Bayesian inference in camera trapping studies for a class of spatial capture–recapture models

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Abstract. We develop a class of models for inference about abundance or density using spatial capture–recapture data from studies based on camera trapping and related methods. The model is a hierarchical model composed of two components: a point process model describing the distribution of individuals in space (or their home range centers) and a model describing the observation of individuals in traps. We suppose that trap- and individual-specific capture probabilities are a function of distance between individual home range centers and trap locations. We show that the models can be regarded as generalized linear mixed models, where the individual home range centers are random effects. We adopt a Bayesian framework for inference under these models using a formulation based on data augmentation. We apply the models to camera trapping data on tigers from the Nagarahole Reserve, India, collected over 48 nights in 2006. For this study, 120 camera locations were used, but cameras were only operational at 30 locations during any given sample occasion. Movement of traps is common in many camera-trapping studies and represents an important feature of the observation model that we address explicitly in our application.

Key words: abundance; Bayesian analysis; binomial point process; camera trapping; carnivore surveys; data augmentation; density estimation; hierarchical model; Markov chain Monte Carlo; spatial capture–recapture; tigers; trapping array; trapping grid.

Introduction

Much of the theory and methodology underlying inference about population size from closed capture–recapture models is concerned with animal populations that are well defined in the sense that one can randomly sample individuals that are associated with some location or area and, usually, uniquely identify them. However, for many populations, the spatial area over which individuals occur (and are exposed to capture) cannot be precisely delineated. Movement of individuals onto and off of a putative sample unit induces a violation of the key assumption of "geographic closure," which impacts our ability to interpret the estimates of population size, N, derived from closed population capture–recapture models.

One area of application where this problem is profoundly important is the use of "camera traps" to study secretive animal populations. In particular, the use of arrays of camera traps for estimating abundances of large felids is widespread. They have been used in studies of tigers (Karanth 1995, Karanth and Nichols 1998, Karanth et al. 2004), ocelots (Trolle and Kéry 2003, 2005), jaguars (Wallace et al. 2003, Maffei et al. 2004), and other species which are individually identifiable

from their spot or stripe patterns. In the typical situation, an array of cameras is distributed over the landscape. Over time, the cameras provide encounter history data indicating the occasions of captures of individuals, as well as auxiliary data on spatial location of captures.

The conventional approach to the analysis of density from these systems is to apply closed population models, and then attempt to convert those estimates to densities using a wide range of heuristically motivated but essentially ad hoc methods. For example, ecologists have used auxiliary location information to estimate the mean or maximum distance moved to adjust the effective sample area, or used various other heuristic "adjustments." (Wilson and Anderson 1985*a*, *b*, Karanth and Nichols 1998, Parmenter et al. 2003, Trolle and Kéry 2003). The standard approach (Karanth and Nichols 1998) places a buffer strip around the trap array (or a convex hull containing the array) that is equal to half the mean maximum distance moved by individuals captured in more than one trap. While these procedures seem to work adequately in practice, the model or range of conditions for which they might work is poorly understood and difficult to characterize theoretically, and there is no basis for their extension. Formalization of the use of auxiliary spatial information requires the precise definition of a model: the linkage of encounter location to some notion of territory or home range (and perhaps movements, see Royle and Young 2008).

In this paper, we describe a general class of hierarchical models for encounter data from studies that use camera traps and related methods. By considering an array of traps in which each trap functions independently of all other traps, individuals in the population may be captured in multiple traps during any capture occasion and even multiple times in the same trap. This is realistic in studies based on camera trapping and other sampling methods which do not physically capture individuals. We describe a hierarchical model for the observed spatial encounter history data which recognizes that individual trap encounter histories are the outcome of two processes: distribution of individuals across the landscape and an encounter process that describes whether or not individuals are encountered by traps as a function of their location. We specify a model for the distribution of individuals in space in terms of a simple binomial point process, where $\mathbf{s}_i$, $i = 1, 2, \ldots, N$, is the realization of such a process for the N individuals in the population. We interpret the point locations as individual activity centers (or home range centers, or centroids; Borchers and Efford 2008, Royle and Young 2008, Gardner et al. 2009, Royle et al. 2009). We consider two distinct observation models that are defined conditional on the underlying point process realization: In the most general model, we allow that an individual can be caught an arbitrary number of times in each of an arbitrary number of traps. In principle, this is a reasonable model for camera trapping and other situations (e.g., hair or dung sampling to obtain DNA data), except that data, for processing reasons, are often reduced to single encounters for each trap. Moreover, when sample intervals are short (e.g., nights), it seems likely that multi-trap encounters should be highly correlated with one another, and so there may be little loss of efficiency in discarding such data. Therefore, we consider a second model in which individuals can be caught at most one time per trap, but in an arbitrary number of traps. This model is a formal restriction of the more general model, which can be obtained by imposing an explicit restriction on the observed random variables.

We demonstrate that these spatial capture–recapture models have simple formulations as classical generalized linear models with random effects (i.e., generalized linear mixed models; GLMMs). Analysis of the models is technically challenging because there are many latent variables (random effects) in the model. In particular, the activity centers of each individual are unknown. Moreover, the number of such activity centers (i.e., the population size N) is also unknown. To attack inference under these models, we adopt a Bayesian analysis of the model based on data augmentation (Royle et al. 2007), which has been applied to a number of related models (e.g., Royle and Dorazio 2008, Gardner et al. 2009, Royle 2009). Using data augmentation, the spatial capture–recapture models are formulated as zero-inflated Poisson or binomial regression models with random

effects. The models may be implemented in the freely available software WinBUGS (Gilks et al. 1994), which we believe yields an accessible platform for extension of the models described in our paper.

CAMERA TRAPPING: THE NAGARAHOLE DATA

Photographic captures of felid species that possess individually unique spot or stripe patterns, permit estimation of their abundance and density using closed capture recapture models. Such surveys have been conducted for tigers (Karanth and Nichols 1998, Karanth et al. 2004), leopards (Henschel and Ray 2003), jaguars (Wallace et al. 2003, Maffei et al. 2004, Soisalo and Cavalcanti 2006), and ocelots (Trolle and Kéry 2003), for example. These surveys are typically conducted over a short period of 30–60 days to ensure demographic closure, and involve photo-capturing both flanks of the cat in order to assign a unique identity to the individual. To increase capture probabilities, the traps are placed at ecologically optimal sites chosen based on the expertise of biologists, resulting in an irregular pattern of trap locations across the sampled area.

The tiger population in Nagarahole Reserve in the state of Karnataka, southwestern India, has been studied via camera trap methods by Karanth and associates from 1991 until the present (e.g., Karanth 1995, Karanth and Nichols 1998, Karanth et al. 2006; see Plate 1). The specific data set examined here was obtained in 2006 from sampling at 120 trap stations, each referenced by latitude and longitude and by UTM coordinates (Fig. 1). Two camera traps (unambiguous identification requires photographs of both flanks of each detected animal) were placed at each location. The sampling took place over 48 nightly intervals between 24 January and 16 March 2006.

All photographic captures of tigers obtained were labeled with auxiliary data such as date, time and location of capture, and the two corresponding flank images were linked using these data to establish the identity of each tiger. Multiple independent captures of individuals in the same night and trap is generally rare (fewer than four such events). As a result, in earlier published analyses of these data based on classical (nonspatial) closed population capture–recapture models (e.g., Karanth et al. 2004), multiple captures of the same individual at different trap locations or multiple captures at one location, during the same night, were combined into single binary "capture" events. We consider models that could accommodate capture both in multiple traps and also multiple captures in the same trap. However, we only address the former in our analysis of the data because our data have been processed into binary encounter history data. In addition, as we noted previously, we believe that within-trap recaptures in the same night are liable to be highly correlated (e.g., due to individuals moving past a camera multiple times in quick succession), and this
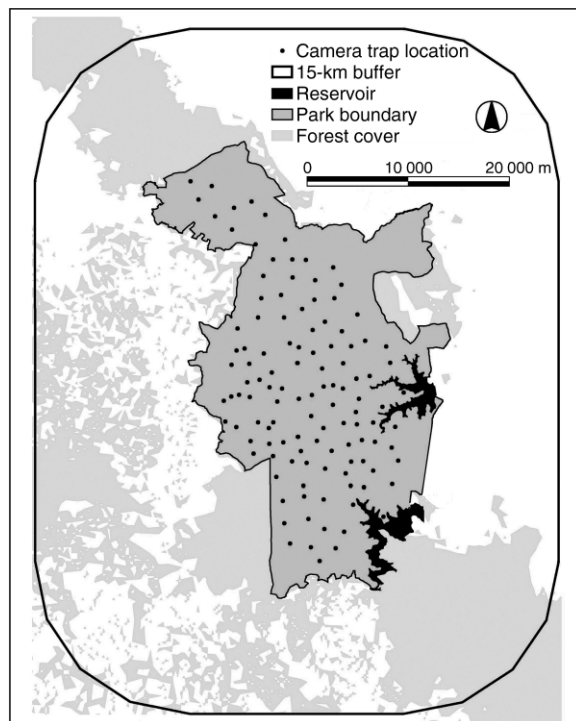
Fig. 1. Nagarahole Reserve tiger camera-trapping study area, Karnataka, southwestern India, with 15-km buffer outlined and non-habitat whited out.

may introduce an additional model selection/sensitivity issue while providing information that is less informative about density than captures among traps (see *Discussion*).

Sampling over this period resulted in encounter history data on 44 individuals during the 48 nightly sampling occasions. Thus, each encounter history was a $J \times K$ (120 traps × 48 nights) matrix, where a 0 was recorded for each occasion and trap location where the animal was not detected and a 1 was recorded for each occasion and trap location where a detection occurred. The number of distinct traps and capture occasions in which each of the 44 individuals was captured is shown in Table 1. We see that 15 individuals were captured in more than one trap. There were 65 unique individual/occasions and a total of 68 encounter events. Thus there were only three "extra-trap captures" during the study, that is, individuals captured in >1 trap on the same sampling occasion (night). In both instances, this corresponds to individuals captured in a single occasion: one individual captured at two traps and another individual captured at three traps.

An important feature of the study design is that not all 120 trap stations were operated simultaneously. Instead, the reserve was subdivided into four blocks of approximately 30 trapping stations each, and each block was run for 12 consecutive days. Then, cameras were moved to the next block for another 12 days and the process repeated until all four blocks were sampled. This

design follows sample design four of Karanth and Nichols (2002:133). Thus, some of the zeros are structural zeros (as opposed to sampling zeros), which we accommodate in the analysis of these data as described in *Spatial capture–recapture as a GLM with individual effects*.

In a previous analysis of these data (Royle et al. 2009) a multinomial capture model was applied, assuming that individuals could be captured in at most one trap per survey occasion. However, this model mis-specifies the true observation process. Because camera traps do not physically retain individuals, an individual tiger can be captured in multiple traps during any night. Failure to accommodate this information in the model induces some loss of efficiency in estimating density (see *Analysis of Nagarahole data*). We also note that in the analysis of Royle et al. (2009) there were $n = 45$ individuals. Subsequent reanalysis of the photographs revealed that one of these individuals represented only a recapture. Thus, the data analyzed here has one fewer individual, but one additional recapture compared to the analysis in Royle et al. (2009).

Model Formulation

The basic deficiency with the application of closed population models to data from trapping arrays is that space and movement have no explicit manifestation in such models. i.e., the models are not "spatial." Under these traditional models, N is just an integer-valued parameter that has no spatial context whatsoever. Thus, we seek to formalize the manner in which spatial organization of individuals is relevant to how they are observed.

State process model

A natural framework for developing spatial models of abundance is based on point process models, and point processes have been considered as the basis for spatial capture–recapture models in a number of recent efforts (Efford 2004, Borchers and Efford 2008, Royle and Young 2008). To develop this notion, we suppose that each individual in the population has a fixed point associated with it, its center of activity, $\mathbf{s}_i = (s_{1i}, s_{2i})$, a two-dimensional coordinate representing a point in space about which the movements of individual i are

TABLE 1. Summary encounter frequency data on tigers in the Nagarahole Reserve, India, camera trapping study during 48 nightly sampling occasions using 120 camera trap locations (e.g., nine tigers were captured on two nights and at two distinct camera trap locations).

Number of distinct traps	Number of occasions				
	1	2	3	4	5
1	28	1	0	0	0
2	1	9	1	0	0
3	1	0	1	0	1
4	0	0	0	1	0

concentrated. We suppose that these point locations represent the realization of a binomial point process. That is, we suppose there exists a population of N independent centers $\mathbf{s}_i$, $i = 1, 2, \ldots, N$, distributed uniformly over some region, say S, the state-space of the point process. We denote this assumption by

$$\mathbf{s}_i \overset{\text{ind}}{\sim} \text{Uniform}(\text{S}).$$

In practice, S will be prescribed (e.g., by specifying coordinates of some polygon that contains a trapping array).

The basic inference problem is to obtain an estimate of density, the number of activity centers per unit area of S, that is equivalent to an estimate of N under the point process model. We may also wish to estimate the number of activity centers in specific subsets of S, say some polygon $\text{P} \in \text{S}$. For example, P might be a national park, a reserve, or some block of contiguous habitat. We describe the model in some detail and then address this inference problem explicitly in *Estimating derived parameters*.

This uniform point process model represents a prior distribution for individual activity centers. While the assumptions of independence and uniformity are biologically untenable in many cases, we will see in our analysis of the tiger data that independence and uniformity of point locations in the prior does not preclude clustering or patchiness of point locations in the estimated posterior density of $\mathbf{s}$.

Observation models

Next we describe the juxtaposition of individual activity centers with the camera trapping array. We suppose that sampling is carried out by a network of J camera traps, having locations $\{\mathbf{x}_j, j = 1, 2, \ldots, J\}$. Further, we suppose that cameras function independently of one another. In particular, encounter by cameras is not mutually exclusive so that individuals can be encountered by multiple cameras. In the subsequent development of the observation models we will suppose that the probability of an individual being encountered by some camera j is a function of the distance from the camera to its activity center, and one or more parameters that will be estimated. Let $d_{ij} = ||\mathbf{s}_i - \mathbf{x}_j||$ be the distance between an individual i's activity center and camera j where $||\cdot||$ is the normal Euclidean distance.

In an ideal situation where cameras are operational continuously and individual encounter events are independent in time, an individual may be captured an arbitrary number of times yielding encounter frequencies y_{ijk} for individual i, in trap j, during interval k. One possible model for such encounter frequency data is the Poisson model:

$$y_{ijk} \sim \text{Poisson}(\lambda_0 g_{ij}) \tag{1}$$

where λ_0 is the baseline encounter intensity and g_{ij} is some function of distance between individual i and camera trap j which we will suppose equals 1 for $d_{ij} = 0$. Thus, for a trap that is located precisely at an individual's activity center, λ_0 is the expected number of captures in that trap. For example,

$$g_{ij} = \exp(-d_{ij}^2/\sigma) \tag{2}$$

which is a common "detection function" used in distance sampling and in the model described by Efford (2004). It can also be related explicitly to movement in some situations (Royle and Young 2008). In our analysis (below), we will also consider an exponential form for g_{ij}, i.e., $g_{ij} = \exp(-d_{ij}/\sigma)$ in order to assess the sensitivity to choice of model relating encounter to distance.

For the case where individuals can be captured at most once per trap, the observations are binary: $y_{ijk} = 1$ if individual i is captured in trap j during sample occasion k, and $y_{ijk} = 0$ otherwise. We will view the binary observations conceptually as reductions of the counts that we could have observed in the more general case. This might be most realistic for bear hair snare studies (and other DNA-based sampling) where an individual might be encountered a number of times during any period, and the biological material (hair, and so on) accumulates but cannot be partitioned into distinct visits after it is collected. In addition, as in our case, while camera traps may yield multiple captures during each occasion, it is difficult to imagine that such multiple captures are independent. Instead of either applying an arbitrary and subjective rule to determine how to partition events into independent recaptures, or devising a model of within-trap dependence, it is natural to reduce such data into binary encounter events. To formalize this, suppose we obtain binary observations y_{ijk} which are Bernoulli outcomes,

$$y_{ijk} \sim \text{Bernoulli}(\pi_{ij}) \tag{3}$$

with success probability that arises as the positive mass of the Poisson model described above:

$$\Pr(y_{ijk} = 1) = 1 - \exp(-\lambda_0 g_{ij}). \tag{4}$$

We will refer to the two models in Eqs. 1 and 3 as the Poisson and Bernoulli encounter models, respectively. Note that the parameters of the two distinct models are fundamentally equivalent, but the observable data under the second model is a reduced-information summary of what we would prefer to observe, the actual trap frequencies (see Royle and Nichols [2003] and Royle [2004] for a similar pairing of models).

SPATIAL CAPTURE–RECAPTURE AS A GLM WITH INDIVIDUAL EFFECTS

Note that the Bernoulli observation model, with $y_{ijk} \sim$ Bernoulli(π_{ij}) and $\pi_{ij} = \Pr(y_{ij} = 1) = 1 - \exp(-\lambda_0 g_{ij})$, can be viewed as a logistic-regression type of model. Specifically, with the choice of g from Eq. 2 we have

$$\text{cloglog}(\pi_{ij}) = \log(\lambda_0) - (1/\sigma)d_{ij}^2$$

where cloglog(argument) = log[–log(1 – argument)] is the complementary log–log transform. For Poisson observations, we have a standard Poisson regression formulation:

$$\log(\lambda_{ij}) = \log(\lambda_0) + (1/\sigma)d_{ij}^2.$$

This specification reveals the essential simplicity of spatial capture–recapture models as GLM type models, and it elucidates a number of important aspects of this model.

(1) The model is closely related to both "individual heterogeneity" (Link 2003, Dorazio and Royle 2003) models and also individual covariate models (Royle 2009) with individual covariate "distance" being a deterministic function of the latent variable s_i. The model is not precisely an individual covariate model because the variables s_i are unobserved even for the captured individuals. However the model is not entirely an individual heterogeneity model because they are partially observed for the captured individuals. In a sense, spatial capture–recapture models represent a conceptual intermediate between the two classes of models.

(2) We see that factors that influence λ_0 are linear effects on the cloglog π_{ij} scale. Thus, very general models can be represented as simple logistic-regression type models.

(3) We see that the (squared) distance between each trap and s_i is also a linear effect on the complementary log–log scale. Changing the distance function to be exponential produces a linear distance effect. Thus, in general, choice of distance function determines a transformation applied to the individual covariate.

Covariates that may influence detectability among individuals, or traps or through time may be modeled directly on the parameter λ_0 (regardless of the observation model under consideration). One situation that we will consider is the possibility of a behavioral response. In this case, we allow λ_0 to vary by individual and occasion so that

$$\log(\lambda_{0,ik}) = \alpha + \beta c_{ik}$$

where c_{ik} is an indicator covariate of previous encounter. Under this model, an individual's encounter probability may increase or decrease after initial encounter. The general model that we consider in our application (see *Analysis of Nagarahole data*) is of the form:

$$\text{cloglog}(\pi_{ijk}) = \alpha + \beta c_{ik} - (1/\sigma)d_{ij}^2.$$

A special kind of covariate is effort. In the context of camera trapping studies, this might be the time that a camera was operational, which could be modeled as described above (as a covariate on λ_0). In the Nagarahole study, traps were moved around such that only 30 of the 120 locations contained a trap on any particular night. This is a standard design both for camera trap studies, as well as so-called "hair snares" used for

obtaining DNA, and other methods of detecting individuals. In this case, the parameter λ_0 has to be forced to 0 for such instances so that $\Pr(y = 1) = 0$. This is simple to handle in the analysis by defining

$$\Pr(y_{ijk} = 1) = 1 - \exp(-\lambda_0 m_{jk} g_{ij})$$

where $m_{jk} = 1$ if trap j is operational during occasion k and $m_{jk} = 0$, otherwise. Thus, whenever a trap is not operational, $\Pr(y_{ijk} = 1) = 0$, as it should.

ANALYSIS OF THE MODEL WITH KNOWN N

If we knew **s** and N then the models are simple Poisson or logistic regression models and inference would be no more difficult than under those conventional models. To introduce readers to analysis of the models, we provide the basic specification of the models in WinBUGS for this situation. This "conditional-on-**s**" formulation of the model reveals the simplicity of the hierarchical model for camera trap array data. Further, the extension of the model to allow for **s** to be unknown is technically and conceptually straightforward. We formally address that situation in the following section.

As our analysis of the Nagarahole data makes use of the Bernoulli model, we consider that model here. The WinBUGS model specification for the Poisson model is provided in the Appendix. The implementation of this model in WinBUGS is given in Fig. 2 where the model is described in the standard WinBUGS pseudo-code. We can improve the efficiency of fitting the model in some restricted cases (e.g., when λ_0 is not time varying) by recognizing that the total number of captures of each individual in trap j is a binomial random variable based on a sample of size K. Then, the data can be reduced to the $n \times J$ matrix of capture frequencies (number of captures out of K samples).

INFERENCE WHEN N IS UNKNOWN

While we have described the models conditional on the variables s_i, $i = 1, 2, \ldots, N$, they are unobservable quantities. Conceptually, these can be thought of as random effects in the usual sense of the concept as it is used in classical statistics. For analysis of random effects models, we adopt a prior distribution ("random effects distribution") for **s** and proceed with standard methods for analyzing such models. Precisely how we proceed depends in large part on whether we adopt a classical approach to the analysis of random effects or a Bayesian approach. In the classical treatment of random effects, we would remove them from the likelihood by integration. This was the strategy recently adopted by Borchers and Efford (2008) in a similar class of spatial capture–recapture models. Alternatively, Bayesian analysis of the random effects model is relatively straightforward. We have previously specified this random effects distribution under the binomial point process as

$$\mathbf{s} \sim \text{Uniform}(S).$$

```
model {
    sigma~dunif(0,5)
    lam0~dgamma(.1,.1)

    for(i in 1:nind){
        for(j in 1:ntrap){
            dist2[i,j]<- ( pow(sx[i]-trap[j,1],2)  +  pow(sy[i]-trap[j,2],2) )
            mu[i,j]<- 1-exp( -lam0*exp(-dist2[i,j]/sigma) )
            for(k in 1:K){
                y[i,k,j] ~ dbern(mu[i,j])
            }
        }
    }
}
```

FIG. 2. WinBUGS model specification for the Bernoulli encounter model when $\mathbf{s}_i$ are known for $i = 1, 2, \ldots, N$ independent centers (where $\mathbf{s}_i$ is a two-dimensional coordinate representing a point in space about which the movements of individual i are concentrated). In this model description, sx and sy are the x- and y-coordinates of each individual activity center, respectively.

Whereas when N is known, the model is just a form of generalized linear mixed model (with random effects $\mathbf{s}_i$), the difficulty in analyzing the model with unknown N is that the dimension of the parameter space (the number of "random effects") is itself an unknown quantity. It is this problem that motivated the analysis of similar models using the method of data augmentation (Royle et al. 2007, Royle and Dorazio 2008). In effect, data augmentation allows us to analyze a version of the "complete data" model: the model with a fixed number of activity centers.

To implement data augmentation, we physically augment the n observed encounter histories with some large number of "all-zero" histories, say $M - n$ such histories. In the present case, the encounter history for each augmented individual is the two-dimensional array of $J \times K$ zeros. We assume that this list of M pseudo-individuals includes the actual N individuals in the population as a subset. We must choose M sufficiently large so as that the posterior of N is not truncated. This can be achieved by trial and error with no philosophical or practical consequence. Given the augmented data set, the key result (Royle et al. 2007) is that the model for the augmented data is a zero-inflated version of the "known-N" model, i.e., that corresponding to the case where N is known. There are no additional parameters to estimate, but the parameter N is replaced by a zero-inflation parameter, say $1 - \psi$. The parameter ψ is the probability that an individual on the list of size M is a member of the population of size N that was exposed to sampling by the trap array.

Analysis by data augmentation has a formal Bayesian development, which can be motivated by the assumption of a discrete uniform prior for N on the integers $0, 1, \ldots, M$. This prior can be specified hierarchically in the form of a Binomial prior for N: $N \sim \mathrm{Bin}(M, \psi)$ and a uniform prior for ψ: $\psi \sim \mathrm{Unif}(0, 1)$. Integration of the binomial prior for N over the uniform prior for ψ yields the discrete uniform prior for N. This hierarchical specification is useful because it yields a convenient Bayesian implementation. Namely, we introduce $M - n$ observations of $y_i = 0$ for $i = n + 1, n + 2, \ldots, M$. For these individuals, there is no trap information and thus the encounter history record is $y_{ijk} = 0$ for all j and k as well. Given the augmented data set, we now introduce a set of latent indicator variable w_i, $i = 1, 2, \ldots, M$, such that $w_i = 1$ if the ith element of the augmented list is a member of the population of size N, and $w_i = 0$ otherwise (an "excess zero"). We impose the model $w_i \sim \mathrm{Bern}(\psi)$. With a uniform(0, 1) prior on ψ, the induced prior distribution on $N = \Sigma_i w_i$ is uniform on the integers $0, 1, \ldots, M$, as noted above.

Estimating derived parameters

In some instances, there will be interest in derived parameters. That is, parameters that are not canonical or structural parameters of the model (i.e., λ_0, σ, and ψ introduced by data augmentation). For example,

$$N(S) = \sum_{i=1}^{M} w_i$$

is the population size of individuals on the set S and $D(S) = N(S)/A(S)$ is the density on S (here, $A(S)$ denotes the area of S). Similarly, the number of activity centers in any prescribed polygon, say P, is the quantity denoted by $N(P)$. This is calculated by simply tallying up the number of $\mathbf{s}_i$ contained in P, and for which $w_i = 1$ (the data augmentation indicator variable), at each iteration of the Markov chain Monte Carlo (MCMC) algorithm. The resulting sequence of $N(P)$ (one value for each iteration of the MCMC algorithm) constitutes a sample from the desired posterior distribution. In addition, density, say $D(P) = N(P)/A(P)$, is also a derived parameter.

```
model {
    sigma~dunif(0,20)
    lam0~dgamma(.1,.1)
    psi ~ dunif(0,1)
    for(i in 1:nind){
        w[i]~dbern(psi)
        sx[i]~dunif(Xl,Xu)
        sy[i]~dunif(Yl,Yu)

        for(j in 1:ntrap){
            dist2[i,j]<- ( pow(sx[i]-trap[j,1],2)  +  pow(sy[i]-trap[j,2],2) )
            mu[i,j]<-w[i]*(1-exp(-lam0*exp(-dist2[i,j]/sigma)))
            y[i,j] ~ dbin(mu[i,j],K)
        }
    }
    N<-sum(w[1:nind])
}
```

FIG. 3. WinBUGS model specification for the Bernoulli encounter model for unknown $\mathbf{s}_i$ and N. In this model description, sx and sy are the x- and y-coordinates of each individual activity center, respectively.

Implementation

While developing the MCMC algorithm for analysis of the augmented data under the models is straightforward, we avoid those technical details because the model can also be implemented in WinBUGS. Applications of data augmentation in similar models can be found in Royle and Young (2008), Royle (2009), and Gardner et al. (2009). One detail that we have avoided discussion of is that Bayesian analysis requires that we specify prior distributions for model parameters. In the analyses below, we used a uniform(0, 1) prior for the data augmentation parameter ψ, and flat normal priors for any regression coefficients in the model, including the intercept, behavioral response and log($1/\sigma$) (as this is essentially a regression coefficient on the distance covariate). The WinBUGS specification of the Bernoulli model for unknown N is shown in Fig. 3. As shown in Fig. 3, the encounter histories have been aggregated over the number of sampling occasions. In that case, the total number of encounters of each individual, and in each trap, is a binomial random variable with sample size K, as indicated in Fig. 3. Additional models for the Poisson encounter model are given in the Appendix.

ANALYSIS OF NAGARAHOLE DATA

For the analysis of the Nagarahole data, we excluded areas that were judged to be non-habitat within a 15 km buffer area containing the trap array (Fig. 1). This renders the definition of a uniform prior for the activity centers difficult because the polygon is highly irregular. As such, we described this region of suitable habitat by a grid of 9961 equally spaced points, each representing approximately 0.336 km^2 over the buffered region. Of these, 4898 (1645.7 km^2) were judged to represent suitable habitat. The activity centers $\mathbf{s}_i$ were therefore assumed to be uniformly distributed over this discrete space of 4898 points, an area of approximately 1645.7 km^2. We developed an implementation of the model for this discrete state-space situation in the R programming language. The coordinate system was scaled so that a standard unit was 5 km, and thus also are the units of σ.

As described in *Spatial capture–recapture as a GLM with individual effects*, we considered the Bernoulli encounter model which allows a single capture per trap in each occasion. The general model considered was of the form

$$\text{cloglog}(\pi_{ijk}) = \alpha(1 - c_{ik}) + \beta c_{ik} - (1/\sigma)d_{ij}^2 \qquad (5)$$

where c_{ik} is an indicator covariate that takes on the value $c_{ik} = 1$ if individual i was encountered in a sample occasion prior to k. Here, we have reparameterized the intercept α in order to interpret α and β as the log-encounter intensity parameters for individuals pre- and post-encounter, respectively. Bayesian analysis of this model was carried out using flat priors for the regression coefficients α and β and for log($1/\sigma$). We considered also a model with a linear distance term, which corresponds to an exponential detection function as noted previously.

Given the simple formulation of the model for encounter probability as a generalized linear mixed model, we could conceivably extend the model to arbitrary levels of complexity. For example, time effects or individual heterogeneity (Dorazio and Royle 2003) could also be considered. However, because of the sparsity of our data set and low encounter rate (24 total recaptures), we made several intentional decisions to limit the complexity of the model. In particular, we have more sampling occasions than individuals (48 vs. 44), and they are short intervals (nightly), and so we opted

TABLE 2. Posterior summaries of model parameters for the tiger camera trapping data.

Parameter	Mean	SD	2.5%	Median	97.5%
Half-normal model					
σ	0.3130	0.0761	0.2010	0.3006	0.4957
α	0.0159	0.0043	0.0083	0.0150	0.0246
β	0.0297	0.0088	0.0149	0.0289	0.0478
$1/\sigma$	3.3734	0.7710	2.0172	3.3261	4.9742
ψ	0.4970	0.1008	0.3364	0.4839	0.7335
p_1	0.0157	0.0042	0.0082	0.0149	0.0243
p_2	0.0292	0.0086	0.0148	0.0285	0.0467
D	13.4132	2.6484	9.2968	13.0641	19.5658
Exponential model					
σ	0.2348	0.0328	0.1808	0.2317	0.3093
α	0.0435	0.0130	0.0224	0.0419	0.0688
β	0.0451	0.0187	0.0245	0.0379	0.0939
$1/\sigma$	4.3407	0.5925	3.2333	4.3159	5.5299
ψ	0.5078	0.1041	0.3367	0.4965	0.7521
p_1	0.0425	0.0124	0.0221	0.0411	0.0665
p_2	0.0440	0.0176	0.0242	0.0372	0.0897
D	13.7066	2.7508	9.3576	13.3679	20.2340

Notes: Summaries in the top half of the table correspond to the half-normal detection function, and summaries in the bottom half of the table correspond to an exponential distance function; 2.5% and 97.5% are posterior percentiles. The parameters p_1, p_2, and density, D, are derived parameters. Density units are individuals per 100 km^2, p_1 is the encounter probability for individuals that have not previously been encountered, and p_2 is the encounter probability for individuals subsequent to their initial encounter.

not to consider the additional complexity of temporal variation in detectability. We also did not consider individual heterogeneity in detection probability. Such models would be poorly identifiable with only 44 individuals (Dorazio and Royle 2003), and exhibit extreme sensitivity to model choice (Link 2003). We believe that spatial proximity of individuals to traps should be the predominant mechanism responsible for heterogeneity and seek to effectively model that phenomenon using the spatial covariate. In light of Link (2003), we believe that researchers should make their own judgment as to whether individual heterogeneity should be fit in addition to a spatial covariate because this is a decision that cannot be made objectively in small samples.

Results

Posterior summaries from fitting the model with the half-normal detection function (i.e., corresponding to a quadratic distance effect) and "behavioral response" to capture are given in Table 2. Recall that the number of unique individuals observed was 44. The estimate (posterior mean) of tiger density over S is 13.4 tigers/100 km^2, with a 95% posterior interval of (9.3, 19.6). We contrast these estimates with those reported for a misspecified multinomial observation model (Royle et al. 2009) who reported an estimated density over S of approximately 14.30 with a 95% posterior interval of (2.8, 20.5). We observe a similar estimate of density but a substantial increase in precision. The result suggests that the "non-encounters," which are independent observations under the Bernoulli model considered here, provide considerable information about model parameters. Note that the data set analyzed here has one fewer

individual, and so this contributes to the lower estimated density.

Fig. 4 shows the posterior density of the point process **s**. Each pixel is marked with $\log(E[N(\mathbf{s}) \mid \text{data}])$ where $N(\mathbf{s})$ is the number of activity centers located in pixel **s**. We note the extreme spatial variation and the high density in the western corner of the trap array which is an area known to have high prey densities (S. Kumar, *unpublished data*). The scale in Fig. 4, roughly −4 to −2, equates to a density range from approximately 0.14 to 0.018 (tigers per 0.336-km^2 pixel), respectively. Scaling these figures to 100 km^2 yields a density range between 5.35 and 42 tigers per 100 km^2. Thus the highest density areas have a density of eight times that of the lowest density areas.

The distance covariate appears to be highly important. The posterior mean of the coefficient, $1/\sigma$ is very positive and the posterior mass is concentrated away from 0 (95% interval: (2.017, 4.974)). There appears to be a moderate behavioral response to encounter in this model. The encounter probabilities (posterior means) for individuals pre- and post-initial encounter are $p_1 = 0.0157$ and $p_2 = 0.0292$, respectively. These are related to α and β according to $1 - \exp(-\alpha)$ and $1 - \exp(-\beta)$. Thus, once individuals are captured, there appears to be almost a doubling of encounter probability in subsequent occasions. The estimated difference is imprecise, however. The posterior probability of a positive response is $\Pr(\beta - \alpha > 0) = 0.92$. While a positive trap response ("trap-happiness") is indicated, this is not realistic biologically. We believe that this is likely a result of some non-independence among encounters. For example, if space usage (i.e., movement) is not random for individuals, we think this could appear as a

positive behavioral response. This might happen if individual tigers favor certain trails for moving about their territory.

We also fitted the exponential detection model (Table 2). We see that the summaries of N and density are little changed, and we don't have any intuition as to whether or not we would expect sensitivity in this regard. Interestingly, the behavioral response appears much less important (the posterior was nearly centered at 0).

Assessment of model adequacy

We evaluated the fit of each model using a Bayesian P value (Gelman et al. 1996). The basic idea is to describe a metric of model adequacy and then compare posterior draws of that metric to those obtained from data sets simulated from the posterior distribution. If we denote a posterior sample of this metric for the observed data set as $D_i^{(obs)}$ for posterior sample i and for a data set simulated from the posterior distribution as $D_i^{(new)}$, then the Bayesian P value is $\Pr(D_i^{(obs)} > D_i^{(new)})$. For a model that provides an adequate description of the data this should be near 0.50. Thus, extreme values (near 0 or 1) indicate a lack of model adequacy.

A practical problem with this approach in the context of the model under consideration is the lack of an obvious omnibus fit statistic. For our analysis we considered two distinct measures of model adequacy: One to assess the model's ability to describe the encounter frequency distribution and another statistic to evaluate the clustering of individual captures in space. For the former we considered a sum-of-squares between the observed trap and occasion encounter frequencies and their fitted values. That is, $FIT_1 = \Sigma_k (n_k - E[n_k])^2$ where n_k is the number of individuals captured k times (or in k traps). We aggregated the sum of squares of both components (traps and occasions). For the assessment of clustering (say FIT_2), we used recaptures of individuals to compute within-individual sum of squares of capture locations (this is analogous to the SSE of an ANOVA with individuals as blocks).

The spatial model with either half-normal or exponential detection functions showed about the same fit by both fit statistics. For the half-normal model the P values for FIT_1 and FIT_2 were 0.48 and 0.47, respectively. For the exponential model, the P values were 0.52 and 0.61. For comparison, we also computed the Bayesian P values for model M_0 which is the model described previously setting $1/\sigma$ and β to 0. The statistic based on encounter frequencies suggested a fit of that model as well ($P = 0.58$), which is perhaps not surprising given the sparsity of the observations (see Table 1). Conversely, the assessment of spatial clustering using FIT_2 indicated inadequacy of model M_0 ($P < 0.001$).

DISCUSSION

One of the fundamental objectives of many camera trapping studies is the estimation of abundance and density of the species under study. Historically, this
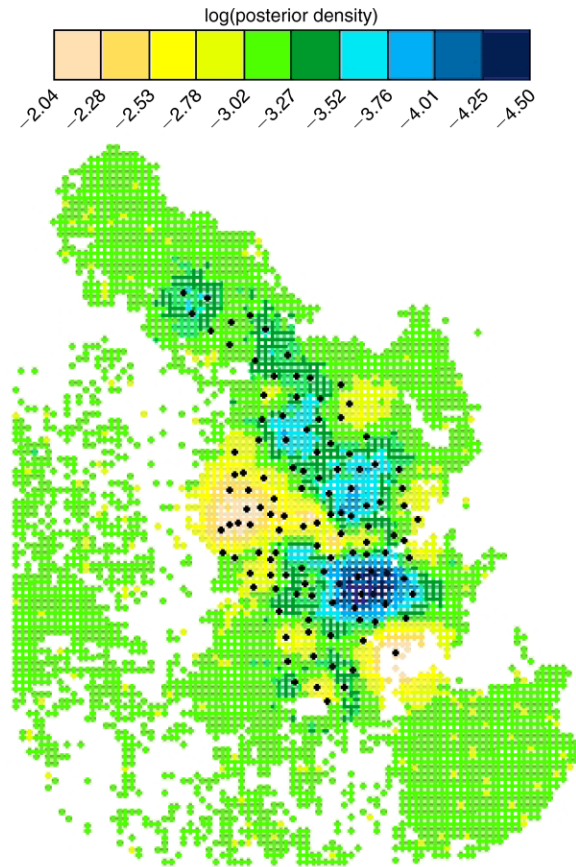

FIG. 4. Logarithm of the estimated posterior density of tigers in the Nagarahole reserve. Each pixel is marked with $\log(E[N(\mathbf{s}) \mid \text{data}])$ where $N(\mathbf{s})$ is the number of points at pixel $\mathbf{s}$. Lighter colors (yellow) indicate higher densities, while darker colors (blue) correspond to lower densities.

estimation problem has been addressed using a large number of essentially ad hoc or heuristic methods based on closed population capture–recapture estimators of population size applied to individual encounter history data. The conceptual limitation of closed population estimators is that, while the estimate of N may be valid in the sense of estimating the size of a population exposed to sampling, the effective sample area of the trapping array is unknown. Conventional methods have sought to estimate effective sample area using methods not formally linked (by a statistical model) to the observed spatial encounter history data. For example, N might be estimated by a conventional estimator of population size for closed populations, and then a buffer applied to the trapping grid based on observed movements of individuals. Because the underlying models are not specified precisely, they are not sufficiently flexible or extensible. For example, the formal treatment of multiple captures has not been integrated directly into such analyses.

Here we described a hierarchical modeling framework for inference from spatial capture–recapture data for

PLATE 1. Camera trap data from tigers in Nagarahole Reserve, India, have facilitated the development of spatially explicit capture–recapture models. Photo credit: WCS/K. U. Karanth.

trapping methods wherein the traps function independently of one another such that multiple encounters of an individual may occur during each sampling occasion. This is typical of camera trapping studies as well as other methods including DNA sampling from arrays of "hair snares." The spatial capture–recapture model is developed by conditioning the encounter history data on the realization of an underlying point-process that describes the distribution of individuals in space. This concept was first adopted in the context of spatial capture–recapture models by Efford (2004), and also exploited recently by Royle and Young (2008), Borchers and Efford (2008), and Royle et. al. (2009) for estimating density in the context of a multinomial observation model wherein an individual can be captured in only a single trap.

We noted that models in which traps function independently of one another can be formulated as generalized linear models (GLMs) with random effects (i.e., generalized linear *mixed* models; GLMMs), similar to other classes of models in capture–recapture including individual heterogeneity models ("Model M_h") and individual covariate models. For models in which individuals can be captured >1 time in a single trap, a natural model for the count frequencies is a Poisson model but obviously other models for count frequencies could be considered (see discussion below). A binary encounter model can be derived as a reduction of the model for the frequency encounter model (i.e., as the

event that $y > 0$). Technically, these spatial capture–recapture models are GLMMs only when N is known. In this case, the activity centers, **s**, are the random effects. When we allow for N to be unknown, the resulting models (when reformulated using data augmentation) are essentially zero-inflated versions of the corresponding generalized linear mixed models. Analysis of these models can be achieved in WinBUGS, which we believe makes them generally accessible to practitioners. However, in our analysis of the Nagarahole camera trapping data, we developed an implementation of the models in R for the case where the point process has a discrete state-space, allowing us to distinguish between suitable and unsuitable habitat. In addition to the conceptual and technical relationships between spatial capture–recapture models and generalized linear models, there is one other class of models that are similar in form to spatial capture–recapture models. If we consider aggregating total detections by trap, the Poisson model has a structural similarity to the Poisson-Gamma convolution models described by Wolpert and Ickstadt (1998) for modeling spatially indexed counts. However, in this case we have a single intensity parameter and allow the "support points" s_i to be unknown. Thus, potentially, the model developed here could be employed in similar contexts to that of Wolpert and Ickstadt (1998), perhaps permitting a lower-dimensional set of support points that adapts to the data.

While the Poisson model (or other model for count frequencies) might be applicable for some camera trapping studies because individuals can potentially be encountered multiple times at the same camera location during any particular sampling occasion, the data are often reduced to binary encounter events either for convenience or because recaptures are seldom independent within short sampling periods (i.e., nights). Another reason to reduce within-occasion recaptures to binary events is that attention to modeling the within trap/occasion variability becomes necessary. Moreover, this information may not be directly informative about density. Heuristically, information in spatial capture–recapture data originates from spatial clustering of recaptures. Thus, an individual that is only ever captured in the same trap is providing no information about the parameter that governs detection as a function of distance (σ in our model). Another reason to be concerned with modeling this extra source of variability is related to the results of Link (2003) who argued that N is not an identifiable parameter in individual heterogeneity models when the mixture distribution is not known. Consider adding an extra source of noise to the linear predictor (Eq. 5) in order to allow for extra-Poisson variation in trap-specific encounter frequencies. This type of heterogeneity, while seemingly natural to try to model, leads immediately to a model that resembles the classical individual heterogeneity model of the type that Link (2003) addressed. Thus, for most practical situations involving a small number of individuals, a priori limiting the complexity of the model is probably advisable.

We have adopted a Bayesian formulation of spatial capture–recapture models in this paper. However, these models could also be analyzed by integrated likelihood which is the technical approach adopted by Borchers and Efford (2008). However, we believe the hierarchical formulation adopted in our analysis (and in Royle and Young 2008) will prove more flexible in the development of model extensions. For example, a fundamental component of the hierarchical model is the underlying point process model that governs the distribution of individual activity centers. The models have been developed here under the assumption that individuals are distributed uniformly in space. As the underlying point process model is made more complex (e.g., containing interactions and conditional dependencies) the integration required for inference by integrated likelihood may become computationally prohibitive. However, Bayesian analysis of the hierarchical formulation only requires (in principle) the capability to carry out conditional simulation of the activity center locations. That is, we need only be able to simulate from general point processes in order to carry-out inference within a Markov chain Monte Carlo framework.

While extensibility of the point process model is a potential virtue of the Bayesian formulation of spatial capture–recapture models, we feel that the biggest practical advantage apparent at this time has to do with the validity of inferences achieved by Bayesian analysis. In particular, classical inference procedures are asymptotic and as such their relevance to small sample situations is questionable. Conversely, Bayesian inferences do not rely on asymptotic arguments and are valid regardless of the sample size. There seems to be a prevailing view in statistical ecology that classical likelihood-based procedures are virtuous because of the availability of simple formulas and procedures for carrying out inference, such as calculating standard errors, doing model selection by AIC, and assessing goodness of fit. In large samples, this is an important practical benefit of classical likelihood-based inference. However, the practical validity of these procedures cannot be asserted in most situations involving small samples. In the study which motivated our analysis, there were a total of 68 encounter events on 44 individuals. Only 24 of these are recaptures, from which the information about the encounter process is obtained. Reliance on conventional asymptotic procedures seems difficult to justify in this context. We note that the size of our data set is similar (or even larger) than many spatial capture–recapture studies on carnivores that we are familiar with, including a study of ocelots (Trolle and Kéry 2003), black bears (Gardner et al. 2009), Pampas cats in Argentina (B. Gardner, J. Reppucci, M. Lucherini, and J. A. Royle, *in review*), European wildcats in Switzerland (M. Kéry, B. Gardner, T. Stoeckle, D. Weber, and J. A. Royle, *unpublished manuscript*) and wolverines in Alaska (Magoun et al. 2008). We also believe that some restraint should be exercised in developing many (or overly complex) models for small data sets. While our framework is quite general and flexible in terms of model development (as a generalized linear mixed model) the ability to fit models of arbitrary complexity should not be perceived as a requirement to do so.

Modern technology has greatly advanced our ability to obtain information about the demography and population dynamics of secretive animal populations. Photographic identification, DNA from dung, and hair snares, or identification of individuals from scent dogs are now widely used in studies of many taxa. Almost universally these methods generate spatial encounter histories and also data which deviate from the standard multinomial structure of one capture per sample occasion. For such data, generalizations of the capture–recapture modeling framework, such as those models we have presented here, are necessary to make efficient use of sparse data that is typically expensive of both time and effort to obtain.

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APPENDIX

Analysis of the Poisson Encounter Model (*Ecological Archives* E090-230-A1).