Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies

Beth Gardner,[1,3] Juan Reppucci,[2] Mauro Lucherini,[2] and J. Andrew Royle[1]

[1]*U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA*
[2]*CONICET, GECM Mammal Behavioural Ecology Group, Departmento de Biologia, Bioquímica y Farmacia, Universidad Nacional del Sur, San Juan 670, 8000 Bahía Blanca, Argentina*

Abstract. We develop a hierarchical capture–recapture model for demographically open populations when auxiliary spatial information about location of capture is obtained. Such spatial capture–recapture data arise from studies based on camera trapping, DNA sampling, and other situations in which a spatial array of devices records encounters of unique individuals. We integrate an individual-based formulation of a Jolly-Seber type model with recently developed spatially explicit capture–recapture models to estimate density and demographic parameters for survival and recruitment. We adopt a Bayesian framework for inference under this model using the method of data augmentation which is implemented in the software program WinBUGS. The model was motivated by a camera trapping study of Pampas cats *Leopardus colocolo* from Argentina, which we present as an illustration of the model in this paper. We provide estimates of density and the first quantitative assessment of vital rates for the Pampas cat in the High Andes. The precision of these estimates is poor due likely to the sparse data set. Unlike conventional inference methods which usually rely on asymptotic arguments, Bayesian inferences are valid in arbitrary sample sizes, and thus the method is ideal for the study of rare or endangered species for which small data sets are typical.

Key words: Andes Mountains; Argentina; Bayesian analysis; camera trapping; data augmentation; hierarchical model; Jolly-Seber model; Pampas cats; spatial capture–recapture; trapping arrays.

Introduction

Estimating demographic parameters such as abundance (or density), survival, and recruitment, is a fundamental objective of many studies of animal populations, and such information is necessary in the conservation and management of any species. To that end, there are a large number of quantitative techniques used to obtain information about demographic parameters of populations. One broad class of methods, known as capture–recapture models (Seber 1965, Williams et al. 2002), is based on encounters of individuals resulting from repeated sampling of populations over time. Capture–recapture models represent a flexible class of methods that are in widespread use for many taxa. When applied to demographically closed populations (that is, populations not experiencing recruitment or mortality), these models provide information about population size, or density. A number of extensions (Cormack 1964, Jolly 1965, Seber 1965, Lebreton et al. 1992, Schwarz and Aranson 1996) relevant to demographically open systems allow for estimation of survival, recruitment, and other vital parameters.

Capture–recapture methods are classically applied to situations in which physical capture and marking of individuals is possible (e.g., live traps for small mammals, or mist nets for birds). However, recent advances in technology have spawned new methods of obtaining encounter data on wildlife populations without having to physically capture individuals. Two passive or noninvasive sampling methods that are growing in popularity include DNA sampling methods (Woods et al. 1999, Mowat and Strobeck 2000, Boulanger and McLellan 2001, Mulders et al. 2007) and camera trapping (Karanth 1995, Karanth and Nichols 1998, Trolle and Kéry 2003, Jackson et al. 2006). These methods make the application of capture–recapture models practical for many species for which they are otherwise impractical due to the difficulty of capturing individuals.

Spatial arrays of detection devices produce individual encounter histories for which capture–recapture methods may be applied. However, they also yield auxiliary spatial information in the form of a location of capture for each encounter. Historically, this information has either been discarded or used to compute ad hoc adjustments to nominal trap area based on observed movements so that an estimate of density could be obtained. To date, recent work on formalizing the use of spatial information to obtain density estimates has focused on closed populations (Efford 2004, Borchers

and Efford 2008, Royle and Young 2008, Gardner et al. 2009). There have been no formal treatments of auxiliary spatial information in open population models. However, Karanth et al. (2006) apply a Jolly-Seber model, and then adjust the effective trap area based on heuristic considerations in order to estimate density, as is commonly done in closed population studies (Karanth 1995, Karanth and Nichols 1998, Trolle and Kéry 2003).

In this paper, we develop a formal framework for parametric inference about density, survival, and recruitment in open populations from camera traps and related methods that produce encounter history data and auxiliary spatial data. Our modeling framework is based on a formulation of a Jolly-Seber type model that is amenable to modeling individual effects, including individual covariates. We extend this model by describing the encounter history data as a function of a latent variable (a random effect) interpreted as an individual's activity (or home range) center. Inference under this hierarchical model is formalized by Bayesian analysis using a method known as data augmentation (Tanner and Wong 1987, Royle et al. 2007).

While we expect the extension of spatial capture–recapture models to open populations to have broad applicability, we emphasize the importance of the Bayesian framework for inference in small samples sizes. Classical inference methods based on likelihood are asymptotic and thus of questionable utility in many practical situations where studies of rare or elusive species produce very small data sets. This is common in studies of carnivores which occur at low densities even for common species, but especially in rare species that are of special conservation concern and therefore the primary focus of considerable field work that generates spatial encounter history data. Attention to the importance of small sample inference in the capture–recapture literature has been very limited; however, we believe that this should be addressed explicitly in all applications of statistical procedures to studies of rare species.

Development of this open population modeling framework was motivated by a study of the Pampas cat (*Leopardus colocolo*) in Argentina, which we report on in this paper. This camera trapping study was conducted in 2006 and 2007 in the Jujuy province of Argentina. We note that this highly elusive cat is difficult to trap, even using camera trapping methods. This results in very small sample sizes in any given year. Nevertheless, interest in this species necessitates a rigorous treatment of available data, and the use of open population models provides the most efficient manner in which to integrate multiple years of sparse data for the purpose of obtaining vital rate estimates for the species.

Methods

Spatial capture–recapture model

We suppose that sampling occurs at J camera trap locations (traps) with coordinates $\{\mathbf{x}_j = (x_{1j}, x_{2j}); j = 1, 2, \ldots J\}$. The observations from camera trapping studies are encounter histories y_{ijk}, for individual $i = 1, 2, \ldots, n$, trap $j = 1, 2, \ldots, J$, and sample occasion $k = 1, 2, \ldots, K$. Typically k indexes daily or other discrete intervals. Each individual can be captured in any number of traps during a particular sampling occasion, and can be captured an arbitrary number of times when the cameras are functioning properly. Thus, the observations y_{ijk} are encounter frequencies, the number of times that individual i is captured in trap j during sample k, and $y_{ijk} = 0$ indicates that the individual was not captured.

In the context of closed populations, the basic strategy for modeling spatial encounter history data is to augment the standard observation model for a closed population with a point process model describing the distribution of individual home range centers, territories, or "activity centers." Poisson (Efford 2004, Borchers and Efford 2008) or binomial (Royle and Young 2008, Gardner et al. 2009) point process models have been adopted in closed population applications. These models assume that the N activity centers, $\mathbf{s}_i = (s_{1i}, s_{2i})$; $i = 1, 2, \ldots, N$, are distributed uniformly over some region S

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

for each $i = 1, 2, \ldots, N$, where S is the state-space of the point process. Thus, the probability density function for the latent variables $\mathbf{s}_i$, which are assumed to be independent, is constant over S. The state-space S is chosen as an arbitrarily large region containing the sampling devices or suitable habitat.

The key concept underlying spatial capture–recapture models is the linkage of this notion of individual activity center to encounter observations. For camera trap studies in which individuals can be encountered repeatedly by any camera during an interval, a natural model is to assume that encounter frequencies are Poisson random variables where the Poisson mean is a function of the distance between $\mathbf{s}_i$ and each trap, i.e.,

$$y_{ijk} \sim \text{Pois}\left(\lambda_0 g(\mathbf{s}_i, \mathbf{x}_j)\right)$$

where y_{ijk} is the encounter frequency for individual i in trap j during interval k and $g_{ij} \equiv g(\mathbf{s}_i, \mathbf{x}_j)$ is a decreasing function of distance between individual activity center $\mathbf{s}_i$ and trap $\mathbf{x}_j$. We assume that $g(\mathbf{s}_i, \mathbf{x}_j) = \exp(-d_{ij}^2/\sigma^2)$, where $d_{ij} = ||\mathbf{s}_i - \mathbf{x}_j||$ is the Euclidean distance between individual i's activity center and trap j and σ is a parameter that determines the rate of decline in detection rate at a trap as a function of distance. This choice of g is a common detection function in distance sampling (Buckland et al. 2001), and other applications (Efford 2004). The expected number of captures is λ_0 when an individual's activity center is located precisely at that trap.

Note that

$$\log(E[y_{ijk}]) = \log(\lambda_0) + (-1/\sigma^2)d_{ij}^2$$

and thus the basic model is a Poisson regression model with distance as a "covariate." In fact, because the individual activity centers are unknown (they are regarded as "random effects"), distance is a latent variable and the resulting model is a type of generalized linear mixed model (GLMM; Royle et al. 2009) similar to classical individual covariate models (e.g., Royle 2009). Given this representation, σ^2 is the inverse of the regression coefficient on distance-squared. It can be related to movement rates or home range size in some circumstances (Royle and Young 2008). Formal inference can be achieved either by classical methods based on integrated likelihood, wherein the random effects are removed from the likelihood by integration (Borchers and Efford 2008) or by Bayesian analysis of the conditional model directly (Royle and Young 2008, Gardner et al. 2009).

Alternative observation models can be considered. For example, it is common practice to reduce y to a binary encounter history which can be related to the Poisson encounter rate model by specifying $\Pr(y=1) = 1 - \exp[-\lambda_0 g(\mathbf{s}_i, \mathbf{x}_j)]$ (Royle et al. 2009). Also, the Poisson model gives rise, by conditioning, to a class of multinomial observation models, i.e., "single catch" trapping devices, where an individual can only visit one trap per sample interval (Borchers and Efford 2008).

Open populations

Natural populations experience mortality and recruitment over time. The standard framework for modeling open populations is based on the Jolly-Seber model (Jolly 1965, Seber 1965). Data arise from repeated sampling over seasons or years (*primary* sample periods) within which one or more samples (e.g., nights) might be taken (often referred to as *secondary* or sub- samples), a sampling design referred to as the "robust design" (Pollock 1982). While this subsampling structure is not necessary to estimate parameters of open population models, this data structure is common due to the historical treatment of data from these studies using classical capture–recapture methods (e.g., Karanth and Nichols 1998, Karanth et al. 2006). Moreover, it often becomes necessary to consider explicit time-varying covariates in models for encounter rate. As such, we develop a general formulation of open models that accommodates robust design data structure, keeping in mind that the case $K = 1$ (i.e., no formal secondary periods) is a special case.

To extend our spatial model to open populations, we adopt the individual-level parameterization of the Jolly-Seber model described in Royle and Dorazio (2008) in which a model for the observations is described conditional on the latent state variables $z(i, t)$, the "alive state," which describe whether individual i is alive ($z(i, t) = 1$) or not ($z(i, t) = 0$) during each of $t = 1, 2, \ldots, T$ *primary* periods.

The observation model is equivalent to that described above for closed population models (*Spatial capture–*recapture model*), but it is conditional on the state variable $z(i, t)$. In particular, let y_{ijkt} indicate the observed encounter frequency for individual i in trap j, during sample $k = 1, 2, \ldots, K$ of primary period t. The Poisson observation model, specified conditional on $z(i, t)$, is

$$y_{ijkt} \mid z(i, t) \sim \text{Pois}\big(\lambda_0 g_{ij} z(i, t)\big).$$

Thus, if individual i is alive at time t ($z(i, t) = 1$), then the observations are Poisson. Conversely, if the individual is not alive ($z(i, t) = 0$), then the observations must be zero with probability 1. Therefore, the model is a form of zero-inflated Poisson regression model.

The dynamics of the open population are manifest in a model for the latent state variables $z(i, t)$ describing individual mortality and recruitment events. An important aspect of the hierarchical formulation of the model that we adopt here is that the model for the state variables is described conditional on the total number of individuals ever alive during the study (a parameter we label N) based on T periods, as in Schwarz and Arnason (1996). This induces a special interpretation on the latent state variables $z(i, t)$. In particular, "not alive" includes individuals that have died, or individuals that have not yet been recruited. Using this formulation simplifies the state model and also allows it to be implemented directly in the WinBUGS software (Royle and Dorazio 2008). For example, considering the case $T = 2$ (the Pampas cat data is based on two primary periods; see Appendix B for a description of the process in the case of $T > 2$), the state model is composed of the following two components: First the initial state is described by

$$z(i, 1) \sim \text{Bern}(\gamma_1)$$

where γ_1 is the probability that an individual is alive at time 1 of the study. Second, a model describing the transition of individual states from $t = 1$ to $t = 2$ is given by

$$z(i, 2) \sim \text{Bern}\big(\phi z(i, 1) + \gamma_2[1 - z(i, 1)]\big).$$

Thus, if $z(i, 1) = 1$, then the individual may survive (apparent survival) with probability ϕ; whereas, if $z(i, 1) = 0$, then the individual may be recruited with probability γ_2. While the state model is conditional on N, we must deal with the fact that N is unknown (see *Bayesian analysis*). Note that under this parameterization of the Jolly-Seber model (Schwarz and Arnason 1996), recruitment parameters are interpreted as "conditional entrance probabilities" and not per-capita recruitment. Also note that, conditional on N, then $\gamma_2 = 1 - \gamma_1$ and standard applications using likelihood methods focus on estimating N and $T - 1$ recruitment parameters, while the Tth recruitment parameter is derived as a function of the other two. In Bayesian analysis by data augmentation (*Bayesian analysis*) we

estimate directly T recruitment parameters and N is a derived parameter, total number ever alive.

We extend the model of individual encounter histories by specifying an additional model component that describes the spatial distribution of individual activity centers. A plausible null model for the distribution of individual activity centers is to assume they are static over time, i.e., $s_i \sim \text{Unif}(S)$. One of the key demographic parameters to be estimated is the population density which is equivalent to the density of individual activity centers in the region S. While this model is exceptionally simple, we adopt it in our analysis of the Pampas cat data due to the sparsity of the data. However, with larger data sets having more recaptures (and hence more information about individual location) we could allow the activity center to change across years. One possibility is to assume that $s(i, t) \sim \text{Normal}[s(i, t - 1), \tau_2\mathbf{I}]$ for $t > 1$ so that individual home range centers are perturbed randomly from their previous value. Using such models we could conceivably test hypotheses about home range dynamics. We note the conceptual and technical parallels of spatial capture–recapture models with individual covariate models. See Bonner and Schwarz (2006), King et al. (2008), and Royle and Young (2008) for some context related to time-varying individual covariates.

Modeling time effects either within or across primary periods is technically straightforward, though potential issues may arise with the estimation and identifiability of parameters which should be examined further. To include time effects, define $\lambda_0 \equiv \lambda_0(k, t)$ and then we can develop log-linear models for $\lambda_0(k, t)$ as in ordinary Poisson regression (trap-specific effects could be modeled analogously). We note that formal regard of the sampling within primary periods is not necessary unless time-varying covariates are being modeled. Clearly if K samples are made in a given primary period then an individual's encounter frequency is Poisson with mean $K\lambda_0 g_{ij}$. Thus, the data can be reduced to "total" encounters per primary period, which does not affect the basic model structure outlined above.

Bayesian analysis

Spatial capture–recapture models can be formulated as generalized linear models (GLMs) with random effects corresponding to the activity centers, s (Royle et al. 2009). Bayesian analysis is a natural paradigm for inference in such models because general algorithms exist for simulating from the posterior given the model as specified conditional on the random effects. The fundamental challenge in carrying out inference under this model is that the parameter N (the total number of individuals alive during at least one time period) is not known. To accommodate this difficulty, we use a general method known as data augmentation (Tanner and Wong 1987) adapted to general capture–recapture type models by Royle et al. (2007) and applied in closed

population models by Royle and Young (2008) and Gardner et al. (2009).

Formally, data augmentation (DA) is equivalent to assuming a Uniform(0, M) prior for the parameter N, for M sufficiently large (Royle et al. 2007), which is a natural non-informative prior for N. A convenient formulation of this uniform prior (Royle et al. 2007) is equivalent to "zero-inflating" the data set (i.e., augmenting the data) with a large number, say $M - n$, of "all zero" encounter histories corresponding to hypothetical individuals that were not captured. The model for the augmented data is a zero-inflated Poisson (or binomial depending on the nature of the observations) which can be analyzed without difficulty. See Royle and Dorazio (2008: chapters 9 and 10) for additional context.

As a result of the reparameterization of the model under DA, the interpretation of the recruitment parameters γ_t is affected. In particular, data augmentation creates a population of available recruits that is depleted over time. The γ_t parameters are therefore the marginal probabilities that one of these available recruits enters the population at time t. It can be shown (Royle and Dorazio 2008: chapter 10) that the conditional entrance probabilities are confounded with a zero-inflation parameter introduced by DA (i.e., the parameter ψ in Royle et al. 2007). Specifically, under DA, recruitment parameters are the product of conditional entrance probabilities and ψ. Thus, use of DA in the open population model merely changes the interpretation of the recruitment parameters so that recruitment is expressed relative to the number of "available recruits" in the augmented data set of size M, and not the population size at time t. We note that alternative parameterizations are possible, see Royle and Dorazio (2008: chapter 10).

While the model is not parameterized directly in terms of annual population size, N_t, or per-capita recruitment, R_t, these parameters can be derived as a function of the latent state variables $z(i, t)$. In particular, the total number of individuals alive at time t is

$$N_t = \sum_{i=1}^{M} z(i, t)$$

and the number of recruits is

$$R_t = \sum_{i=1}^{M} \big[1 - z(i, t - 1)\big] z(i, t)$$

which is the number of individuals *not* alive at time $t - 1$ but alive at time t. Finally, we are interested in estimates of density, which is the number of individual activity centers in S divided by its area:

$$D_t = N_t / \|S\|$$

where $\|S\|$ is the area of S. An advantage of our formulation of the JS model using data augmentation is
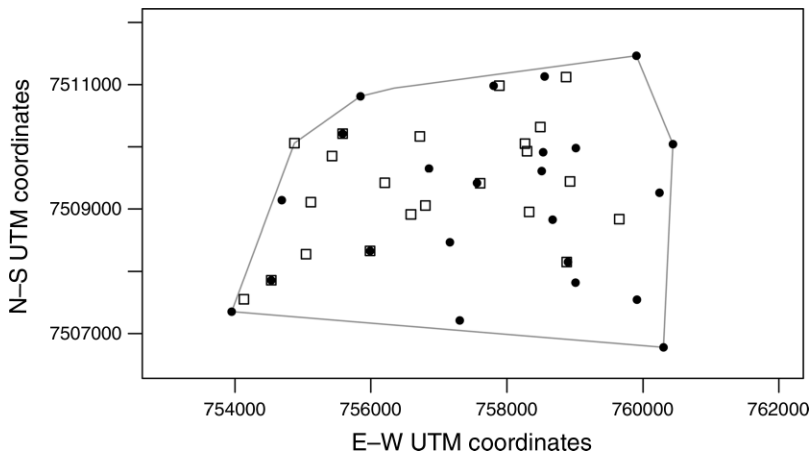
Fig. 1. The study area is shown in UTM Zone 19 South coordinates. The squares are the trap locations for 2006, and the circles are the trap locations for 2007. Some trap locations are the same in both years. The convex hull of all the trap locations is shown by the outline that encloses the symbols.

that it can be implemented directly in WinBUGS (Gilks et al. 1994) (model specification is provided in Appendix A).

Simulation study

Due to the small sample size in the study that motivated development of the model (see next section), we evaluated estimates obtained by this model in small-sample situations using a Monte Carlo simulation study. We simulated situations with average population sizes (for all years) of 50, 100, and 200 individuals in the state-space and varied the detection rate parameter to produce typical data sets of 16 to 164 captured individuals over a three-year time frame. We expect that estimators will generally exhibit bias in realistic (i.e., small) sample sizes and wish to evaluate the degree of bias and relative precision of estimators. See Appendix C for details on the simulation study design.

APPLICATION

Data collected from a camera trapping study on Pampas cats in northern Argentina motivated the development of this model (see Appendix A for more details on the study area and data). This study was conducted during $T = 2$ periods, separated by approximately six months (October–December 2006 and April–June 2007) using an irregular array of camera traps. Thus the model contains a single partial year survival probability parameter and a per capita recruitment parameter. Sampling within each time period was subdivided into weekly intervals. We assume that the observed individual- and camera-specific encounter frequencies follow the Poisson encounter model. We note that trap locations moved within and among years (Fig. 1, see Appendix A). A total of 22 individuals were identified by their unique coat spot patterns. The area of a convex hull placed over the trapping array was approximately 23 km^2. In the analysis, we defined the

state-space of the point process (i.e., the region S) to be a rectangle of 168 km^2 containing the convex hull of the study area.

An assessment of the model fit was computed using a Bayesian P value (Gelman et al. 1996), producing a P value of 0.72, indicating that the model adequately describes the data. The posterior mean of ϕ was 0.79 and the posterior mean for the per capita recruitment (R/N_1) was 0.24 (Table 1). We note that these parameters should be interpreted as *apparent* survival and recruitment because the population is susceptible to permanent emigration and immigration which affect estimators of survival and recruitment, respectively. For example, individuals that move off of the study area permanently appear (under the model) as mortalities and this leads to a negative bias in estimates of ϕ.

The estimated population sizes (posterior means), i.e., the number of activity centers, for the area of S was 125.00 and 131.51 for 2006 and 2007, respectively (Table 1). Density (D_1 and D_2) is derived as the number of Pampas cats per 1 km$_2$, i.e., by standardizing N_t by the area of S. The estimated density per 1 km^2 was 0.74 with a 95% posterior interval of (0.30, 1.48) in 2006 and 0.78 with a 95% posterior interval of (0.30, 1.46) for 2007 (Table 1).

The parameter λ_0 corresponds to the expected capture frequency of some individual whose activity center is located precisely at a trap location, the posterior mean estimate was 0.02 (Table 1). Thus, the probability of capture for such an individual is: $1 - \exp(-\lambda_0) = 0.02$. The estimated posterior mean for σ was 1.91 (Table 1).

The model can be used to produce spatial maps of density or individual locations. One useful summary is a map of the posterior density of activity centers which is $E[N(b) \mid \text{data}]$, where $N(b)$ is the number of activity centers located in a pixel b. The posterior densities of both captured and uncaptured individuals are shown in Fig. 2. We note that the resulting posterior density is not

TABLE 1. Posterior summaries of model parameters for the Pampas cat trapping data.

Parameter	Mean	SD	2.5%	Mode	97.5%
N_1	125.00	51.02	50.00	97.52	248.00
N_2	131.51	49.71	55.00	97.05	246.00
D_1	0.74	0.30	0.29	0.57	1.48
D_2	0.78	0.30	0.32	0.56	1.46
σ	1.91	0.43	1.25	1.69	2.87
λ_0	0.02	0.01	0.01	0.02	0.04
ρ	0.24	0.22	0.01	0.22	0.82
ϕ	0.79	0.15	0.44	0.88	0.98

Notes: The number of unique individuals observed over both years was 22. N_1 and N_2 are the number of estimated activity centers in the boundary box (S) for 2006 and 2007, respectively. Density (D_1 and D_2) is calculated as the number of Pampas cats per 1 km². The per capita recruitment, ρ, is R/N_1. The units of σ, the shape parameter in the detectability function, are given in kilometers. The expected number of encounters per interval for an individual with an activity center located precisely at a given trap is λ_0. The apparent survival between the two sampling seasons is ϕ.

uniform and indicates some areas of higher density within the study area, as well areas of lower density.

Our simulation study results suggest that the model provides good estimates for the survival parameters (ϕ_1 and ϕ_2), σ, and λ_0, with little bias in the estimates across nine different cases of $N = 200$, 100, and 50 and $\lambda_0 = 0.05$, 0.10, and 0.20. Using the posterior mean as a point estimator of N (or density) exhibits relatively high bias in small sample situations due to strong skew of the posterior distribution. However, a point estimator based on the posterior mode shows much lower bias. For a case producing similar sized data sets to our study (specifically $N = 100$, $\lambda_0 = 0.05$), point estimators of N exhibit fairly high levels of bias (15–25%) due to extreme posterior skew. However, coverage of posterior intervals was 94.33% across all three years, which is only slightly less than the nominal 95%.

DISCUSSION

We developed a hierarchical extension of the Jolly-Seber model for modeling spatially explicit encounter history data. The model generalizes existing Jolly-Seber type models by allowing for temporary emigration via movement of individuals onto and off the trapping array, and it generalizes existing spatial capture–recapture models (Efford 2004, Borchers and Efford 2008, Gardner et al. 2009, Royle et al. 2009) by allowing violation of demographic closure. Our model allows for explicit estimation of density as well as population vital rates (survival, recruitment) for species that are studied by camera trapping and related methods. While our development was motivated by the need for an inference framework for a camera trapping study on the Pampas cat, it is applicable to other sampling methods that produce spatial encounter history data on geographically and demographically open populations, such as
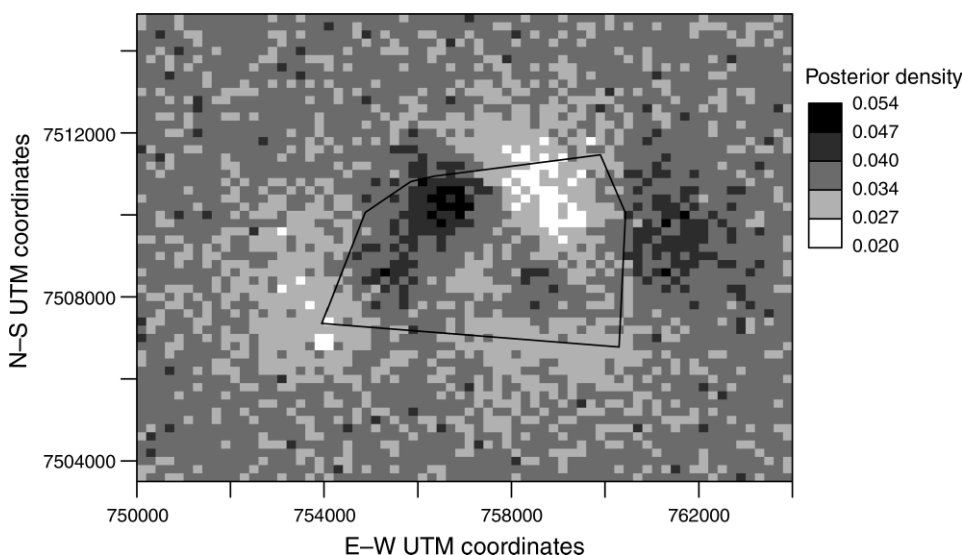

FIG. 2. Map of the posterior density of activity centers from both years of the study. Specifically, the map shows $E[N(b)\,|\,\text{data}]$, where $N(b)$ is the number of activity centers located in a pixel b. The convex hull around the trap array (the polygon) is shown; the map is displayed in UTM Zone 19 South coordinates.

data arising from DNA sampling from hair snares or scat (Gardner et al. 2009) or mist net studies of bird populations.

Many rare and elusive species are difficult to capture which can lead to sparse data sets for species of conservation concern, despite intensive efforts and substantial funding directed at the study of such species. As a result, there have been few attempts to estimate densities of elusive felids, such as the Pampas cat. In our example, only 22 individual Pampas cats were captured during the two-year period. Similar studies report small sample sizes as well; for example, Trolle and Kéry (2005) reported only nine individual ocelots captured, and Jackson et al. (2006) captured six individual snow leopards using camera trapping. In such cases, multiple years of data are required to get enough recapture information for estimating population abundance or density. In our Pampas cat study, there were 15 individuals captured in 2007, of which 13 were captured only one time during that year. However, of those 13 individuals, five of them were also captured in 2006, thus providing considerably more direct information about the encounter process which can be used to better inform the model. In order to collect enough data for estimating density, many studies on rare species must be conducted over large time periods or multiple years which necessarily violate the demographic closure assumptions of current spatial capture–recapture models. Thus, open population models that enable statistical aggregation of data (e.g., combining data across years) are essential for making efficient use of available data, in addition to allowing for estimation of population vital rates.

Gathering reliable information on evasive species is often difficult, and yet it is invaluable because these species are typically of the highest conservation concern (Thompson 2004). Carnivores of the High Andes, including the Pampas cat and the endangered Andean cat, considered one of the rarest felids in the world, are among the least studied (Napolitano et al. 2008). Basic knowledge of population demography is necessary in order to make appropriate management and conservation decisions. The methodological framework developed here is useful not only for estimating density, but also is the first formal approach available for estimating vital rates (survival and recruitment) for the Pampas cat. Statistical approaches that provide rigorous inferences for small data sets resulting from studies of rare species can allow for a greater biological understanding and therefore aid the conservation and management of such species.

Literature Cited

Bonner, S., and C. Schwarz. 2006. An extension of the Cormack Jolly Seber model for continuous covariates with application to *Microtus pennsylvanicus*. Biometrics 62:142–149.

Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for capture–recapture studies. Biometrics 64:377–385.

Boulanger, J., and B. McLellan. 2001. Closure violation in DNA-based mark–recapture estimation of grizzly bear populations. Canadian Journal of Zoology 79:642–651.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, UK.

Cormack, R. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429–438.

Efford, M. 2004. Density estimation in live-trapping studies. Oikos 106:598–610.

Gardner, B., J. A. Royle, and M. T. Wegan. 2009. Hierarchical models for estimating density from DNA mark–recapture studies. Ecology 90:1106–1115.

Gelman, A., X. Meng, and H. Stern. 1996. Posterior predictive assessment of model fitness via realized discrepancies. Statistica Sinica 6:733–759.

Gilks, W., A. Thomas, and D. Spiegelhalter. 1994. A language and program for complex Bayesian modelling. Statistician 43:169–177.

Jackson, R. M., J. D. Roe, R. Wangchuk, and D. O. Hunter. 2006. Estimating snow leopard population abundance using photography and capture–recapture techniques. Wildlife Society Bulletin 34:772–781.

Jolly, G. 1965. Explicit estimates from capture–recapture data with both death and immigration: stochastic model. Biometrika 52:225–247.

Karanth, K. U. 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture–recapture models. Biological Conservation 71:333–338.

Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862.

Karanth, K., J. Nichols, N. Kumar, and J. Hines. 2006. Assessing tiger population dynamics using photographic capture–recapture sampling. Ecology 87:2925–2937.

King, R., S. Brooks, and T. Coulson. 2008. Analysing complex capture–recapture data in the presence of individual and temporal covariates and model uncertainty. Biometrics 64:1187–1195.

Lebreton, J., K. Burnham, J. Clobert, and D. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Mowat, G., and C. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark–recapture analysis. Journal of Wildlife Management 64:183–193.

Mulders, R., J. Boulanger, and D. Paetkau. 2007. Estimation of population size for wolverines *Gulo gulo* at Daring Lake, Northwest Territories, using DNA based mark–recapture methods. Wildlife Biology 13:38–51.

Napolitano, C., M. Bennett, W. E. Johnson, S. J. O'Brien, P. A. Marquet, I. Barría, E. Poulin, and A. Iriarte. 2008.

Ecological and biogeographical inferences on two sympatric and enigmatic Andean cat species using genetic identification of faecal samples. Molecular Ecology 17:678–690.

Pollock, K. 1982. A capture–recapture design robust to unequal probability of capture. Journal of Wildlife Management 46: 757–760.

Royle, J. A. 2009. Analysis of capture–recapture models with individual covariates using data augmentation. Biometrics 65:267–274.

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press, San Diego, California, USA.

Royle, J. A., R. M. Dorazio, and W. A. Link. 2007. Analysis of multinomial models with unknown index using data augmentation. Journal of Computational and Graphical Statistics 16:67–85.

Royle, J. A., K. U. Karanth, A. M. Gopalaswamy, and N. Kumar. 2009. Bayesian inference in camera trapping studies for a class of spatial capture–recapture models. Ecology 90: 3233–3244.

Royle, J. A., and K. Young. 2008. A hierarchical model for spatial capture–recapture data. Ecology 89:2281–2289.

Schwarz, C., and A. Arnason. 1996. A general methodology for the analysis of capture–recapture experiments in open populations. Biometrics 52:860–873.

Seber, G. 1965. A note on the multiple-recapture census. Biometrika 52:249–259.

Tanner, M. A., and W. H. Wong. 1987. The calculation of posterior distributions by data augmentation. Journal of the American Statistical Association 82:528–540.

Thompson, W. L., editor. 2004. Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters. Island Press, Washington, D.C., USA.

Trolle, M., and M. Kéry. 2003. Estimation of ocelot density in the Pantanal using capture–recapture analysis of camera-trapping data. Journal of Mammology 84:607–614.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Woods, J. G., D. Paetkau, D. Lewis, B. N. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging of free-ranging black and brown bears. Wildlife Society Bulletin 27: 616–627.

APPENDIX A

Details about Pampas cats and the Pampas cat study (*Ecological Archives* E091-239-A1).

APPENDIX B

Survival and recruitment for $T > 2$ (*Ecological Archives* E091-239-A2).

APPENDIX C

Details of the simulation study with the Jolly-Seber extension to our spatially explicit capture–recapture model (*Ecological Archives* E091-239-A3).

SUPPLEMENT

The R code with embedded WinBUGS specification to run the simulation study and a separate WinBUGS file with specification for the spatially explicit open population model used in the Pampas cat study (*Ecological Archives* E091-239-S1).