

A HIERARCHICAL MODEL FOR SPATIAL CAPTURE–RECAPTURE DATA

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Abstract. Estimating density is a fundamental objective of many animal population studies. Application of methods for estimating population size from ostensibly closed populations is widespread, but ineffective for estimating absolute density because most populations are subject to short-term movements or so-called temporary emigration. This phenomenon invalidates the resulting estimates because the effective sample area is unknown. A number of methods involving the adjustment of estimates based on heuristic considerations are in widespread use. In this paper, a hierarchical model of spatially indexed capture–recapture data is proposed for sampling based on area searches of spatial sample units subject to uniform sampling intensity. The hierarchical model contains explicit models for the distribution of individuals and their movements, in addition to an observation model that is conditional on the location of individuals during sampling. Bayesian analysis of the hierarchical model is achieved by the use of data augmentation, which allows for a straightforward implementation in the freely available software WinBUGS. We present results of a simulation study that was carried out to evaluate the operating characteristics of the Bayesian estimator under variable densities and movement patterns of individuals. An application of the model is presented for survey data on the flat-tailed horned lizard (*Phrynosoma mcallii*) in Arizona, USA.

Key words: abundance estimation; animal movement models; Bayesian analysis; data augmentation; density estimation; distance sampling; hierarchical modeling; *Phrynosoma mcallii*; spatial point process; trapping grid; trapping web.

INTRODUCTION

Estimating abundance is a fundamental goal of many animal sampling problems, and it forms the basis of a vast body of literature on statistical methods in animal ecology (e.g., Seber 1982, Williams et al. 2002). An important consideration in estimating abundance of most animal populations is that individuals cannot be observed perfectly. That is, the probability of encountering or detecting an animal is less than 1.0 in most survey situations. A number of methods for dealing with imperfect detection have been devised, including capture–recapture, its many variations, distance sampling (Buckland et al. 1993), and approaches that are more distinctly model based (e.g., Royle and Nichols 2003, Royle 2004).

However, an equally important component of sampling animal populations is the spatial organization of sample units, and individuals within the broader population that is the object of inference. That is, it is typically not possible to expose all individuals in the population at large to sampling. Instead, one must typically delineate sample units (or at least locations) that will be surveyed.

For example, suppose a 1-ha quadrat is delineated and surveyed. Animals that are encountered are uniquely marked, and the survey is repeated a number of times. It is natural to view the resulting capture–recapture data as being relevant to some form of a demographically closed population, provided the samples were close enough together in time so as to minimize mortality and recruitment. However, lacking a physical barrier around the sample plot, there is likely to be movement of individuals onto and off of the plot, resulting in a lack of geographical closure. This phenomenon of temporary emigration (Kendall and Nichols 1995, Kendall et al. 1997, Kendall 1999) in the simplest case (random temporary emigration) biases detection probability (p) low, hence abundance (N) high. Most importantly, temporary emigration means that the effective sample area is poorly estimated by the nominal, delineated area of the sample. That is, individuals near the borders of the sample unit have lower exposure to sampling, and those near the interior have a higher net exposure to sampling. Thus, while we might have a good quality data set in terms of information content, we do not know the effective area from which animals were sampled by the delineated sample unit. Considerable effort has been focused on the development of methods for estimating or approximating the effective sample area. See Parmenter et al. (2003) for a review of concepts and an extensive evaluation of some popular methods.

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In this paper, we propose a spatially explicit capture–recapture model that applies to area-search sampling wherein a delineated sample unit is searched thoroughly and all captured animals are uniquely marked. The process is repeated T times yielding spatially referenced capture histories on n unique individuals. That is, every time an individual is captured, a corresponding spatial location is recorded. Our approach is to parameterize a hierarchical model in terms of individual activity centers (which we formally describe mathematically here), and then a model for individual movement conditional on the activity centers. Finally, we specify a model for the observations conditional on the location of individuals during each sample occasion. The objective is to estimate absolute density of individuals in the survey plot. Under our model, this is accomplished by estimating the number of activity centers contained within the delineated sample unit. The model is hierarchical in the sense that a formal distinction is made (in the model) between the underlying process model, consisting of the model of individual activity centers and movement, and an observation model which describes the detection of individuals during sampling. When rendered in this way, the model is simple, concise, flexible, and extensible. We adopt a Bayesian analysis based on data augmentation (Royle et al. 2007). Using this approach, the model can be implemented in the freely available software WinBUGS (Gilks et al. 1994) with little more than a few lines of “pseudo-code” that describes the model. The model also produces an estimate of the relevant “super-population” of individuals that are exposed to sampling. Therefore, the method allows one to quantify temporary emigration explicitly without use of the “robust design” (see Pollock 1982, Kendall et al. 1997).

We apply the model to a capture–recapture survey of flat-tailed horned lizards (*Phrynosoma mcallii*) in southwestern Arizona. This species is difficult to monitor due to low densities and detection probabilities (Grant 2005, Grant and Doherty 2007), due in part to its cryptic coloration and habit of burying under the sand when approached (Wone and Beauchamp 1995; see Plate 1). In addition to being difficult to find, these lizards can move over fairly large distances, and movement varies annually (K. Young, *unpublished data*) and seasonally (Grant and Doherty 2006). Hence, even when capture–recapture techniques yield an estimate of p , estimating the effective sample area (and hence actual density) can be problematic due to movement or temporary emigration (Grant and Doherty 2007).

MODEL FORMULATION

Suppose that each individual in the population has a center of activity, or home range center. We will avoid associating a biological meaning to this concept, but instead provide a concise mathematical definition. The home range center for individual i is the point $\mathbf{s}_i = (s_{1i}, s_{2i})$, about which the movements of animal i are

distributed (in a manner to be described precisely) according to some probability rule.

Thus, \mathbf{s}_i ; $i = 1, 2, \dots, N$ represent the home range centers for all individuals in the population, which will be defined to be those individuals within some large region S that contains the sample unit as a strict subset. The sample unit (e.g., a transect, plot, or quadrat) will be denoted by the set $D \subset S$. We will assume that the \mathbf{s}_i are uniformly distributed over S . In practice, we will prescribe S (e.g., by specifying coordinates of some polygon that contains the sample unit). As an example, consider Fig. 1 (which is described more fully below). The smaller square is a hypothetical sample unit (i.e., D) of dimension 10×10 , and this is nested within a larger polygon (the dashed line), S , which is a square of dimension 16×16 . The need for a formal definition of S is related to the construction of the model (described subsequently). The model postulates, due to movement, that there are individuals captured having an \mathbf{s}_i that is located outside of the physical area that was sampled. The model therefore implies the existence of some S , and we must choose it to be sufficiently large so that it does not influence the parameter estimates. More practically, we specify the model in terms of a point process model that governs the distribution of the points \mathbf{s}_i , and we adopt a Bayesian approach to analysis of the model based on Markov chain Monte Carlo which requires that we simulate draws of each \mathbf{s}_i from the posterior distribution. We must therefore describe, explicitly, the region within which those \mathbf{s}_i are simulated, and that region is S . Essentially, S is a prior distribution on the potential location of captureable individuals.

We suppose that an individual moves around randomly according to some probability distribution function, $g(\mathbf{s}; \theta)$. We will denote the coordinates at sample times t as $\mathbf{u}_{it} = (u_{1,it}, u_{2,it})$ to distinguish them from the individual centers. In the application below, we suppose that the random variables (u_1, u_2) are independent normals so that $u_{1,it} \sim \text{Normal}(s_{1i}, \sigma_1)$ and $u_{2,it} \sim \text{Normal}(s_{2i}, \sigma_2)$. In practice, we do not observe the individual centers, \mathbf{s}_i , nor do we observe a complete set of $(u_{1,it}, u_{2,it})$ pairs for each individual due to imperfect sampling of individuals. We will describe the model for the observation process subsequently.

Given the observation model, we will devise the joint probability distribution of the observations and underlying process (the locations of the individuals), and this will enable us to estimate the number of individual activity centers located within the sample unit, or in any, arbitrary region of S .

The observation model

The previous description of the activity centers and time-specific locations of all individuals in the population constitutes the biological process component of the model. This is the process about which we would like to learn. As is typical in ecology, we cannot obtain perfect observations of this process. Instead, we must settle for

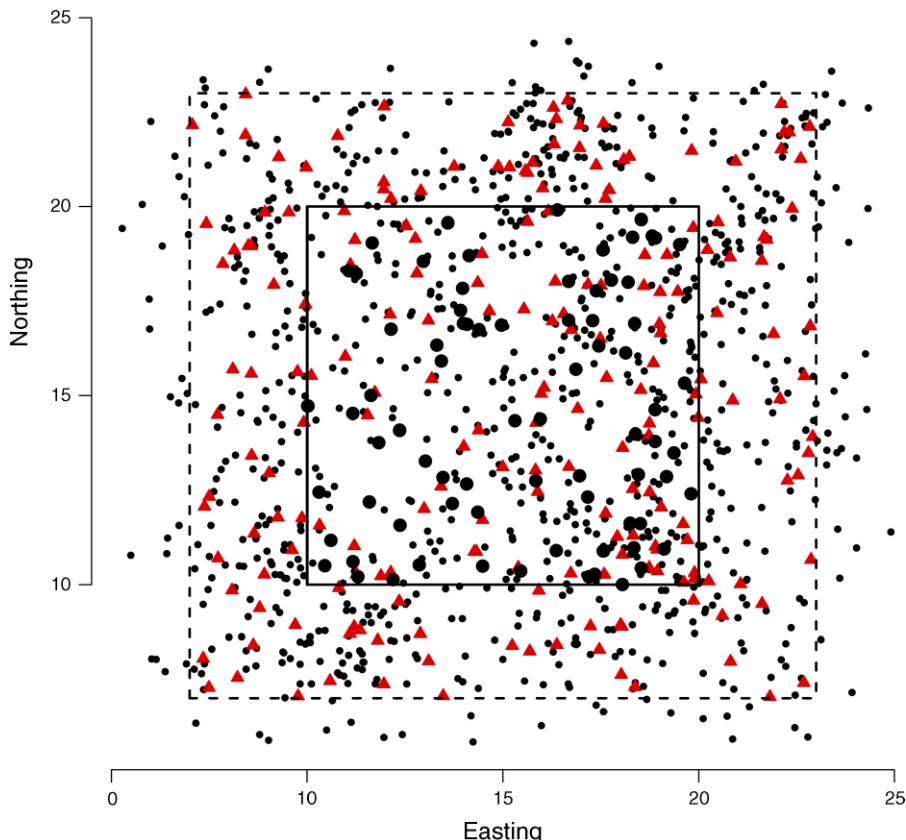


FIG. 1. Simulated 10×10 sample unit nested within S , a 16×16 square, containing 200 individual activity centers (red triangles) of which 46 are contained within the sample unit. The large and small black dots are all locations of each individual for each of $T = 5$ hypothetical survey occasions. The large black dots correspond to capture locations.

data that arise under some observation model that induces uncertainty about the underlying state process.

Let $y(i, t)$ be the binary observations indicating whether individual i is encountered during sample t [$y(i, t) = 1$] or not [$y(i, t) = 0$]. In practice, we obtain these encounter histories on $i = 1, 2, \dots, n \leq N$ individuals, which we will organize in the array $\mathbf{Y}_{n \times T}$. In addition to these encounter histories, there is a corresponding pair of coordinates $\mathbf{u}_{it} = (u_{1,it}, u_{2,it})$ for each occasion in which individual i was captured. We emphasize that the sample method addressed here is an “area search” and so these observed coordinates may be anywhere in D . They are *not* restricted to locations that correspond to trap locations. We require an observation model that describes the manner by which the \mathbf{u}_{it} pairs are observed. We only observe \mathbf{u}_{it} whenever $y(i, t) = 1$. Otherwise, the \mathbf{u}_{it} will be viewed as missing data.

The observation model is derived as follows. If \mathbf{u}_{it} is contained in D during the survey at t , then individual i is detected with probability p . Otherwise, the individual cannot be detected and $y(i, t) = 0$ with probability 1. That is, $y(i, t)$ is a deterministic zero in this case. These two possibilities are manifest precisely in the following model for the observations:

$$\begin{aligned}
 y(i, t) &= 0 && \text{if } \mathbf{u}_{it} \notin D \\
 y(i, t) &\sim \text{Bernoulli}[p(i, t)] && \text{if } \mathbf{u}_{it} \in D.
 \end{aligned}$$

As described here, we have assumed no behavioral response to capture (e.g., trap happiness or trap shyness), which we feel is sensible for the lizard survey described in *Flat-tailed horned lizard data*, which are captured by hand during an exhaustive area search by crews of several individuals. However, we have the usual flexibility for modeling $p(i, t)$, for example as a function of time or covariates, where such considerations are relevant.

This model is a special case of what are usually referred to as “individual covariate” models (see Pollock 2002). The individual covariate in this case is \mathbf{s}_i , and it is unobserved. Secondly, this model is a model of temporary emigration, under a more general form of temporary emigration than random temporary emigration considered by Kendall (1999).

Illustration: simulated data

Fig. 1 shows an example of a realization from the process model described above and the resulting pattern of observations. As noted previously, the sample unit is a square of dimension 10×10 units, and this is nested

within S , a larger square of 16×16 units. We simulated $N = 200$ individuals and subjected them to sampling with $p = 0.25$. Their movement was bivariate normal with $\sigma_1 = 1$ and $\sigma_2 = 1$. The small and large black dots are all locations of each individual for each of $T = 5$ hypothetical survey occasions (some of which are not captures). The large black dots were the actual capture locations within the sample unit.

In all, 81 of the 200 individuals had their center of activity (red triangles) within the sample unit. A total of 57 individuals were observed in the sample, and this included 46 individuals having their center of activity within the sample unit. The remaining 11 captured individuals were among the 119 having their centers outside of the sample unit. The 57 captured individuals were observed a total of 76 times during the five samples, with $p = 0.25$.

The statistical objective is to estimate the number of centers within the 10×10 sample unit, when confronted only with the capture histories of the 57 individuals, and the locations of the large black circles in Fig. 1. In the following Section, we describe a Bayesian analysis of this model, and its implementation in WinBUGS.

BAYESIAN ESTIMATION BY DATA AUGMENTATION

The model is a specialized case of the individual covariate models, wherein the individual effect is latent (i.e., unobserved). Analysis of the classical individual covariate or heterogeneity models using likelihood methods is relatively straightforward integrated likelihood (e.g., Coull and Agresti 1999, Dorazio and Royle 2003, Royle 2008). However, it is not immediately apparent how to carry out such an analysis in the present problem. In particular, the location of individuals at each sample occasion are realizations of a partially observed random variable, and they must be removed from the conditional likelihood by integration. Alternatively, Bayesian analysis can be accomplished very directly using methods of Markov chain Monte Carlo (MCMC). Within the MCMC framework, the unobserved locations are removed by Monte Carlo integration thus avoiding the necessity of explicit integration. We adopt a general strategy here based on a method of “data augmentation” (Tanner and Wong 1987). Here, we will avoid the technical details which justify the following, instead focusing on its heuristic motivation and practical implementation. The mathematical justification for a related class of models is given in Royle et al. (2007).

Data augmentation can be formally motivated by the assumption of a discrete uniform prior on N having support on the integers $N = 0, 1, \dots, M$ for some large M . Under a reparameterization, the model is equivalent (Royle et al. 2007) to physically augmenting the observed data set with a large number, $M - n$, of “all zero” encounter histories. Thus, the size of the data set (M) becomes a fixed quantity, and the model is reparameterized to be technically equivalent to what

are sometimes referred to as “site occupancy” models (e.g., MacKenzie et al. 2006). While the technical derivation is precise, the augmented zeros are something of an abstraction, corresponding to what one might call “pseudo-individuals,” only a subset of which are members of the population of size N that was exposed to sampling. We assert that M is sufficiently large so 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, we now introduce a latent indicator variable, say z_i $i = 1, 2, \dots, M$, such that $z_i = 1$ if the i th element of the augmented list is a member of the population of size N , and $z_i = 0$ otherwise. We impose the model $z_i \sim \text{Bernoulli}(\psi)$, where ψ will be referred to as the inclusion probability. This is the probability that an individual on the list of pseudo-individuals is a member of the sampled population of size N . Under this formulation, the resulting model is a zero-inflated version of the “known- N ” model, which provided some of the motivation underlying the formulation put forth by Royle et al. (2007). Specifically, $1 - \psi$ is the zero-inflation parameter, and ψ is related to N in the sense that $N \sim \text{Binomial}(M, \psi)$ under the model for the augmented data. This relationship between N and ψ has been noted elsewhere in the context of site occupancy models and closed population size estimation (Karanth and Nichols 1998, Royle et al. 2007).

While developing the MCMC algorithm for analysis of the augmented data is straightforward under this model, we avoid those technical details because the model can also be implemented directly in WinBUGS, which is the approach adopted here. We provide the WinBUGS implementation in the Supplement so that readers may experiment with the model and its analysis under various scenarios. Some results of simulations are provided in the following section.

MCMC methods obtain a sample of the model parameters from the posterior distribution by Monte Carlo simulation. Typically, a large sample of dependent draws from the posterior is obtained after an initial sample (referred to as the “burn-in”) is discarded to ensure that subsequent draws are being generated from the target distribution. There are many practical aspects to Bayesian analysis and MCMC which are discussed extensively in a large number of recent publications including the WinBUGS manual (Gilks et al. 1994), and recent review articles including Link et al. (2002) and Ellison (2004).

Within the MCMC framework, the individual activity centers are regarded as missing observations, and they are estimated by Monte Carlo sampling from the posterior distribution. That is, we obtain a sample of each $s_i^{(j)}$ for Monte Carlo iterations $j = 1, 2, \dots$. Various estimands of interest are derived parameters under the model formulation put forth here. For example, the parameter N is the number of individual centers in the region S , and this is obtained by calculating $\sum_{i=1}^M z_i$ for

TABLE 1. Summary of encounter history frequencies, expected number of individuals captured ($E[n]$), and mean detection probability ($E[p]$) for individuals in simulated populations.

σ	Density	Encounter frequency distribution						$E[n]$	$E[p]$
		0	1	2	3	4	5		
4	0.234	0.900	0.085	0.013	0.001	0	0	27	0.023
4	0.352	0.902	0.082	0.015	0.002	0	0	40	0.023
4	0.469	0.900	0.085	0.013	0.002	0	0	54	0.023
4	0.586	0.903	0.083	0.013	0.001	0	0	66	0.023
4	0.781	0.902	0.083	0.013	0.001	0	0	88	0.023
2	0.234	0.713	0.209	0.063	0.014	0.001	0	33	0.077
2	0.352	0.716	0.205	0.063	0.014	0.002	0	48	0.077
2	0.469	0.711	0.211	0.062	0.014	0.001	0	66	0.077
2	0.586	0.713	0.205	0.065	0.015	0.002	0	81	0.077
2	0.781	0.709	0.211	0.064	0.015	0.001	0	110	0.077
1	0.234	0.668	0.214	0.093	0.022	0.003	0	20	0.098
1	0.352	0.669	0.209	0.091	0.027	0.003	0	30	0.098
1	0.469	0.665	0.215	0.091	0.025	0.004	0	40	0.098
1	0.586	0.662	0.216	0.092	0.026	0.004	0	51	0.098
1	0.781	0.665	0.212	0.095	0.024	0.003	0	67	0.098

Notes: Populations were simulated under five levels of density, with movement rate parameter $\sigma \in \{1, 2, 4\}$. Density is the number of individuals per unit area; encounter history frequency distribution is the probability that an individual is captured 0, 1, 2, 3, 4, or 5 times. Individuals in simulated populations had home range centers within 2 SE of the trapping grid, and were subject to encounter on a 10×10 unit area.

each iteration of the MCMC algorithm. Similarly, the number of centers within the sample unit, $N(D)$, and the density of individuals (which is just a scaled version of $N(D)$), are derived parameters, which can be computed from the posterior draws of the individual activity centers. That is, we tally up those activity centers which are within D during each iteration of the MCMC algorithm. Our WinBUGS model specification does this explicitly using the WinBUGS model specification syntax (see Supplement).

EXAMPLES

Simulated data

The model was fit to the data set described in *Illustration: simulated data*. Recall that 81 of the 200 individuals had their center of activity within the sample unit, and, with $p = 0.25$, a total of 57 individuals were observed in the sample, including 46 of those 81 individuals having their center of activity within the sample unit.

The posterior mean (SD; 95% confidence interval) of $N(D)$ was 79.06 (12.84; 59–109). For the detection probability, the posterior mean was 0.200 (0.036; 0.134–0.275). The posterior means (SD) of σ_1 and σ_2 were 0.962 (0.039) and 1.054 (0.051), respectively. In this case, $\sigma_1 \approx \sigma_2$, consistent with the data-generating model in which the two variance components were both set to 1.0.

We expanded our use of simulated data under more variable conditions by considering populations having $\sigma \in \{1, 2, 4\}$, five levels of density (see Table 1), while keeping the 10×10 unit sample area fixed and $p = 0.25$. The range of densities correspond to population sizes within the 100 unit² sample area of roughly 23–78. Summary statistics of populations under these scenarios are given in Table 1. We note that the average p of

individuals in the population is only 0.023 for $\sigma = 4$ and increases to only 0.098 for $\sigma = 1$. These are extraordinarily low detection probabilities and we therefore believe the results of the density estimator should reflect worst-case scenarios. In particular, when the movement parameter is $\sigma = 4$, we expect to capture only about 10% of the individuals in the population (with $T = 5$) and only about 10% of those are captured more than one time.

For each level of density (five levels) and σ (three levels), we simulated 100 data sets to which the model was fitted in WinBUGS based on 10 000 post burn-in draws from the posterior. Summaries of the estimated density (posterior mean) across all 100 replicates for each of the 15 cases are given in Table 2. We have provided the mean, median, and standard deviation across replicates as well as the coverage of a nominal 95% posterior interval, which was computed as the 2.5th and 97.5th percentiles. As expected (i.e., in small samples), the estimator appears slightly biased, and the bias is more pronounced for the lower density situations due to the very small sample sizes (see Table 1). We note that the bias diminishes rapidly from about 15% to about 4% as density increases from the lowest level (0.234) to the highest (0.781). We see that the mean and median are not too different, and typically close to the data-generating value. The bias affects the confidence interval coverage (mostly at the lower value of σ), generating a typical coverage (averaged across levels of density) close to 90% for $\sigma = 1$ and $\sigma = 2$, and then about 96% for the high-movement case.

Flat-tailed horned lizard data

Here we apply the model to estimate the density of the flat-tailed horned lizard in southwestern Arizona from a

TABLE 2. Summaries of Bayesian estimator of density under the spatial model based on a Monte Carlo simulation of 100 replicate data sets under five levels of density and three values of the movement parameter σ .

True density	$\sigma = 1$				$\sigma = 2$				$\sigma = 4$			
	Mean	Med.	SD	CI	Mean	Med.	SD	CI	Mean	Med.	SD	CI
0.234	0.272	0.268	0.073	0.86	0.269	0.273	0.066	0.90	0.269	0.272	0.067	0.98
0.352	0.372	0.372	0.075	0.92	0.380	0.372	0.087	0.91	0.358	0.349	0.084	0.96
0.469	0.508	0.516	0.096	0.86	0.509	0.500	0.098	0.89	0.497	0.509	0.097	0.97
0.586	0.623	0.623	0.105	0.91	0.625	0.622	0.110	0.89	0.591	0.565	0.127	0.94
0.781	0.810	0.802	0.102	0.94	0.822	0.796	0.155	0.91	0.805	0.774	0.152	0.99

Note: "Mean," "Med.," and "SD" are the mean, median, and standard deviation across the 100 replicates of the Bayesian point estimate (posterior mean), and "CI" is the percentage of 95% posterior intervals that contained the true density.

capture–recapture study that was carried out on a 9-ha plot of dimension 300×300 m. There were 14 capture occasions over 17 days (14 June to 1 July 2005). A total of 68 individuals were captured 134 times. The distribution of capture frequencies was (34, 16, 10, 4, 2, 2) for one to six captures, respectively, and no individual was captured more than six times. The plot boundaries in a scaled coordinate system, along with the capture locations, are shown in Fig. 2.

The model was fit in WinBUGS using the data augmentation parameterization described in *Bayesian estimation by data augmentation* (Supplement). The MCMC simulation was run for 44 000 iterations, the first 4000 were discarded as "burn-in" (as described in *Bayesian estimation by data augmentation*), and posterior summaries were computed from the remaining 40 000 iterations. Posterior summaries are provided in Table 3 where $N(D)$ is the number of activity centers within the sample unit boundaries and the parameter ψ is the complement of the zero-inflation parameter described in *Bayesian estimation by data augmentation*. That is, it is the inclusion probability for a member of the augmented list of size M .

The results are summarized by the following points: Approximately 80 individuals are estimated to have home range centers within the 9-ha study plot. The posterior mean density per ha, i.e., the posterior mean of the quantity $D = N(D)/9$, is 8.784 lizards/ha, with a 95% Bayesian confidence interval (7.667–10.220). The posterior means of both spatial movement parameters were about 0.15. Recall that the plot was scaled to be 3×3 units, so $\sigma = 0.15$ represents about 5% of the dimension, or about 15 m relative to the original dimension of 300 m.

It is useful to put this estimate into context with that obtained using a typical closed-population estimator of N , say under the standard null model in which p is constant (usually referred to as "Model M_0 ") for which, in practice, we never know the effective sample area. Fitting this closed-population model to the data yields $\hat{N} = 82.02$ and $\hat{p} = 0.117$. These estimates are consistent with the expected influence of temporary emigration, but in this case the difference is only about 3.5%, owing to the relatively small (i.e., relative to the plot dimension) estimated movement range of lizards about their

territory center. While this difference is small, we note that it would be impossible to gauge the reasonableness of the closed-population estimator of N in any particular instance, in the presence of temporary emigration. In the present case, excessive bias due to temporary emigration was mitigated to some extent by the large plot size. The plot size here is much larger than has been suggested as being practical in operational monitoring efforts for this species (Grant and Doherty 2007). Also, the plot was chosen specifically because a high density of individuals was present, and high densities typically correspond to less movement in this species (K. Young, *unpublished data*).

DISCUSSION

In many animal sampling problems, it is convenient to prescribe an areal sample unit that is surveyed repeatedly in the context of a capture–recapture study. However, it is not generally feasible to impose strict geographic closure on the survey area, and movement onto and off of the survey plot is typical. This phenomenon has been termed temporary emigration, and its effects are widely known (Kendall 1999).

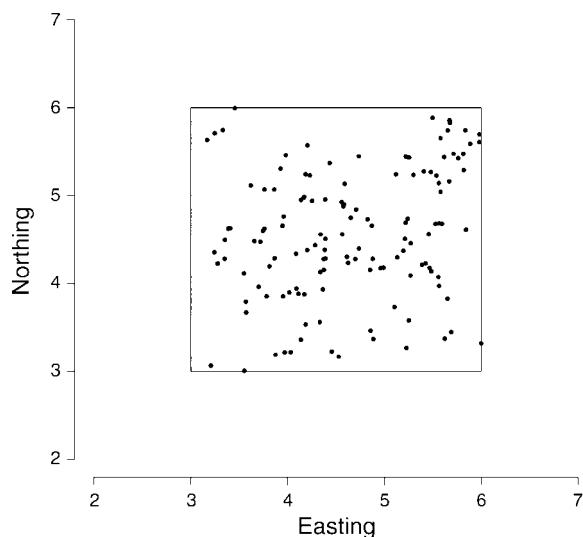


FIG. 2. Locations of 68 flat-tailed horned lizards (*Phrynosoma mcallii*) captured a total of 134 times on a 9-ha plot in southwestern Arizona, USA.



PLATE 1. Not only does the flat-tailed horned lizard (*Phrynosoma mcallii*) match the color of its sandy habitat, but it typically presses against or buries under the sand rather than fleeing, adding to the difficulty of detecting this species. Photo credit: K. V. Young.

Unfortunately, it has not generally been possible to account for temporary movements in the absence of additional information such as replicate surveys carried out under the so-called “robust design” (Kendall et al. 1997). This notion has been used in other herptile surveys by Bailey et al. (2004a, b), and the basic concepts and existing methods have recently been reviewed by Parmenter et al. (2003).

In this paper, we described a hierarchical model of the temporary emigration phenomenon that is informed by location-of-capture information. The model is hierar-

chical in the sense that it is comprised of an explicit process model, and an observation model that is conditional on the underlying state process. The process model describes the spatial organization of home-range centers, and the movement of individuals over time. The observation model describes the probability of encounter as a function of an individual’s location at the time of sample, and a probability of detection parameter.

Bayesian analysis of this hierarchical analysis is straightforward with the aid of data augmentation (Royle et al. 2007). Under data augmentation, the

TABLE 3. Parameter estimates for the lizard data.

Parameter	Mean	SD	Posterior percentiles		
			2.5%	50%	97.5%
$N(D)$	79.23	5.947	69.0	79.0	92.000
β	8.784	0.659	7.667	8.667	10.220
p	0.122	0.013	0.097	0.121	0.149
σ_1	0.154	0.011	0.136	0.153	0.176
σ_2	0.150	0.001	0.133	0.150	0.172
ψ	0.626	0.077	0.483	0.626	0.781

Notes: $N(D)$ is the number of home range centers located within the 9-ha study plot, and β is the estimated density (no. individuals/ha). The parameter ψ is the zero-inflation parameter, which is related to the total population of exposed individuals as described in *Bayesian estimation by data augmentation*.

observed sample of size n is physically augmented with a large number of all-zero encounter histories. This leads to a reparameterization of the model: the resulting model being a zero-inflated version of the “known N ” model. That is, the reparameterized model explicitly admits that the augmented data set contains an excess of zeros. Data augmentation was devised as a method for facilitating the Bayesian analysis of models with individual effects of which the present model is a specialized case, having an individual effect (individual activity center) that is not observed. One of the important advantages of data augmentation is that it yields a fairly accessible implementation by MCMC. The model proposed here can be implemented directly in WinBUGS with little difficulty.

In the flat-tailed horned lizard example, the method was used to obtain an estimate of density that allows for bias due to movement of individuals into and out of the sample plot. The typical movements (embodied in the parameter σ) were found to be small relative to the total plot dimension ($\hat{\sigma} = 0.15$ relative to a standardized plot dimension of three units). This was expected to a certain extent as the large plot size was chosen in part to minimize the effects of temporary emigration. However, in general, there could be some advantage to using plots of smaller size (e.g., more plots could be sampled, thereby achieving more diverse landscapes and hence a more representative sample), in which case the effects of movement would be more acute. In such cases, there would probably be a need to model additional structure in the parameter σ as home-range size would be expected to change in response to density and local conditions (e.g., see Discussion in Grant and Doherty 2007). The flat-tailed horned lizard is a difficult species to monitor because of its low detection probabilities, which are due, in part, to movement or temporary emigration. The method presented here provides an alternative to conventional methods (capture–recapture and distance sampling) that allows for temporary emigration and enables sampling on arbitrary plot sizes.

Using simulation studies, we evaluated the performance of the proposed estimator under situations in which the movement-to-plot-dimension ratio was considerably larger than for the flat-tailed horned lizards. For a 10×10 unit plot, we considered $\sigma \in \{1, 2, 4\}$, which is approximately 2 \times , 4 \times , and 8 \times the movement-to-plot-dimension ratio found in the lizard data. These simulations suggested tolerable levels of small-sample bias (5–15%) in the estimator (posterior mean) even under situations for which typical data sets contain few individuals captured more than one time (see Table 1).

There are a number of conventional solutions for obtaining estimates of density when the effective trap area is unknown, or the study is subject to temporary emigration. Some of these involve modification of the basic survey method and design from conventional capture–recapture methods (e.g., distance sampling [Buckland et al. 1993], or trapping grids [Wilson and

Anderson 1985b]), while others involve various adjustments to the nominal plot area (e.g., by the radius of a home range [Otis et al. 1978] or by mean maximum distance moved [Wilson and Anderson 1985c]), or the use of “nested grids” (Wilson and Anderson 1985a). These adjustments are used in camera trap surveys of tigers in India (Karanth and Nichols 1998, Nichols and Karanth 2002), small mammal trapping (Parmenter et al. 2003), and in many other settings. Another form of adjustment is based on auxiliary data from telemetry information (White and Shenk 2001) when it is practical to obtain such information. Oftentimes, however, information necessary to apply such adjustments is obtained from the literature on the species in question, i.e., from prior, similar studies. The problem with the use of such prior information is that the estimate used to formulate the adjustment comes from somewhere else—some other place, some other time, under different conditions. That is, a different population of individuals. Thus, the estimate of density for the population under study is only as good as the relevance of the extrinsic estimate of home range size which cannot be assessed, in general, and likely varies in response to a host of factors. On the other hand, the method that we have described produces an “adjustment” that is intrinsic to the data set at hand, i.e., the same data set that produces the estimate of N . While this is immediately useful for obtaining estimates of density of the population under study, the model also allows for the consideration of models for the movement range parameter, σ , in response to environmental conditions, or demographic factors.

A number of useful extensions of this model are possible. One in particular is to the case where sampling is based on a fixed array of trap devices, such as camera traps, or hair snares. Such a model appears to have much in common with Efford’s models (Efford 2004) which represent a novel approach to the incorporation of spatial location in the development of density estimation from trapping arrays. Efford (2004) uses a simulation-based method of fitting the models to trap array data, as opposed to one of the more conventional paradigms of inference (e.g., likelihood or Bayesian). We believe that the modification of the present hierarchical model to the trap array situation is the conceptual equivalent of the Efford models.

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SUPPLEMENT

WinBUGS model specification for the lizard example in the paper (*Ecological Archives* E089-130-S1).