximized. Bootstrapping of capture histories is potentially useful, but for the moment prohibitively slow.

6. More General Models

In the interests of readability, our development thus far has dealt with relatively simple spatially explicit capture–

recapture models. In this section we discuss more complicated models. While our models are considerably more general than those considered by Otis et al. (1978), their notation for categorizing models has become standard in the capture–recapture literature, and we use it here as a convenient means of structuring the more general models.

The first generalization is inclusion of observed covariates, which is an important generalization with wide application. The capture function can be made to depend on covariates (which we denote z) and/or animal density can be made to depend on covariates. Dependence of density on covariates can be achieved in a number of ways, including (a) making the rate parameter of the Poisson distribution of home-range centers ($D(\mathbf{X})$) depend on them and (b) specifying a joint distribution for \mathbf{X} and z . The joint distribution might conveniently be specified using the marginal of \mathbf{X} and the conditional distribution of z given \mathbf{X} ($f(z | \mathbf{X})$). Knowledge of the spatial distribution of z will help in formulating a suitable form for $f(z | \mathbf{X})$ and conversely, inferences about $f(z | \mathbf{X})$ from the capture–recapture study may be of interest in themselves.

We assume in the discussion below that the capture function has the proportional hazards form and depends on covariates z : $h(d_k(\mathbf{X}), z) = h_0(z)g(d_k(\mathbf{X}), z)$. The covariate vector z could contain categorical, ordinal, or continuous variables and these variables could occur at the survey level (e.g., occasion index, time traps were out, etc.) or at the trap level (e.g., trap type) or at the environment level (e.g., kind of habitat) or at the individual animal level (e.g., an indicator of previous capture, age, size, etc.).

With dependence on z , the rate parameter of the observed Poisson process becomes $\lambda = \int \int D(\mathbf{X}, z)p(\mathbf{X}, z) dz d\mathbf{X}$. Evaluation of the likelihood then requires that a suitable form for the density surface ($D(\mathbf{X}, z)$) be specified and this adds complexity. Variables z , which occur at the survey level, rather than attached to individual animals, and which can be observed throughout the survey region, are relatively easy to incorporate. If, for example, z represented habitat, one might have a separate density parameter for each habitat: $D_{\mathbf{z}}(\mathbf{X})$ for habitat z . Animal-level z s present the greatest difficulty because, unlike the survey-level case, not all the z s for the population are observed and inference about the density of unobserved z s may depend heavily on the model chosen for $D(\mathbf{X}, z)$.

For the general case in which $p(\mathbf{X}, z)$ and $D(\mathbf{X}, z)$ depend on \mathbf{X} and z , we define $a(z) = E[n(z)]/D(z)$, where $E[n(z)] = \int p(\mathbf{X}, z)D(\mathbf{X}, z) d\mathbf{X}$ and $D(z) = \int D(\mathbf{X}, z) d\mathbf{X}$. When D is constant and there are no covariates, this reduces to the a of equation (2). The quantity a can be thought of as the effective sampling area: If all animals in an area of size a were detected and none outside of it were detected, the expected n would be the same as that from the actual survey.

6.1 M_t and M_b Models

There are a variety of ways in which the capture function can be made to depend on trapping occasion (M_t) and whether animals have been captured previously (M_b). A model in which only h_0 is a function of occasion is appropriate if individual animals' ranges remain unaltered over trapping occasions, but their capture probability changes between occasions. Similarly, h_0 could be made a function of an index, b_{si} say, which

is 1 if animal i has been captured prior to occasion s and is zero otherwise.

If traps are left for different lengths of time on different occasions, it makes sense to consider a capture function model that accommodates this. The hazard formulation does so easily (see equation 3).

One might want to consider models in which range changed in response to capture or between occasions. This could be implemented through the scale parameter(s) of $g(d(\mathbf{X}))$. For example, in the case of a circularly symmetric hazard with normal PDF shape, $g(d(\mathbf{X}), s) = \exp\{-d(\mathbf{X})^2/(2\sigma_s^2)\}$, where σ_s is an occasion-specific scale parameter.

6.2 M_h Models

M_h models deal with differences in animal-level capture probability (individual heterogeneity). This can cause substantial bias if it is not accommodated appropriately in estimation. While the methods of this paper have been developed specifically to accommodate individual heterogeneity due to proximity to traps, there may be additional individual heterogeneity.

Some sources of individual heterogeneity may be due to observable variables (animals' age, sex, etc.) and some due to unobservable sources. Huggins (1989) and Alho (1990) developed methods for incorporating observable variables causing heterogeneity in estimation, while Burnham (1972), Agresti (1994), Norris and Pollock (1996), Pledger (2000), and Dorazio and Royle (2003) developed methods for accommodating heterogeneity due to unobserved variables.

The finite mixture methods developed by Pledger (2000) are adapted below for our spatially explicit models. "Infinite mixture" models like those of Dorazio and Royle (2003) could also be adapted. We define a nominal unobservable variable $u = 1, \dots, U$ to index the U notional subpopulations comprising the population of interest. Following Pledger (2000), we assume that animals independently become members of subpopulation u , with probability ψ_u ($\sum_{u=1}^U \psi_u = 1$).

Different subpopulations have different capture probabilities and there is a variety of ways to model this. Either the intercept $h_0(\cdot)$ or the scale parameter of the $g(\cdot)$ can be made dependent on u as a means of giving different subpopulations different capture probabilities. If individual differences manifest themselves primarily through differences in ranges, the latter seems more appropriate. This model accommodates heterogeneity in capture probability due to heterogeneous home ranges. If differences manifest themselves in a way that leaves home ranges unchanged, then a formulation for the hazard function like $h(d, u) = h_{0u}g(d(\mathbf{X}))$ is natural.

Including u in the capture function (as a factor with U levels) makes the probability of observing capture history ω depend on u , so we now write it as $\Pr(\omega | \mathbf{X}, u)$. This leads to the following finite mixture model likelihood:

$$L(N, \theta, \phi, \psi) = \binom{N}{n} \prod_{i=1}^n \sum_{u=1}^U \psi_u \int \Pr(\omega_i | \mathbf{X}, u) \pi(\mathbf{X}) d\mathbf{X} \\ \times \left[\sum_{u=1}^U \psi_u \int \{1 - p(\mathbf{X}, u)\} \pi(\mathbf{X}) d\mathbf{X} \right]^{N-n},$$

where $\psi = (\psi_1, \dots, \psi_U)$ and $\pi(\mathbf{X}) = D(\mathbf{X}) / \int D(\mathbf{X}) d\mathbf{X}$.

By including u as an unobserved random variable in equation (1), we construct a Poisson mixture model:

$$L(\theta, \phi, \psi) = \frac{\lambda^n e^{-\lambda}}{n!} \prod_{i=1}^n \sum_{u=1}^U \int f(\mathbf{X}, u | \omega_i > 0) \\ \times \Pr(\omega_i | \mathbf{X}, u) / p(\mathbf{X}, u) d\mathbf{X},$$

where $\lambda = \sum_{u=1}^U \psi_u \int D(\mathbf{X}) p(\mathbf{X}, u) d\mathbf{X}$, and $f(\mathbf{X}, u | \omega_i > 0)$ is equal to $D(\mathbf{X}) p(\mathbf{X}, u) \psi_u / (\sum_{u=1}^U \int D(\mathbf{X}) p(\mathbf{X}, u) \times \psi_u d\mathbf{X})$.

6.3 Habitat Type and Non-uniform Spatial Distribution

The development in Section 3.1 specifically allows non-uniform distribution of home-range centers in space. If a suitable parametric functional form is available for $D(\mathbf{X})$ then estimation presents no difficulties in principle. If $D(\mathbf{X})$ is to be modeled nonparametrically (using smoothing splines, for example) direct maximization of the likelihood may be more difficult. If environmental variables that affect density are available, $D(\mathbf{X})$ can be made a function of these as well as of location, \mathbf{X} .

6.4 Other Extensions

Different trap types are readily accommodated in the model by having h_0 depend on an index for trap type (h_{0j} for trap type j). Alternatively, if there is some continuous variable(s) z associated with the trap that might affect capture probability, h_0 could be made a continuous function of z . A log-linear form $h_0(z) = \exp(\theta_z^T z)$ as is commonly used with proportional hazard models, might be appropriate.

It may be desirable to relocate some/all traps from one capture occasion to the next. Our model readily accommodates this by allowing x_k and h_i to depend on occasion: $x_{ks} h_{i,s}$. Similarly, the addition or removal of traps on any occasion presents no problem for the model.

Known deaths can be accommodated by setting the number of occasions considered (S) to be equal to r_i , where r_i is the occasion on which the animal died.

6.5 Model Selection and Diagnostics

Likelihood-based methods of model selection, and Akaike's information criterion (AIC) in particular (Akaike, 1973) can be used to select between competing models for the capture function. Decisions include the form the dependence of the capture function on covariates, which covariates to include and, if a mixture model of the sort described in Section 6.2 is used, how many mixtures to use. Similar decisions may be required for the spatial intensity function $D(\mathbf{X})$.

We follow Cooch and White (2006) and use a Monte Carlo test based on the scaled deviance $[-2 \log(\hat{L}) + 2 \log(L_{\text{sat}})] / \Delta df$. Here \hat{L} is the value of the likelihood evaluated at its maximum, L_{sat} is the likelihood of the saturated model (below) at its maximum, and Δdf is the difference between the degrees of freedom of the saturated model and that of L . In the case of the conditional likelihood, the saturated log likelihood evaluated at its maximum is $\log(n!) - \sum_{\omega} \log(n_{\omega}!) + \sum_{\omega} n_{\omega} \log(\frac{n_{\omega}}{n})$; that for the homogeneous Poisson full likelihood equation (2) is $n \log(n) - n - \sum_{\omega} \log(n_{\omega}!) + \sum_{\omega} n_{\omega} \log(\frac{n_{\omega}}{n})$, where \sum_{ω} is the sum over the

observed capture histories, n_ω is the number of animals with capture history ω and $n = \sum_\omega n_\omega$.

7. Simulation Testing

For comparison with the results of Efford (2004) and inverse prediction method performance, we simulated surveys from a square grid of 144 traps at 30-meter intervals, over 5 trapping occasions. The true capture function was $p_s^i(\mathbf{X}) = h_0 g(d(\mathbf{X}))$ where $h_0 = 0.1$ and $g(d(\mathbf{X}))$ is half-normal density function with scale parameter $\sigma = 40$. (The parameter h_0 is equivalent to the “g(0)” parameter of Efford (2004).) Animals were generated in a square region extending 5σ beyond the grid of traps. This corresponds to a region that would contain 99.99% of captured animals and simulated animal with range center at the edge of this area has less than 1 chance in 10,000 of being caught over five occasions. The number of animals within the region was drawn from a Poisson distribution with mean DA ($A = 53.29$ ha) and animals’ locations were draws from a two-dimensional uniform density function on the region. Capture probability contours are shown in Figure 2.

Density and capture function parameters were estimated by maximizing the likelihood equation (2). Variance was estimated using the inverse of the estimated information matrix. Simulations were conducted using program DENSITY version 4.0 (Efford, 2007; available from <http://www.otago.ac.nz/density>).

Results from simulations with density $D = 0.5$ and 5.0 animals per hectare are shown in Table 1. The low-density scenario has a mean number of unique animals captured just less than 14, while that of the high-density scenario is just under 140. In both scenarios the MLEs of density (\hat{D}) are unbiased

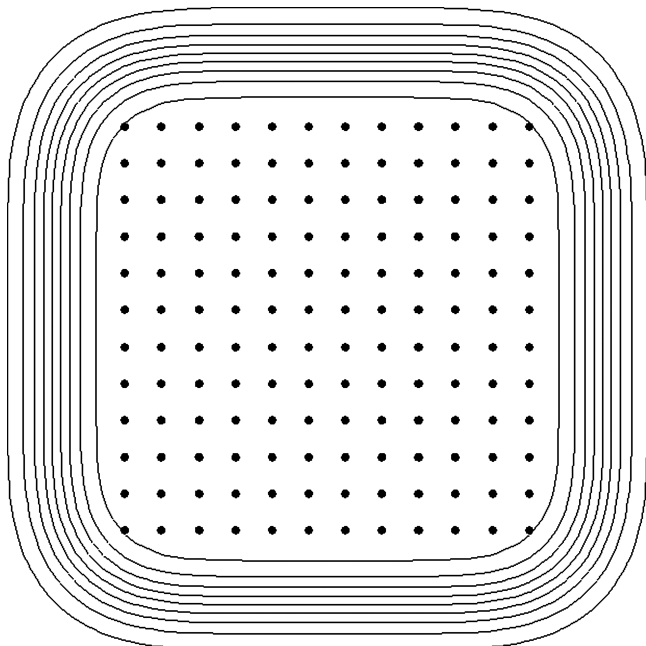


Figure 2. Trapping grid used in simulations. The curves are 10% contours (from 10% to 90%) of estimated capture probability $p(\mathbf{X})$ as a function of animal location, \mathbf{X} . The integral of this function is the effective sampling area.

with both integration buffer widths (IBWs). The MLEs of the standard errors of the density estimates are very nearly unbiased.

Because these simulated data were from a large grid we may obtain comparable estimates with the conventional “nested subgrid” method of MacLulich (1951) as implemented by Otis et al. (1978). Efford (2004, Table 1) found that method gave estimates with large bias (>20%) for density in the range 0.5 to 5 ha⁻¹ when detection parameters matched those we used; nominal precision was similar to our present simulation results, but confidence interval coverage was poor.

8. Application

Birds were mist-netted in forest on the Patuxent Research Refuge, Maryland, U.S.A., by C. S. Robbins each year from 1961 to 1972. Nets on a 4 × 11 grid, with spacing 100 m between rows and 61 m along rows, were operated for six non-consecutive days in early summer. Birds were banded with uniquely numbered aluminum bands (see Efford et al., 2004, for details). Some birds were captured in more than one year, but each annual sample was analyzed as if from a separate closed population. We chose to analyze data for the most commonly caught species, Red-eyed Vireo (*Vireo olivaceus*), which yielded 721 within-year capture histories.

8.1 Model Description

A variety of models for these data were considered. Our models (and the likelihoods developed above) contain two kinds of parameters: those associated with density, and those associated with capture probability. It is useful to consider the capture function parameters in two categories: those relating to the scale parameter (σ), and those relating to the intercept (h_0). The models support a wide variety of parameterizations of density and of capture probability parameters. We denote them using the following subscripts:

- \cdot : Constant parameter value. For example, a model with σ has a single shape parameter.
- y : Separate parameter for each year. For example a model with D_y has a separate density parameter for each year and h_{0y} has a separate h_0 parameter for each year.
- v : Constant density within 3-year strata but separate density parameters for each multi-year stratum. From a biological perspective, models with constant density over years or density changing between years are sensible and of interest. We consider temporal stratification by 3-year strata purely for comparability with the results of Efford et al. (2004). The subscript v is used to denote multiyear stratum, as follows: $v = (1961-1963), (1964-1966), (1967-1969), (1970-1972)$. For example, a model with σ_v has four shape parameters, one for each multiyear stratum.
- ψ_U : Random parameter individual heterogeneity model such that the parameter being subscripted is drawn from a distribution supported at U points, with probability mass ψ_u at the u th point ($u = 1, \dots, U$). For example, σ_{ψ_3} denotes a model with support at three values of σ , with probability ψ_u of being σ_u ($u = 1, 2, 3$).

Table 1

Mean and standard error (in parentheses) of estimates from 100 independent simulations with density (D) of 0.5 and 5.0 animals per hectare and two levels of IBW. IBW was preset to a multiple of the known home-range width parameter σ . \hat{D} is the mean estimated density; n^+ is the mean number of captures per simulation including recaptures; n is the mean number of different animals caught per simulation; SE denotes standard error; %Bias(\hat{D}) is the percentage bias of \hat{D} (i.e., $100(\hat{D} - D)/D$); and h_0 is the intercept parameter of the capture function.

IBW	$D = 0.5$ animals per ha				$D = 5.0$ animals per ha			
	3σ		5σ		3σ		5σ	
n^+	28.1	(0.89)	28.9	(0.99)	291.2	(2.8)	290.8	(2.9)
n	13.6	(0.39)	13.8	(0.41)	138.1	(1.1)	139.3	(1.2)
%Bias \hat{D}	0.6	(3.2)	3.0	(3.2)	-0.4	(0.82)	1.2	(0.88)
\hat{D}	0.503	(0.016)	0.515	(0.016)	4.98	(0.041)	5.06	(0.044)
$\widehat{\text{se}}(\hat{D})$	0.148	(0.003)	0.153	(0.005)	0.448	(0.002)	0.453	(0.002)
\hat{h}_0	0.103	(0.003)	0.108	(0.004)	0.101	(0.001)	0.101	(0.001)
$\widehat{\text{SE}}(\hat{h}_0)$	0.035	(0.001)	0.037	(0.001)	0.010	(10^{-4})	0.010	(10^{-4})
$\hat{\sigma}$	40.3	(0.62)	39.4	(0.64)	40.1	(0.17)	29.8	(0.17)
$\widehat{\text{SE}}(\hat{\sigma})$	6.31	(0.19)	6.10	(0.21)	1.79	(0.02)	1.79	(0.02)

b: Trap-response such that individuals that have been captured have a different value for the parameter being subscripted from as yet uncaptured individuals. For example, a model denoted h_{0b} has two h_0 parameters, one for as yet uncaptured animals and another for animals that have been captured before.

In addition, we consider density models with exponential change between years, which we denote $D(y)$, where $D(y) = \exp(\beta_0 + \beta_1 y)$ for year y . Note that with this model $\exp(\beta_1)$ is the finite population growth rate parameter (often denoted λ).

The half-normal form (denoted “ hn ”) and the hazard-rate form of Hayes and Buckland (1983) (denoted “ hz ”) were considered for the capture function. So for example, $hn(h_0, \sigma_{\psi_2})$ denotes a half-normal capture function model with a single h_0 parameter and a two-component finite mixture of σ parameters (with probability ψ_1 of parameter σ_1 and probability $\psi_2 = (1 - \psi_1)$ of parameter σ_2), while $hz(h_{0\psi_2}, \sigma)$ denotes a hazard-rate capture function model with a two-component finite mixture of h_0 parameters (with probability ψ_1 of parameter h_{01} and probability $\psi_2 = (1 - \psi_1)$ of parameter h_{02}), and

a single σ parameter (as well as a single shape parameter, b , which for brevity we do not show explicitly in our notation).

8.2 Comparison with Inverse Prediction Estimates

In their analysis, Efford et al. (2004) aggregated data within each 3-year stratum and for comparison, we do the same here. We compare the estimates from a model with capture function $hn(\sigma_v, h_{0v})$ applied separately to each aggregated dataset, to those from the inverse prediction method (Efford et al., 2004) in Table 2. The inverse prediction estimates in this table differ slightly from those of Efford et al. (2004) for the same data as they use model M_0 of Otis et al. (1978) instead of the Mth coverage estimator of Lee and Chao (1994) used by Efford et al. (2004). The MLEs agree well with those obtained by inverse prediction—see Table 2.

8.3 Model Selection and Density Estimation

Table 3 summarizes model selection results based on AIC. The hazard-rate capture function form was consistently found to be preferable to the half-normal model. While one should be cautious of drawing inferences about home range from the capture function (which reflects a combination of home range and catchability), it is interesting that the hazard-rate form

Table 2

Maximum likelihood and inverse prediction method estimates of density \hat{D} and model parameters \hat{h}_0 and $\hat{\sigma}$ (see text for details) for Patuxent Research Refuge Red-eyed Vireo capture data. Estimated standard errors are shown in parentheses; n is the number of different birds captured.

Method	Stratum (v)	n_v	\hat{D}_v	\hat{h}_{0v}	$\hat{\sigma}_v$
Inverse prediction	1961–1963	218	4.02 (0.54)	0.0341 (0.0018)	64.7 (4.3)
	1964–1966	177	2.75 (0.39)	0.0306 (0.0019)	76.3 (5.0)
	1967–1969	213	2.83 (0.33)	0.0372 (0.0021)	77.8 (4.1)
	1970–1972	113	2.49 (0.59)	0.0321 (0.0013)	58.4 (6.6)
Maximum likelihood	1961–1963	218	4.19 (0.48)	0.0356 (0.0059)	62.9 (4.5)
	1964–1966	177	2.89 (0.35)	0.0304 (0.0054)	75.1 (6.2)
	1967–1969	213	2.91 (0.30)	0.0374 (0.0052)	77.1 (5.2)
	1970–1972	113	2.51 (0.46)	0.0278 (0.0073)	64.4 (7.5)

Table 3

Summary of maximum likelihood models for Patuxent Research Refuge Red-eyed Vireo capture data. Model notation is given in the text. ΔAIC is the difference between the AIC of the model in question and the model with lowest AIC.

Model index	Density model	Capture model	Number of parameters	$\log(L)$	AIC	ΔAIC
M1	D	$hn(\sigma, h_0)$	3	-5449.83	10,905.66	161.51
M2	$D(y)$	$hn(\sigma, h_0)$	4	-5437.61	10,883.21	139.06
M3	D_y	$hn(\sigma, h_0)$	14	-5423.85	10,875.70	131.55
M4	D	$hz(\sigma, h_0)$	4	-5401.24	10,810.47	66.32
M5	$D(y)$	$hz(\sigma, h_0)$	5	-5389.01	10,788.03	43.88
M6	$D(y)$	$hz(\sigma_{\psi_2}, h_0)$	7	-5385.96	10,785.93	41.78
M7	$D(y)$	$hz(\sigma, h_{0\psi_2})$	7	-5383.89	10,781.78	37.63
M8	$D(y)$	$hz(\sigma, h_0)$	6	-5380.58	10,773.16	29.01
M9	D	$hz(\sigma, h_{0y})$	15	-5371.55	10,773.10	28.95
M10	$D(y)$	$hz(\sigma_y, h_0)$	16	-5369.58	10,771.17	27.02
M11	$D(y)$	$hz(\sigma, h_{0y})$	16	-5369.34	10,770.67	26.52
M12	$D(y)$	$hz(\sigma, h_{0b})$	6	-5376.06	10,764.12	19.97
M13	D_y	$hz(\sigma, h_{0b})$	16	-5362.31	10,756.62	12.47
M14	$D(y)$	$hz(\sigma_y, h_{0yb})$	28	-5346.65	10,749.31	5.16
M15	$D(y)$	$hz(\sigma_y, h_{0b})$	17	-5355.08	10,744.15	0.00

allows a “shoulder” in the capture function form (i.e, near-constant capture probability out to some distance from the home-range center), similar to the platykurtic home range forms considered by Horne and Garton (2006), while the less flexible half-normal form does not.

We find that model M15, with log-linear density trend over years, a behavioral response in capture function intercept parameter (h_0) and a year-specific scale parameter (σ) has lowest AIC. The results suggest behavioral response (trap shyness), temporal effects on the range over which animals are catchable and declining temporal trend in density. It is clear that the simpler models in Table 3 are inappropriate. The simplest model (M1, with 3 parameters), for example, has an AIC which is 162 larger than that of model M15 (which has 17 parameters).

Estimates obtained from the best model (M15) are shown in Table 4. The model involves a trend in density estimates. For comparison with estimates in Table 2, the density estimates for the first and last years of the study are: 2.2 ha⁻¹ in 1962 and 1.4 ha⁻¹ in 1971. These densities are substantially less than those in Table 2 because model M15 includes a behavioral response.

9. Discussion

Our models introduce into likelihood-based capture–recapture models a spatial component that has been absent to date. While there are contexts in which the spatial component will not be useful, in many capture–recapture studies the spatial nature of the sampling process is a key determinant of capture probability. Modeling this is important for two reasons. Firstly, an intrinsic problem for capture–recapture methods is that to avoid substantial bias in estimating abundance, they must model the capture probabilities of the least catchable members of the population well. When capture probability depends on location, as it does in many situations, it is therefore important to model this dependence. Our models do this.

Secondly, and perhaps more importantly, our models allow one to use the capture–recapture data to provide well-defined estimates of animal density. Without a spatially referenced capture function, the spatial extent of capture–recapture sampling is unknown. This in turn means that the

Table 4

Maximum likelihood model M15 parameter estimates for the Patuxent Research Refuge Red-eyed Vireo capture data. Parameters are as follows: β_0 and β_1 are estimates of the log-linear density parameters ($D(y) = \exp(\beta_0 + \beta_1 y)$); σ_y is the hazard-rate model capture function scale parameter for year y , b is the hazard-rate model shape parameter; and h_0 is the capture function intercept parameter for as yet uncaptured animals; previously captured animals have capture functions with intercept rh_0 .

Parameter	Estimate	SE	95% confidence interval
β_0	0.889	0.135	(0.626; 1.154)
β_1	-0.050	0.021	(-0.090; -0.009)
σ_1	36.27	6.46	(25.64; 51.30)
σ_2	30.77	5.54	(21.68; 43.65)
σ_3	37.39	6.14	(27.16; 51.48)
σ_4	37.76	6.15	(27.49; 51.87)
σ_5	34.25	6.12	(24.20; 48.48)
σ_6	33.15	6.19	(23.06; 47.65)
σ_7	50.18	8.47	(36.12; 69.71)
σ_8	42.33	7.23	(30.35; 59.03)
σ_9	41.80	7.49	(29.50; 59.22)
σ_{10}	31.69	6.26	(21.59; 46.50)
σ_{11}	27.44	6.30	(17.59; 42.79)
σ_{12}	30.15	5.99	(20.51; 44.33)
b	2.782	0.247	(2.344; 3.315)
h_0	0.186	0.044	(0.114; 0.287)
r	0.436	0.064	(0.327; 0.581)

“population” whose abundance is estimated is not well defined, and estimates of population size cannot be converted to estimates of density.

The models are general and flexible, spanning the full range of closed-population capture–recapture models, including models with behavioral response, observable heterogeneity, and unobservable heterogeneity.

They do of course have limitations. They are not currently able to accommodate traps that fill up, or whose efficacy changes when they contain animals. While this is also true of nearly all closed-population models currently available, accommodating changing trap efficacy due to traps containing animals is a feature that it would be useful to have in a model. Nor are the models presented here able to deal with captures in continuous time, although the hazard-rate formulation of the detection function provides a framework for extension to this case.

We have only implemented a homogeneous Poisson process for animal home-range locations, but the methods accommodate more general processes, including clustered point processes, although implementation with such processes is likely to be more challenging. There may be merit in considering more flexible capture function forms than we have used as one can think of situations in which capture probability does not decline monotonically with distance—if animals patrolled a circle about some notional home-range center, for example. However, we think such situations are rare.

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