Bayes and Empirical Bayes Estimators of Abundance and Density from Spatial Capture-Recapture Data

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Abstract

In capture-recapture and mark-resight surveys, movements of individuals both within and between sampling periods can alter the susceptibility of individuals to detection over the region of sampling. In these circumstances spatially explicit capture-recapture (SECR) models, which incorporate the observed locations of individuals, allow population density and abundance to be estimated while accounting for differences in detectability of individuals. In this paper I propose two Bayesian SECR models, one for the analysis of recaptures observed in trapping arrays and another for the analysis of recaptures observed in area searches. In formulating these models I used distinct submodels to specify the distribution of individual home-range centers and the observable recaptures associated with these individuals. This separation of ecological and observational processes allowed me to derive a formal connection between Bayes and empirical Bayes estimators of population abundance that has not been established previously. I showed that this connection applies to every Poisson point-process model of SECR data and provides theoretical support for a previously proposed estimator of abundance based on recaptures in trapping arrays. To illustrate results of both classical and Bayesian methods of analysis, I compared Bayes and empirical Bayes estimates of abundance and density using recaptures from simulated and real populations of animals. Real populations included two iconic datasets: recaptures of tigers detected in camera-trap surveys and recaptures of lizards detected in area-search surveys. In the datasets I analyzed, classical and Bayesian methods provided similar – and often identical – inferences, which is not surprising given the sample sizes and the noninformative priors used in the analyses.

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Introduction

In capture-recapture and mark-resight surveys, movements of individuals both within and between sampling periods can alter the susceptibility of individuals to detection over the region of sampling. In these circumstances spatially explicit capture-recapture (SECR) models, which incorporate the observed locations of individuals, allow population density and abundance to be estimated while accounting for differences in detectability of individuals.

A variety of SECR models have been developed to accommodate different kinds of sampling protocols and capture methods [1]. The spatial point process used to model the distribution of individual home-range centers is an important component of these models. This process determines the expected size of the population within any finite region, and it specifies how the expected density of individuals is assumed to vary across the region. Many SECR models use a Poisson point process to specify the spatial distribution of home-range centers [2–7]. The parameters of these models have been estimated using classical statistical methods (maximum likelihood), and freely available software exists to fit these models (programs DENSITY [8] and secr (written using the R software program [9]). Other SECR models use a binomial point process to specify the spatial distribution of home-range centers [10–16]. In these models the

number N of home-range centers located within an arbitrarily large (but finite) region is assumed to be constant, unlike the Poisson point-process models wherein N is a random outcome. By assuming a constant value for N , the binomial point-process models can be fitted using Bayesian methods and data augmentation [17]. In this approach the actual data set is augmented with a known number of “all zero” detection histories and a zero-inflated version of the base SECR model is fitted to the augmented data set. These models have been implemented using freely available software (programs WinBUGS (<http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml>) and JAGS (<http://mcmc-jags.sourceforge.net>)). Program SPACECAP provides a more specialized implementation of this approach [18].

If the region occupied by the population is sufficiently large, the Poisson limit theorem suggests an asymptotic equivalence between the Poisson and binomial SECR models and their estimators of N . For example, in a Bayesian analysis using data augmentation, a $\text{binomial}(M, \psi)$ distribution is used to specify prior uncertainty in N . In this context the N individuals may be viewed as a subset of M individuals whose home-range centers are distributed in a region $\mathcal{R}$ that encompasses the region $\mathcal{S}$ occupied by the subpopulation of size N . Suppose a homogeneous binomial point process is used to model the home-range centers of all M individuals; then $\psi = A(\mathcal{S})/A(\mathcal{R})$, where $A(\mathcal{S})$ and $A(\mathcal{R})$ denote the respective areas of the two regions. The Poisson limit theorem

establishes that if the both M and $A(\mathcal{R})$ tend to infinity while keeping the binomial mean $MA(\mathcal{S})/A(\mathcal{R})$ constant, the asymptotic distribution of N is Poisson with mean $MA(\mathcal{S})/A(\mathcal{R})$. The intensity of this point process is $M/A(\mathcal{R})$, so the expected value of N equals the product of the intensity and $A(\mathcal{S})$, as in a homogeneous Poisson process.

The asymptotic equivalence of binomial and Poisson SECR models may not apply in small regions or small populations. In a simulation study where recapture locations were simulated for area-search surveys [7], maximum-likelihood estimates (MLEs) of population density obtained by fitting a Poisson point-process model sometimes exhibited lower relative bias than Bayesian estimates obtained by fitting a binomial point-process model. The differences in bias were most pronounced at the lowest (true) population densities, regardless of whether the posterior mean or mode was used as a Bayesian estimator of density. Similarly, the frequentist coverage of Bayesian credible intervals for population density was sometimes less than the nominal level, whereas the coverage of classical confidence intervals approximated the nominal level in the same simulation scenarios.

The source(s) of the apparent difference in performance of classical and Bayesian estimators of density cannot be inferred from this simulation study. Were the differences associated with differences in modeling assumptions (binomial vs. Poisson) or with differences in methods of inference and point estimators (MLE vs. posterior mean or mode)? Also, owing to the sizeable difference in number of data sets analyzed in each simulation scenario (the binomial model was fitted to 100 data sets whereas the Poisson model was fitted to 1000 data sets), the estimated bias and coverage of the Bayesian estimators may have included substantial Monte Carlo error, casting doubt on the statistical significance of the reported difference in performance of classical and Bayesian methods.

To shed light on this issue and to establish a formal relationship between classical and Bayesian estimators of abundance, I developed two Bayesian models of SECR data using Poisson point processes. One model is for the analysis of recaptures

observed in trapping arrays; the other is for the analysis of recapture locations observed in area searches. In formulating these models I used distinct submodels to specify the distribution of individual home-range centers and the observable recaptures associated with these individuals. This separation of ecological and observational processes allowed me to derive a formal connection between Bayes and empirical Bayes estimators of population abundance that has not been established previously. I showed that this connection applies to *every* Poisson point-process model of SECR data and provides theoretical support for an estimator of abundance proposed for recaptures in trapping arrays [19].

To illustrate the results of both classical and Bayesian methods of analysis, I compared Bayes and empirical Bayes estimates of abundance and density for both simulated and real populations of animals. Surprisingly few analyses of SECR data have assumed spatial variation in individual density [19–21]; therefore, I analyzed recaptures of animals in a simulated trapping array to illustrate how maps of individual density may be estimated for a landscape containing substantial habitat heterogeneity. I also repeated the simulation study of recaptures in area-search surveys [7]. In contrast to [7], I analyzed a larger number of data sets using only Poisson point-process models (classical and Bayesian) and I evaluated the amount of Monte Carlo error in the estimates of bias and frequentist coverage. To illustrate analyses of real data with the Poisson point-process models, I used two iconic datasets: recaptures of tigers detected in camera-trap surveys [12,13,17] and recaptures of lizards detected in area-search surveys [7,10]. I conclude the paper with a discussion of the relative merits of classical and Bayesian SECR models and a description of some useful extensions of these models.

Methods of Analysis for Spatial Capture-Recapture Data

In this section I describe two SECR models, one for the analysis of recaptures observed in trapping arrays and another for the analysis of recaptures observed in area searches. These models can be specified hierarchically using one component to describe the process that generates the spatial distribution of individuals in the population and a second component to describe the process that leads to an observable sample of individuals. The first component, a Poisson point-process model, is identical for both SECR models; therefore, I describe this component first and follow with descriptions of the underlying assumptions and likelihood functions of the two observation models.

Poisson Point-process Model of Individual Activity Centers

This component of the SECR models is similar to the model of home-range centers (more generally, activity centers) proposed by [2] and extended by [3]. Consider a population of individuals that reside within a bounded, geographic region $\mathcal{S} \subset \mathbb{R}^2$ that has scientific or operational relevance. Each individual is assumed to move randomly around its activity center $s \in \mathcal{S}$, so that the spatial distribution of activity centers defines the population.

I assume that the activity centers are a realization of an inhomogeneous Poisson point process parameterized by a first-order intensity function $\lambda(\mathbf{v}(s)) = \exp(\beta' \mathbf{v}(s))$ that includes a vector of regressors $\mathbf{v}(s)$ at location s and a vector of parameters β . (I use a prime symbol to denote the transpose of a matrix or vector.) To simplify notation, I will use $\lambda(s)$ instead of $\lambda(\mathbf{v}(s))$ to express the implied functional dependence of λ on location s .

In the context of SECR models, $\lambda(s)$ denotes the limiting, expected density of individuals (number of individuals per unit area)

Figure 1. Map of spatial variation in habitat quality for a simulated population of individuals exposed to an array of 100 traps. Trap locations are superimposed on map. doi:10.1371/journal.pone.0084017.g001

at location $\mathbf{s}$. That is, for a small region $d\mathbf{s}$ of area $A(d\mathbf{s})$ centered at $\mathbf{s}$,

$$\lambda(\mathbf{s}) = \lim_{A(d\mathbf{s}) \rightarrow 0} E\{N(d\mathbf{s})\}/A(d\mathbf{s})$$

for the Poisson point process $N(\cdot)$ [22]. Furthermore, the number $N(\mathcal{S})$ of individuals in $\mathcal{S}$ – that is, the size of the population – is a Poisson random variable that depends on the mean intensity of the process over region $\mathcal{S}$: $\mu = \int_{\mathcal{S}} \lambda(\mathbf{s}) d\mathbf{s}$. In other words, $N(\mathcal{S}) \sim \text{Poisson}(\mu)$. Given a realized population of size $N(\mathcal{S}) = N$, the N activity centers are independent and distributed with probability density function $\lambda(\mathbf{s})/\mu$. Therefore, under the assumptions of the point-process model the conditional density of the N locations is

$$[s_1, s_2, \dots, s_N | N] = \prod_{i=1}^N \lambda(s_i) / \mu.$$

(Note that I specify probability density functions using bracket notation wherein $[x, y]$ denotes the joint density of random variables x and y , $[x|y]$ denotes the conditional density x given y , and $[x]$ denotes the unconditional (marginal) density of x [23]. In addition, I do not distinguish random variables and their realized values by uppercase and lowercase notations. This practice, while common in Statistics, can be cumbersome and can produce notations that are unconventional in Ecology.)

An important, special case of the model of activity centers is the *homogeneous* Poisson point process, wherein $\lambda(\mathbf{s})$ is assumed to be constant at all locations (i.e., $\lambda(\mathbf{s}) = \lambda, \forall \mathbf{s} \in \mathcal{S}$). For this model, the expected size of the population depends only on λ and on the area $A(\mathcal{S})$ of region $\mathcal{S}$ because $\mu = \lambda A(\mathcal{S})$. In addition, the probability density of each activity center is constant since $\lambda/\mu = 1/A(\mathcal{S})$. In other words, under the assumptions of the homogeneous model, the activity centers are independently and uniformly distributed over region $\mathcal{S}$.

Analysis of Recaptures at Trapping Array Locations

In this section I describe a model for recaptures of individuals that may be detected at each of K distinct trapping locations. These locations are often selected to form an array (or grid) of uniformly spaced traps. In practice, these traps often correspond to recording devices (such as cameras or people capable of detecting the presence of uniquely marked individuals) as opposed to devices that capture and retain individuals. [5] have proposed the term “proximity detectors” for these kinds of traps. Throughout this paper, I use the words, *detections* and *captures*, interchangeably to describe observations of marked individuals.

I assume an individual may be detected at the k th trap during each of J_k trapping periods of equal duration. Although multiple detections of an individual at the same trap are possible and easily modeled [12], I consider here a model in which individuals are assumed to be detected only once per trapping period at any trap. Specifically, I assume that each detection of an individual at trap k is an independent Bernoulli outcome in which capture probability $p(\mathbf{s}, x_k)$ is a function of the Euclidean distance between an individual’s activity center $\mathbf{s}$ and the location x_k of trap k . In addition, I assume that recaptures of an individual in different traps occur independently.

Several functional forms for $p(\mathbf{s}, x_k)$ are possible [5]; here, I consider a function based on the Gaussian kernel:

$$p(\mathbf{s}, x_k) = p_0 \exp(-\|\mathbf{x}_k - \mathbf{s}\|^2 / (2\sigma^2))$$

where p_0 denotes the maximum probability of capture (applicable when $\mathbf{s} = x_k$) and where σ denotes a positive-valued scale parameter. If movement of individuals is the mechanism that makes them susceptible to detection, the scale parameter essentially quantifies the spatial extent of movements around the activity centers; however, this distance-based detection function is also applicable in surveys where individual movements are not responsible for differences in capture probability [1]. The essential feature is that $p(\mathbf{s}, x_k)$ is highest when locations $\mathbf{s}$ and x_k coincide and declines monotonically as the distance between $\mathbf{s}$ and x_k increases.

To complete the model description, let $y_k \in \{0, 1, \dots, J_k\}$ denote the number of trapping periods in which an individual is detected at the k th trap. A sum of J_k independent and identically distributed Bernoulli random variables has a binomial distribution; therefore, $y_k | \mathbf{s} \sim \text{binomial}(J_k, p(\mathbf{s}, x_k))$. Moreover, since recaptures of the same individual in different traps are assumed to occur independently, the joint probability of these observations (conditional on the individual’s activity center $\mathbf{s}$) equals the product of trap-specific, binomial probabilities:

$$[y_1, y_2, \dots, y_K | \mathbf{s}] = \prod_{k=1}^K \text{Bin}(y_k | J_k, p(\mathbf{s}, x_k)).$$

(Probability density functions for the binomial, Bernoulli, and normal distributions are abbreviated using Bin, Bern, and N, respectively (as in tables 2.1 and 2.2 of [24]).)

We are now equipped with all of the components needed to derive the likelihood function of the model. Let y_{ik} denote the number of detections of the i th individual at trap k ($i = 1, \dots, N$). For the moment, suppose (counterfactually) that each of the N individuals is detected at least once during trapping. In this case the likelihood function for the unknown parameters $\theta = (\beta, p_0, \sigma)'$ equals the joint density of N and the $N \times K$ matrix Y of individual- and trap-specific counts:

$$\begin{aligned} [Y, N | \theta] &= [N] \prod_{i=1}^N \int_{\mathcal{S}} [s_i | N] [y_{i1}, y_{i2}, \dots, y_{iK} | s_i] ds_i \\ &= \frac{\exp(-\mu) \mu^N}{N!} \prod_{i=1}^N \int_{\mathcal{S}} \frac{\lambda(s_i)}{\mu} \prod_{k=1}^K \text{Bin}(y_{ik} | J_k, p(s_i, x_k)) ds_i \\ &= \frac{\exp(-\mu)}{N!} \prod_{i=1}^N \int_{\mathcal{S}} \lambda(s_i) \prod_{k=1}^K \text{Bin}(y_{ik} | J_k, p(s_i, x_k)) ds_i \end{aligned}$$

In classical (non-Bayesian) statistics, the likelihood function is often written as a function of θ (for example, $L(\theta | Y, N)$), emphasizing that θ is the unknown parameter to be estimated given data. I depart from this convention here for reasons that will become clear shortly; however, it should be understood that $[Y, N | \theta] \equiv L(\theta | Y, N)$. The contribution of the i th individual to this likelihood function is based on the marginal probability of the observed counts, $[y_{i1}, y_{i2}, \dots, y_{iK} | \theta]$, obtained by integrating the individual’s activity center s_i (an unobserved random variable) from the joint density of s_i and the observed counts. Although the integrals for μ and each individual’s contribution to $[Y, N | \theta]$ cannot be expressed in closed form, these integrals can be

evaluated numerically by partitioning region $\mathcal{S}$ into a sufficiently fine grid and evaluating a Riemann sum.

In reality, only $n < N$ individuals are detected during trapping, and our objective is to estimate N and the parameters θ given the number of observed individuals (n) and their $n \times K$ matrix Y_{obs} of trap-specific counts. Let $n_0 = N - n$ denote the unknown number of individuals that are *not* detected in any of the K traps. For these individuals, $y_k = 0$ ($\forall k$). The previous likelihood function must be modified to account for the unobserved individuals in the population. Given our modeling assumptions, the probability that an individual in the population was unobserved is

$$\begin{aligned} \pi_0 &= \int_{\mathcal{S}} \frac{\lambda(s)}{\mu} \prod_{k=1}^K \text{Bin}(0|J_k, p(s, x_k)) ds \\ &= \int_{\mathcal{S}} \frac{\lambda(s)}{\mu} \prod_{k=1}^K \{1 - p(s, x_k)\}^{J_k} ds \end{aligned} \quad (1)$$

The likelihood function of the "complete data" (wherein n_0 is treated as observable) is

$$\begin{aligned} [Y_{\text{obs}}, n, n_0 | \theta] &= [N] \frac{N!}{n_0! n!} \pi_0^{n_0} \\ &\quad \prod_{i=1}^n \int_{\mathcal{S}} [s_i | N] [y_{i1}, y_{i2}, \dots, y_{iK} | s_i] ds_i \\ &= \frac{\exp(-\mu) \mu^N}{N!} \frac{N!}{n_0! n!} \left[\int_{\mathcal{S}} \frac{\lambda(s)}{\mu} \prod_{k=1}^K \{1 - p(s, x_k)\}^{J_k} ds \right]^{n_0} \\ &\quad \times \prod_{i=1}^n \int_{\mathcal{S}} \frac{\lambda(s_i)}{\mu} \prod_{k=1}^K \text{Bin}(y_{ik} | J_k, p(s_i, x_k)) ds_i \\ &= \frac{\exp(-\mu) (\mu \pi_0)^{n_0}}{n_0! n!} \prod_{i=1}^n \int_{\mathcal{S}} \lambda(s_i) \\ &\quad \prod_{k=1}^K \text{Bin}(y_{ik} | J_k, p(s_i, x_k)) ds_i \end{aligned}$$

which accounts for the $\binom{N}{n_0}$ ways that n_0 distinct individuals may remain unobserved after sampling a population of size N . We marginalize n_0 (by summation) from this "complete-data" likelihood to obtain the likelihood function of the observable data:

$$\begin{aligned} [Y_{\text{obs}}, n | \theta] &= \sum_{n_0=0}^{\infty} [Y_{\text{obs}}, n, n_0 | \theta] \\ &= \frac{\exp\{-\mu(1 - \pi_0)\}}{n!} \prod_{i=1}^n \int_{\mathcal{S}} \lambda(s_i) \\ &\quad \prod_{k=1}^K \text{Bin}(y_{ik} | J_k, p(s_i, x_k)) ds_i. \end{aligned} \quad (2)$$

The maximum-likelihood estimator (MLE) of θ cannot be expressed in closed form; however, numerical maximization of (2) is straightforward and allows a maximum-likelihood estimate $\hat{\theta}$ to be calculated for any data set. Asymptotic variances and

covariances of the model's parameters may be estimated by inverting the observed information matrix.

Empirical bayes estimator of abundance. To develop an estimator of population size N using classical (non-Bayesian) methods of analysis, we use a single application of Bayes' rule to derive the conditional probability of n_0 given the observed data and the parameters θ :

$$\begin{aligned} [n_0 | Y_{\text{obs}}, n, \theta] &= \frac{[Y_{\text{obs}}, n, n_0 | \theta]}{[Y_{\text{obs}}, n | \theta]} \\ &= \frac{\exp(-\mu \pi_0) (\mu \pi_0)^{n_0}}{n_0!}. \end{aligned} \quad (3)$$

Therefore, the conditional distribution of n_0 is $\text{Poisson}(\mu \pi_0)$ and depends on the observed data (Y_{obs} and n) only indirectly in the sense that μ and π_0 are functions of θ , which must be estimated. The mean of the conditional distribution of n_0 provides the basis for the following empirical Bayes estimator of N :

$$\begin{aligned} \hat{N} &= n + E(n_0 | Y_{\text{obs}}, n, \hat{\theta}) \\ &= n + \hat{\mu} \hat{\pi}_0 \end{aligned} \quad (4)$$

where $\hat{\mu}$ and $\hat{\pi}_0$ correspond to the values of μ and π_0 evaluated at the estimate $\hat{\theta}$.

To estimate $\text{Var}(\hat{N})$, we must account for the expected variance of n_0 based on its conditional (Poisson) distribution and for the uncertainty involved in estimating θ . I derived the following estimator of $\text{Var}(\hat{N})$ by adopting the conceptual framework of [25] and by using the delta method to propagate the uncertainty of $\hat{\theta}$:

$$\widehat{\text{Var}}(\hat{N}) = \hat{\mu} \hat{\pi}_0 + \nabla(\hat{\mu} \hat{\pi}_0)' \widehat{\text{Var}}(\hat{\theta}) \nabla(\hat{\mu} \hat{\pi}_0) \quad (5)$$

where $\widehat{\text{Var}}(\hat{\theta})$ denotes the estimated asymptotic variance-covariance matrix of $\hat{\theta}$ and where $\nabla(\hat{\mu} \hat{\pi}_0)$ denotes the gradient of $\mu \pi_0$ with respect to θ evaluated at $\hat{\theta}$. (See Appendix S1 for the derivation of (5).) A 95% confidence interval for N may be computed by assuming that the sampling distribution of the estimates of n_0 is lognormal with mean $\hat{\mu} \hat{\pi}_0$ and variance $\widehat{\text{Var}}(\hat{N})$.

Though not entirely obvious, it's worth noting that empirical Bayes estimates of N and their variances increase automatically with the size of region $\mathcal{S}$. This occurs because the integral in (1) increases with the size of $\mathcal{S}$. In addition, the abundance of activity centers located within any subset of $\mathcal{S}$ may be estimated using θ without additional computation owing to the independence of events of the Poisson process over $\mathcal{S}$ [22].

Bayes estimator of abundance. To develop an estimator of population size N using Bayesian methods of analysis, we must extend the model to specify uncertainty in the magnitude of θ prior to observing the data. To do this we combine the complete-data likelihood function with a prior density $[\theta]$ to form the (unnormalized) posterior density:

$$[\theta, n_0 | Y_{\text{obs}}, n] \propto [Y_{\text{obs}}, n, n_0 | \theta] [\theta]$$

Note that the parameters of this model include both θ and n_0 . We could instead have chosen the likelihood of the observed data (Equation 2) and obtained the marginal density $[\theta | Y_{\text{obs}}, n]$ of this

posterior directly; however, retaining n_0 as a parameter actually simplifies the Markov chain Monte Carlo (MCMC) algorithm used to fit the model (see Appendix S1).

Since $N = n + n_0$, Bayesian inferences about N are based entirely on the posterior distribution of n_0 , which has probability mass function

$$[n_0 | Y_{\text{obs}}, n] = \int [n_0 | Y_{\text{obs}}, n, \theta] [\theta | Y_{\text{obs}}, n] d\theta \quad (6)$$

Note that the integrand in this equation contains the conditional posterior probability of n_0 , which was derived earlier (Equation 3) and used to compute the empirical Bayes estimator of N . In contrast to that estimator, Bayesian inferences about n_0 – and therefore, about N – integrate over the posterior uncertainty in θ so that additional calculations (as in (5)) are not needed to estimate the uncertainty in N correctly. Summaries of the posterior distribution of N (e.g., mean, mode, quantiles, etc.) may be estimated directly from (6). In addition, these estimates are valid for any sample size and do not rely on asymptotic approximations, unlike the empirical Bayes confidence intervals. Of course, the price of that validity is having to specify a prior distribution for θ , which may influence estimates of N if relatively few individuals have been recaptured.

Analysis of Recapture Locations Observed in Area Searches

In this section I describe a model for recaptures of individuals that may be detected during each of J uniform searches of a sampling region $\mathcal{X} \subset \mathcal{S}$. During these area-search surveys, as they have come to be called, individuals may be detected but their capture locations are not fixed – unlike the recaptures at trapping arrays. In fact, in an area search the capture location of an individual is not even observable if the individual is not detected. Therefore, the detections of individuals and their capture locations are both stochastic outcomes of area-search surveys.

To specify a model of the observable capture (and recapture) locations, I assume that each individual moves randomly around its activity center $s \in \mathcal{S}$. Specifically, I use a bivariate normal distribution to model the locations that arise from each individual's movements. Let x_j denote a random variable for the location of an individual during the j th area-search survey ($j = 1, \dots, J$). Under the bivariate normal model, $x_j | s \sim \text{Normal}(s, \sigma^2 I)$, where I denotes a 2×2 identity matrix. Note that whereas all individuals share the same scale parameter σ , which quantifies the extent of their movements, the locations at which a single individual might be observed depend on its activity center s . [10] and [7] also used the bivariate normal distribution to specify models of area-search data; however, alternative movement models are also possible. The essential feature of the SECR model developed here is the conditional dependence between an individual's locations and its activity center.

To complete the model, we need to specify the process that leads to detections of individuals. Let a random variable $y_j \in \{0, 1\}$ denote whether an individual is detected ($y = 1$) or not ($y = 0$) during the j th search of region $\mathcal{X}$. The value of y_j clearly depends on an individual's location x_j during the j th survey (since $y_j = 0$ if $x_j \notin \mathcal{X}$); therefore, I assume

$$y_j | x_j \sim \text{Bernoulli}(p_0 I(x_j \in \mathcal{X}))$$

where p_0 is the probability that an individual present in region $\mathcal{X}$ is

detected during a single search of the region. ($I(a)$ denotes the indicator function, which equals 1 if argument a is true and 0 otherwise.)

The locations and detections of the same individual in different surveys are assumed to occur independently; therefore, the joint density of these observations (conditional on the individual's activity center s), equals the product of survey-specific densities:

$$\begin{aligned} [x_1, y_1, x_2, y_2, \dots, x_J, y_J | s] &= \prod_{j=1}^J [x_j | s] [y_j | x_j] \\ &= \prod_{j=1}^J N(x_j | s, \sigma^2 I) \text{Bern}(y_j | p_0 I(x_j \in \mathcal{X})) \end{aligned} \quad (7)$$

Recall, however, that an individual's capture location is not observable in surveys where the individual is not detected; therefore, the joint density in (7) cannot be used in the likelihood function of the observable data. Instead, we must factor the joint density into two components, one for the locations of individuals that are detected and another for the marginal probability of the non-detections obtained by integrating the unobserved recapture locations from (7).

The first component of the joint density is associated with the value of $y_j = 1$ (detection). This observation implies $x_j \in \mathcal{X}$; thus, the joint density of x_j and $y_j = 1$ is

$$[x_j, y_j = 1 | s] = N(x_j | s, \sigma^2 I) p_0 \quad (8)$$

The second component of the joint density is associated with the value of $y_j = 0$ (non-detection). In this case the individual's location is unobserved, so the marginal probability of non-detection is

$$\begin{aligned} [y_j = 0 | s] &= \int_{\mathcal{S}} [x_j | s] [y_j = 0 | x_j] dx_j \\ &= \int_{\mathcal{S}} N(x_j | s, \sigma^2 I) \{1 - p_0 I(x_j \in \mathcal{X})\} dx_j \\ &= 1 - \int_{\mathcal{X}} N(x_j | s, \sigma^2 I) p_0 dx_j \end{aligned} \quad (9)$$

Note that (9) is based on the assumption that $\int_{\mathcal{S}} N(x_j | s, \sigma^2 I) dx_j = 1$, which implies that an individual's locations are contained within region $\mathcal{S}$ during the area-search surveys of $\mathcal{X}$. Technically, and depending on the value of σ , this assumption could be violated for individuals whose activity centers are located near the boundary of $\mathcal{S}$. However, the consequences of these “edge effects” for estimation usually can be minimized simply by increasing the size of $\mathcal{S}$, which reduces the relative contribution of these individuals to the likelihood function. If this corrective measure does not solve the problem, then σ may be so high relative to the size of $\mathcal{X}$ that movements of individuals reduce the chances of multiple detections (recaptures of the same individual) and the problem is not tractable anyway [7,26].

We now have all of the elements needed to derive the likelihood function of the model. Let y_{ij} indicate whether the i th individual is detected or not during the j th search of region $\mathcal{X}$ ($i = 1, \dots, N$). Similarly, let x_{ij} denote the location of the i th individual during the j th area-search survey. Our objective is to estimate N and the parameters $\theta = (\beta, p_0, \sigma)$ given the number of observed

individuals (n), the $n \times J$ matrix Y_{obs} of detection indicators, and the partially observed $n \times J$ matrix X_{obs} of locations. Let $n_0 = N - n$ denote the unknown number of individuals that are *not* detected during the J area-search surveys. For these individuals, $y_j = 0$ ($\forall j$). As before, the likelihood function of the observable data must account for the unobserved individuals in the population. Given our modeling assumptions, the probability that an individual in the population was unobserved is

$$\pi_0 = \int_{\mathcal{S}} \frac{\lambda(s)}{\mu} \left\{ 1 - \int_{\mathcal{X}} \text{N}(x|s, \sigma^2 I) p_0 dx \right\}^J ds. \quad (10)$$

The likelihood function of the “complete data” (wherein n_0 is treated as observable) is

$$\begin{aligned} [Y_{\text{obs}}, X_{\text{obs}}, n, n_0 | \theta] &= [N] \frac{N!}{n_0! n!} \pi_0^{n_0} \\ &\times \prod_{i=1}^n \int_{\mathcal{S}} [s_i | N] \left\{ \prod_{j: y_{ij}=1} \text{N}(x_{ij} | s_i, \sigma^2 I) p_0 \right\} \\ &\quad \left\{ 1 - \int_{\mathcal{X}} \text{N}(x | s_i, \sigma^2 I) p_0 dx \right\}^{J-y_i} ds_i \\ &= \frac{\exp(-\mu)(\mu \pi_0)^{n_0}}{n_0! n!} \\ &\times \prod_{i=1}^n \int_{\mathcal{S}} \lambda(s_i) \left\{ \prod_{j: y_{ij}=1} \text{N}(x_{ij} | s_i, \sigma^2 I) p_0 \right\} \\ &\quad \left\{ 1 - \int_{\mathcal{X}} \text{N}(x | s_i, \sigma^2 I) p_0 dx \right\}^{J-y_i} ds_i \end{aligned}$$

where $y_i = \sum_{j=1}^J y_{ij}$ is the number of area-searches in which the i th individual is detected. We marginalize n_0 (by summation) from this “complete-data” likelihood to obtain the likelihood function of the observable data:

$$\begin{aligned} [Y_{\text{obs}}, X_{\text{obs}}, n | \theta] &= \sum_{n_0=0}^{\infty} [Y_{\text{obs}}, X_{\text{obs}}, n, n_0 | \theta] \\ &= \frac{\exp\{-\mu(1-\pi_0)\}}{n!} \\ &\times \prod_{i=1}^n \int_{\mathcal{S}} \lambda(s_i) \left\{ \prod_{j: y_{ij}=1} \text{N}(x_{ij} | s_i, \sigma^2 I) p_0 \right\} \\ &\quad \left\{ 1 - \int_{\mathcal{X}} \text{N}(x | s_i, \sigma^2 I) p_0 dx \right\}^{J-y_i} ds_i. \end{aligned}$$

The maximum-likelihood estimator (MLE) of θ cannot be expressed in closed form; however, numerical maximization of the likelihood function is straightforward. Although the numerical integrations over $\mathcal{S}$ require discretization (as described earlier) and can be computationally intensive, efficient algorithms exist for integrating the bivariate normal density function over $\mathcal{X}$. Asymptotic variances and covariances of the model’s parameters may be estimated by inverting the observed information matrix.

Estimators of abundance. Classical (non-Bayesian) and Bayesian estimators of population size N may be derived using the same approach taken with the trapping array model. For example, a single application of Bayes’ rule reveals that the conditional distribution of the number of unobserved individuals in the population is Poisson:

$$n_0 | Y_{\text{obs}}, X_{\text{obs}}, n, \theta \sim \text{Poisson}(\mu \pi_0)$$

where π_0 is defined in (10). The mean of this distribution provides the basis for the empirical Bayes estimator of N : $\hat{N} = n + \hat{\mu} \hat{\pi}_0$, where $\hat{\mu}$ and $\hat{\pi}_0$ correspond to the values of μ and π_0 evaluated at the maximum likelihood estimate $\hat{\theta}$. Similarly $\text{Var}(\hat{N})$ is estimated using the empirical Bayes estimator (5).

To develop the Bayesian estimator of N , we combine the complete-data likelihood function with a prior density $[\theta]$ to obtain the (unnormalized) posterior density:

$$[\theta, n_0 | Y_{\text{obs}}, X_{\text{obs}}, n] \propto [Y_{\text{obs}}, X_{\text{obs}}, n, n_0 | \theta] [\theta]$$

The MCMC algorithm used to fit this model is given in Appendix S1. Since $N = n + n_0$, Bayesian inferences about N are based entirely on the posterior distribution of n_0 , which has probability mass function

$$\begin{aligned} [n_0 | Y_{\text{obs}}, X_{\text{obs}}, n] \\ = \int [n_0 | Y_{\text{obs}}, X_{\text{obs}}, n, \theta] [\theta | Y_{\text{obs}}, X_{\text{obs}}, n] d\theta \end{aligned} \quad (11)$$

Summaries of the posterior distribution of N may be estimated directly from (11), as described earlier.

Analyses of Real and Simulated Data

Trapping-array Surveys in a Spatially Heterogeneous Habitat

The density of individuals can vary substantially in regions of spatially varying habitat. To mimic this situation, I simulated a population of individuals living in a square (2 km $\times$ 2 km) region with relatively large differences in habitat quality (Figure 1). The limiting expected density of individuals in this region was assumed to vary as a loglinear function of habitat quality $v(s)$ as follows: $\log(\lambda(s)) = \log(80) + 0.5v(s) - 1.0v(s)^2$, where $v(s)$ was centered and scaled to have mean zero and unit variance. Individuals were detected in an array of 100 traps placed within a 1 km $\times$ 1 km square located at the center of the region (Figure 1). I assumed that individuals possessed unique marks for identification and may have been detected during each of five survey periods, as in camera-trap surveys. Maximum detection probability p_0 was assumed to be 0.25, and the scale parameter σ was assumed to be 0.4 km.

Of the total population of 643 individuals, 535 were observed in the trapping-array surveys. Many of these individuals were detected at more than one trap (average = 7.8 traps per individual), but few individuals were observed more than twice at the same trap (average = 1.2 detections per trap).

I fitted the SECR model for recaptures in trapping arrays to these data by partitioning the region occupied by the population into a grid of square pixels (width = 160 m) for numerical integration. Further reductions in pixel width did not change the

value of the maximized log likelihood. I used maximum-likelihood estimates of the model's parameters to initialize the Markov chain used in the Bayesian analysis. In addition, I used $M = 2000$ successive draws of the Gibbs sampler (Appendix S1) to estimate posterior means and quantiles of the model parameters. Monte Carlo standard errors of posterior means and quantiles were computed using the subsampling bootstrap method [27,28] with overlapping batch means of size $\lfloor \sqrt{M} \rfloor$.

Classical and Bayesian estimates of the model parameters and of their 95% confidence or credible intervals are quite similar (Table 1). Strong agreement also exists between the parameter estimates and the parameter values used to generate the data, which is not surprising given the size of the population and sample. This agreement is manifest in predictions of $\lambda(s)$ as a function of habitat quality (Figures 2 and 3). The empirical Bayes and Bayes estimates of population size N are essentially identical (647.8 and 647.6 individuals, respectively) given the Monte Carlo error of the Bayes estimate. The 95% confidence and credible intervals for N are also quite similar since the posterior distribution appears to be approximately lognormal (Figure 4).

Camera-trap Surveys of Tigers

I fitted the SECR model for recaptures in trapping arrays to a set of data that have been analyzed previously using both non-spatial and spatial capture-recapture models [12,13,17]. [12] provide a detailed description of these data. Briefly, the data include photographic recaptures of 44 tigers that were exposed to a spatial array of 120 camera traps established within the Nagarhole Reserve in the state of Karnataka, southwestern India [12]. The identity of each tiger could be established from photographs because these animals possess natural marks (unique stripe patterns). All 120 camera traps were not operated simultaneously. Instead, the reserve was partitioned into four subregions, each containing about 30 traps, and tigers were photographed in each subregion during each of 12 consecutive days. Because individual tigers were rarely detected more than once in the same day and trap, I treated multiple detections on the same day and trap as a single recapture, in accordance with the underlying assumptions of the SECR model. [12] made the same assumption, treating the observations of each tiger as a sequence of binary encounters over 12 days of trapping.

In the absence of spatial covariates of tiger density, I fitted the model based on a homogeneous Poisson point process using both classical and Bayesian methods of analysis. The minimum rectangular region needed to encompass the entire trapping array

spanned an area of 772 km² (20.7 km × 37.3 km). To fit the model, I assigned $\mathcal{S}$ to be the rectangular region that buffers this minimum rectangle by 12.5 km on each side, and I partitioned $\mathcal{S}$ into a grid of square pixels (width = 0.5 km) for numerical integration. Further increases in the size of $\mathcal{S}$ and further reductions in pixel width did not change the value of the maximized log likelihood. To conduct a Bayesian analysis of the data, I used maximum-likelihood estimates of the model's parameters to initialize the Markov chain and I used $M = 12000$ successive draws of the Gibbs sampler (Appendix S1) to estimate posterior means and quantiles of the model parameters. Monte Carlo standard errors of posterior means and quantiles were computed as described earlier.

Classical and Bayesian estimates of the model parameters and their 95% confidence or credible intervals are quite similar (Table 2). The average density of tigers is estimated to be 0.123 individuals km⁻². The probabilities of detecting these tigers appears to be very low since the estimated maximum detection probability is only about 0.02. For comparison with a previous analysis of these data [17], I estimated the number of tigers present in a rectangular region that buffers the minimum rectangle by 5 km on each side (area = 1452 km²). [17] incorrectly reported this region as buffering the minimum rectangle by 7.5 km on each side (area = 1866 km²) (Royle, personal communication). The empirical Bayes and Bayes estimates of N in this region are essentially identical (178.8 and 179.2 tigers, respectively) given the Monte Carlo error of the Bayes estimate. The 95% confidence and credible intervals for N are also quite similar since the posterior distribution appears to be approximately lognormal (Figure 5).

Area-search Surveys of Lizards

I fitted the SECR model for area-search surveys to a set of data that have been described and analyzed previously [7,10]. The data include the recaptures of 68 flat-tailed horned lizards (*Phrynosoma mcallii*) within a 9-ha square plot (width = 300 m) located in southwestern Arizona, USA. During each survey, this plot was searched thoroughly for lizards, which were marked and released after noting their capture locations. A total of 14 surveys were conducted over 17 days producing 134 captures [7].

In the absence of spatial covariates of lizard density, I fitted the model based on a homogeneous Poisson point process using both classical and Bayesian methods of analysis. To fit the model, I assigned $\mathcal{S}$ to be the square region that buffers the surveyed plot by 150 m on each side, and I partitioned $\mathcal{S}$ into a grid of square pixels (width = 5 m) for numerical integration. Further increases in the

Table 1. Estimates of parameters of model fitted to recaptures of individuals in a simulated population.

Parameter (units)	Maximum-likelihood estimates			Bayesian estimates		
	Estimate	2.5%	97.5%	Mean	2.5%	97.5%
β_0	4.412	4.292	4.532	4.415 (0.0030)	4.297 (0.0047)	4.531 (0.0044)
β_1	0.557	0.359	0.755	0.563 (0.0044)	0.370 (0.0061)	0.784 (0.0061)
β_2	-1.123	-1.353	-0.892	-1.143 (0.0067)	-1.367 (0.0091)	-0.911 (0.0091)
ρ_0	0.254	0.244	0.263	0.254 (0.0002)	0.245 (0.0003)	0.263 (0.0003)
σ (km)	0.400	0.393	0.407	0.400 (0.0002)	0.393 (0.0003)	0.407 (0.0003)
N (individuals)	647.8	625.3	674.2	647.6 (0.26)	624 (0.45)	672 (0.62)

N is the abundance of individuals in the population. Lower and upper limits of 95% confidence intervals (based on ± 1.96 asymptotic standard errors) and of 95% credible intervals are given in the columns labeled 2.5% and 97.5%, respectively. Monte Carlo standard errors are given in parentheses.

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Figure 2. Predicted mean density of individuals in a simulated population as a function of habitat quality. Shaded region indicates 95% credible interval. Dotted lines indicate uncertainty of upper and lower credible limits due to Monte Carlo error. Blue dashed line indicates the true relationship between $\lambda(s)$ and habitat quality.
doi:10.1371/journal.pone.0084017.g002

size of S and further reductions in pixel width did not change the value of the maximized log likelihood. To conduct a Bayesian analysis of the data, I used maximum-likelihood estimates of the model's parameters to initialize the Markov chain and I used $M=12000$ successive draws of the Gibbs sampler (Appendix S1) to estimate posterior means and quantiles of the model param-

eters. Monte Carlo standard errors of posterior means and quantiles were computed as described earlier.

Classical and Bayesian estimates of the model parameters and their 95% confidence or credible intervals are quite similar (Table 3). The average density of lizards is estimated to be 8.06

Figure 3. Map of predicted mean density of individuals in a simulated population. Activity centers of individuals are superimposed on the map.
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Figure 4. Posterior distribution of abundance of simulated population. Red line indicates the estimated sampling distribution of empirical Bayes estimates of abundance. Vertical blue line indicates true population size.
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Table 2. Estimates of parameters of model fitted to recaptures of tigers at trap locations.

Parameter (units)	Maximum-likelihood estimates			Bayesian estimates		
	Estimate	2.5%	97.5%	Mean	2.5%	97.5%
λ (tigers km^{-2})	0.123	0.083	0.182	0.123 (0.0013)	0.082 (0.0011)	0.180 (0.0020)
p_0	0.016	0.009	0.027	0.017 (0.0002)	0.009 (0.0002)	0.027 (0.0003)
σ (km)	1.95	1.57	2.44	1.95 (0.0087)	1.59 (0.0080)	2.46 (0.0168)
N (tigers)	178.8	125.6	254.1	179.2 (1.64)	124 (1.20)	256 (2.68)

N is the abundance of tigers in a rectangular region of area 1452 km^2 (trapping rectangle buffered by 5 km). Lower and upper limits of 95% confidence intervals (based on ± 1.96 asymptotic standard errors) and of 95% credible intervals are given in the columns labeled 2.5% and 97.5%, respectively. Monte Carlo standard errors are given in parentheses.

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individuals ha^{-1} . For comparison with previous analyses of these data, I estimated the number of lizards present in the 9-ha surveyed plot. The empirical Bayes and Bayes estimates of N in the plot are essentially identical (82.3 and 82.5 lizards, respectively) given the Monte Carlo error of the Bayes estimate. The 95% confidence and credible intervals for N are also similar (Figure 6).

Simulation Study of Area-search Surveys

I repeated the simulation study of [7] and [26] to compare the operating characteristics of Bayes and empirical Bayes estimators of population abundance and average density based on the area-search models described in this paper. In the simulations a square (1×1 km) plot $\mathcal{X}$ was searched for individuals on $J = 5$ separate occasions. Individuals detected in each survey were marked (if unmarked) and released after noting their capture locations.

Figure 5. Posterior distribution of abundance of tigers in a rectangular region of area 1452 km^2 . Region is defined as trapping rectangle buffered by 5 km. Red line indicates the estimated sampling distribution of empirical Bayes estimates of abundance.
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Movements of individuals were assumed to follow a bivariate normal model with scale parameter σ equal to 0.1 or 0.2 km. The region $\mathcal{S}$ occupied by the population was assumed to be the square that buffers the survey plot $\mathcal{X}$ by 3σ km on each side. The detection probability was assumed to be constant ($p_0 = 0.25$) during each survey. The spatial distribution of individual activity centers was assumed to follow a homogeneous Poisson point process with limiting expected density λ equal to 23.4, 46.9, or 78.1 individuals km^{-2} .

To perform classical and Bayesian analyses of each simulated data set, I partitioned $\mathcal{S}$ into a grid of 2500 square pixels for numerical integration. In the Bayesian analysis of each data set, I used the maximum-likelihood estimate of the model's parameters to initialize the Markov chain and I used 2000 successive draws of the Gibbs sampler (Appendix S1) to estimate the model's parameters. Owing to the computational expense of these analyses, only 300 simulated data sets were analyzed for each combination of model parameters.

Classical and Bayes estimates of population abundance and average density were similar in most of the scenarios of the simulation study (Figures 7 and 8). The mean number of individuals observed ranged from about 20 individuals in the lowest density populations to about 67 or 74 individuals in the highest density populations (depending on the assumed value of σ). Estimates of relative bias of classical and Bayesian estimators were highest at the lowest population density and declined with increases in population density. The frequentist coverage of classical and Bayesian 95% confidence and credible intervals, respectively, was estimated to be at or near the nominal level in almost all simulation scenarios. One exception occurred at the lowest population density (23.4 individuals km^{-2}) with $\sigma = 0.2$, where the estimated coverage of Bayesian intervals was 0.88 (for abundance) and 0.89 (for density).

Discussion

In formulating the SECR models I used a Poisson point process to specify the spatial distribution of individual activity centers. This modeling assumption allowed me to derive estimators of population abundance and density for use in classical or Bayesian analyses and to compare the operating characteristics of these estimators in analyses of real and simulated data sets.

The Bayes and empirical Bayes estimators of population abundance are closely related. Both estimators depend on the full conditional distribution of the number n_0 of activity centers of unobserved individuals (i.e., individuals not detected while

Table 3. Estimates of parameters of model fitted to locations of lizards recaptured during area-search surveys.

Parameter (units)	Maximum-likelihood estimates			Bayesian estimates		
	Estimate	2.5%	97.5%	Mean	2.5%	97.5%
λ (lizards ha^{-1})	8.06	6.23	10.43	8.06 (0.030)	6.15 (0.036)	10.34 (0.055)
p_0	0.124	0.100	0.153	0.125 (0.0003)	0.099 (0.0005)	0.152 (0.0007)
σ (m)	18.5	16.3	21.0	18.7 (0.02)	16.5 (0.04)	21.4 (0.07)
N (lizards)	82.3	74.6	95.1	82.5 (0.11)	74.0 (0.10)	93.0 (0.26)

N is the abundance of lizards in the 9 ha search area. Lower and upper limits of 95% confidence intervals (based on ± 1.96 asymptotic standard errors) and of 95% credible intervals are given in the columns labeled 2.5% and 97.5%, respectively. Monte Carlo standard errors are given in parentheses.

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sampling). This distribution is $\text{Poisson}(\mu\pi_0)$ for every Poisson point-process model of SECR data. The only difference between models is the functional form of π_0 , which depends on the sampling protocol (e.g., compare (1) and (10)). In general, the empirical Bayes estimator of abundance equals the mean of the conditional distribution of n_0 plus the observed number of individuals. However, since the mean of n_0 is a function of the model's parameters θ , additional calculations are needed to ensure that the estimator of $\text{Var}(\hat{N})$ accounts for uncertainty involved in estimating θ (see (5)). In contrast, the fully Bayesian estimator of population abundance is based on the marginal posterior distribution of the number of activity centers of unobserved individuals. This distribution is obtained by integrating the full conditional probabilities over the posterior distribution of θ so that the Bayesian approach automatically accounts for uncertainty in estimating θ .

An estimator of abundance proposed by [19] for the analysis of recaptures in trapping arrays is mathematically equivalent to the empirical Bayes estimator that I derived. In the notation of [19], $D(x; \phi)$ corresponds to $\lambda(s)$ and $1 - p(x; \theta)$ corresponds to

$\prod_{k=1}^K \{1 - p(s, x_k)\}^{J_k}$. [19] also proposed three estimators of $\text{Var}(\hat{N})$; one of these (equation A2 of their appendix) appears to be equivalent to the estimator that I derived in Appendix S1. [19] presented this estimator without derivation, indicating only that it is based on an approximation of mean squared prediction error as described by [29]. I have shown that this estimator of $\text{Var}(\hat{N})$ can be derived from an empirical Bayes view of the problem and is not an ad hoc approximation as suggested by [19]. In fact, the delta-method approximation of $\text{Var}(\hat{\mu}\pi_0)$ can be improved by parametric bootstrapping [25], though the additional calculations would rival those required for a fully Bayesian analysis using MCMC methods.

An empirical Bayes approach for estimating abundance is also feasible if a binomial point-process model is fitted to SECR data. In this case the conditional distribution of the number n_0 of activity centers of unobserved individuals is binomial with index parameter $M - n$ and success probability $\psi\pi_0/(\psi\pi_0 + 1 - \psi)$ [17]. Therefore, an empirical Bayes estimator of N may be computed by adding n and the estimated conditional (binomial) mean of n_0 . As with Poisson models, this approach can be used for every binomial model of SECR data. Only the functional form of π_0 differs among models owing to differences in sampling protocols.

In the datasets I analyzed, classical and Bayesian methods provided similar – and often identical – inferences, which is not surprising given the sample sizes and the noninformative priors used in the analyses. For example, in the analysis of recaptures of tigers in trapping arrays and of lizards in area searches, classical and Bayesian estimates of the model parameters and their 95% confidence or credible intervals were quite similar and were consistent with previous analyses of these data [7,17]. The same was true for Bayes and empirical Bayes estimates of abundance of these populations. In the analysis of recaptures from simulated populations, Bayesian estimates of abundance and average density exhibited levels of bias that were comparable to those of classical estimates (MLEs and empirical Bayes approximations). This result suggests that the differences in maximum-likelihood and Bayesian estimates reported by [7] were either statistically insignificant (due to high Monte Carlo error) or attributed to differences in modeling assumptions (binomial vs. Poisson).

The Bayesian SECR models that I described can be extended in a variety of useful and important ways. For example, the ecological process submodel can be extended to specify stochastic sources of spatial variation in density that induce clustering of individual activity centers (e.g., Cox process models). The Bayesian SECR models also can be revised to include spatial or non-spatial sources of variation in detectability of individuals or alternative functional forms for models of detectability [5]. The observation component of Bayesian SECR models also can be modified to account for

Figure 6. Posterior distribution of abundance of lizards in the 9 ha search area. Red line indicates the estimated sampling distribution of empirical Bayes estimates of abundance.
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Figure 7. Comparison of empirical Bayes and Bayes estimates of population abundance computed from analyses of simulated recaptures in area-search surveys. Estimates of relative bias are plotted in upper row. Estimates of frequentist coverage of 95% credible or confidence intervals are plotted in lower row. Error bars indicate 95% confidence intervals.
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Figure 8. Comparison of maximum-likelihood and Bayes estimates of expected population density computed from analyses of simulated recaptures in area-search surveys. Estimates of relative bias are plotted in upper row. Estimates of frequentist coverage of 95% credible or confidence intervals are plotted in lower row. Error bars indicate 95% confidence intervals.
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different types of sampling methods (e.g., single- or multi-catch traps [5] or proximity detectors of acoustic signals [6]). I anticipate that these extensions of Bayesian SECR models will be developed in the near future.

Supporting Information

Appendix S1 Derivation of empirical Bayes estimator of $\text{Var}(\hat{N})$, and MCMC algorithms used to fit Bayesian models of spatial capture-recapture data. (PDF)

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Author Contributions

Conceived and designed the experiments: RD. Performed the experiments: RD. Analyzed the data: RD. Contributed reagents/materials/analysis tools: RD. Wrote the paper: RD.