Unmarked Populations

18

Traditional capture-recapture models share the fundamental assumption that each individual in a population can be uniquely identified when captured. Often, this can be accomplished by marking individuals with color bands, ear tags, or some other artificial mark that subsequently can be read in the field. For other species, such as tigers (*Panthera tigris*) or marbled salamanders (*Ambystoma opacum*), individuals can be identified using only their natural markings. However, many species do not possess adequate natural markings and are difficult to capture, making it impractical to use standard capture-recapture techniques.

Estimating density when individuals are unmarked can be accomplished using a variety of alternatives to capture-recapture, such as distance sampling (Buckland et al., 2001) and *N*-mixture models (Royle, 2004b). These methods can be very effective when their assumptions are met, but when it is not possible to obtain accurate distance data, or when movement complicates the use of fixed-area plots, these methods may yield biased estimates of density (Chandler et al., 2011). Furthermore, some species are so rare and cryptic that it is nearly impossible to collect enough data using traditional survey methods.

In this chapter, we investigate spatially explicit alternatives for estimating density of unmarked populations, and we highlight the work of Chandler and Royle (2013) who demonstrated that the "individual recognition" assumption of traditional capture-recapture models is not a requirement of spatial capture-recapture models. They showed that, under certain conditions, spatially correlated count data are sufficient for making inferences about animal distribution and density even when no individuals are marked. The Chandler and Royle (2013) "spatial count model" (hereafter the SC model) requires neither distance data nor fixed-area plots. Instead, the observed data are trap- and occasion-specific counts, which are modeled as a reduced-information summary of the *latent* encounter histories. Because the model is formulated in terms of the data we wish we had, i.e., the typical encounter history data observed in standard capture-recapture studies of marked animals, the SC model is just a SCR model with a single extension to account for the fact that the encounter histories are unobserved. However, this results in a drastically different model than the models typically used for count data in ecology because the SC model is parameterized in terms of individuals, and specifically, their locations relative to the sampling device.

The ability to fit SCR models to data from unmarked populations has important implications. For one, it means that SCR models can be applied to data collected using methods like point counts in which observers record simple counts of animals at an array of survey locations. The model can also be fitted to camera trapping data collected on unmarked animals, representing one of the first formal methods for estimating density from such data (but see Rowcliffe et al., 2008). So, is the SC model a free lunch? At face value, it sounds as though it allows for estimation of all the quantities of interest in standard capture-recapture studies, but with very little data. But of course the answer is no—lunch is still not free because with this model come new assumptions, and as was demonstrated by Chandler and Royle (2013), even with "perfect" data, parameter estimates will typically not be very precise. This should not be surprising given that we are asking so much from simple count data.

The real value of the SC model is twofold. First, it demonstrates an important theoretical result, namely that spatial correlation in count data carries information about density and distribution; a result that stands in stark contrast to a prevailing view of spatial correlation as a nuisance to be avoided or modeled out of unsightly residual plots. The second reason why this model is important is that it provides the basis for numerous model extensions that *can* yield precise density estimates. We will discuss some of these possibilities in this chapter, but perhaps the most useful extension—accommodating data from both marked and unmarked individuals—is treated separately in the next chapter. Here, we focus on situations in which all individuals are unmarked, and we begin by presenting the most basic formulation of the model. Then, we proceed by way of a few examples to consider extensions of the model in which ancillary information can be used to increase precision.

18.1 Existing models for inference about density in unmarked populations

When capture-recapture methods are not a viable option, ecologists often collect simple count data or even binary detection/non-detection data. These data are often treated as an index of abundance or occurrence and are analyzed using generalized linear models such as Poisson regression or logistic regression, perhaps with random effects (Zuur et al., 2009). However, index methods cannot be used to make unbiased inferences about abundance or occurrence unless strong assumptions about constant detection probability are valid (Williams et al., 2002; Sollmann et al., 2013b). In particular, index methods can be highly misleading when covariates affect both the ecological process of interest and the observation process. A classic example is given by Bibby and Buckland (1987) who found that songbird detection probability was negatively related to vegetation height, whereas density was positively associated with vegetation height in restocked conifer plantations. This intuitive phenomenon has been demonstrated repeatedly (Kéry, 2008; Sillett et al., 2012) and has led to the development of a vast number of models to estimate population size and occurrence probability when individuals are unmarked and detected imperfectly

(Buckland et al., 2001; Williams et al., 2002; MacKenzie et al., 2006; Royle and Dorazio, 2008). A review of these models is beyond the scope of this chapter, but we mention a few deficiencies of existing methods that warrant the exploration of alternatives for robust inference when standard capture-recapture methods do not apply.

Distance sampling (Buckland et al., 2001; Buckland, 2004), which we briefly introduced in Chapter 4, is perhaps the most widely used method for estimating population density when individuals are unmarked and detection probability is less than 1. This class of methods is known to work impeccably when estimating the number of beer cans in a field or the number of duck nests in a wetland. Distance sampling can also work very well in more interesting situations, and it is an extremely powerful method when the assumptions can be met. However, the assumptions that distance data can be recorded without error and that animals are distributed randomly with respect to the transect can be easily violated by common processes such as animal movement and measurement error. Although numerous methods have been proposed to relax some of these assumptions (Borchers et al., 1998; Royle et al., 2004; Johnson, 2010; Marques et al., 2010; Chandler et al., 2011), a more important issue is that distance sampling is simply not practical in many settings. For example, many species are so rare or elusive that they can only be reliably surveyed using "indirect" methods such as camera traps or hair snares.

In response to the increasing use of camera traps in studies of threatened species, and the problems associated with commonly used indices of abundance (Jennelle et al., 2002; O'Brien, 2011; Sollmann et al., 2013b), several density estimators have been developed for situations in which the population being studied is unmarked (Rowcliffe et al., 2008, 2011). These estimators assume that (1) cameras are randomly placed with respect to animal density, (2) animals neither avoid nor are attracted to the cameras, and (3) detection probability can be either modeled as a function of distance between the animal and the camera or as a function of movement velocity (which must be known or estimated using auxiliary data). Although these methods might represent an important improvement over index-based methods, the assumptions may not hold in many situations, especially when applied to data from standard designs in which camera stations are either baited or placed along trails—issues that can be dealt with directly using SCR models (see Chapters 12 and 13). Nonetheless, empirical studies have found that the assumptions do hold in some cases (Rowcliffe et al., 2008).

Other common approaches to estimating density when individuals are unmarked include double observer sampling, removal sampling, and repeated counts, for which custom models have been developed (Nichols et al., 2000b; Farnsworth et al., 2002; Royle, 2004b,a; Nichols et al., 2009; Fiske and Chandler, 2011). To obtain reliable density estimates using these methods, the area surveyed must be well defined and closed with respect to movement and demographic processes. Given a sufficiently short sampling interval, such as a 5 min point-count, the closure assumption may be reasonable. However, short sampling intervals limit the number of detections, so observers generally visit each survey location multiple times during a season. But then, animal movement may invalidate the closure assumption, and a model of temporary emigration is required (Kendall et al., 1997; Chandler et al., 2011).

Furthermore, distance-related heterogeneity in detection probability can introduce bias in these models, although this bias is negligible when the ratio of plot size to the scale parameter of the detection function is low (Efford and Dawson, 2009).

We mention these issues not to suggest that existing models do not have value—indeed we believe that they can be used to obtain reliable density estimates in many situations—rather, our aim is to highlight the need for alternative methods when the assumptions of existing models cannot be met and when spatially explicit inference is the objective.

## 18.2   Spatial correlation in count data

18.2.1   Spatial correlation as information

All of the previous methods require some sort of auxiliary information to model both abundance and detection. For instance, multiple observers, distance data, or repeated visits may be required to ensure that model parameters are identifiable (but see Lele et al., 2012; Sólymos et al., 2012). The same is true for the SC model, but the auxiliary information comes in the form of spatial correlation, which requires no extra effort to collect.

It is natural to be suspicious of the claim that spatial correlation is a good thing. In fact, elaborate methods have been devised to deal with spatial correlation as a nuisance (Lichstein et al., 2002; Dormann et al., 2007), and ecologists have been admonished for failing to obtain "real" replicates uncontaminated by spatial correlation (Hurlbert, 1984). The following heuristic may be helpful for seeing the value of spatial correlation in the context of density estimation.

Imagine a 10×10 grid of camera traps and a single unmarked individual exposed to "capture" whose home range center lies in the center of the trapping grid. If the individual has a small home range size relative to the extent of the trapping grid, we can envision what the spatial correlation structure of the encounters might look like. If the animal's home range is symmetric around the activity center then the number of times the individual is detected at each trap (the trap count) should decrease with the distance between the home range center and the trap; i.e., traps with the same distance from the activity center will yield counts that are more highly correlated with one another than traps located at different distances from the activity center. Thus, the correlation among the counts tells us something about the location of the activity center. It is relatively intuitive that spatial correlation carries information about distribution, but what about density?

Imagine now that there are two activity centers located in the trapping grid. Using trap counts alone, is it possible to determine the number and location of these activity centers? The answer is yes, at least under certain circumstances. Figure 18.1 shows the locations of the two hypothetical activity centers, and the total counts obtained at each trap after 10 survey occasions. Assuming that animals have bivariate normal home ranges, the fact that there are two areas in the map with high counts that dissipate with distance suggests that the most likely number of individuals given these data is 2.
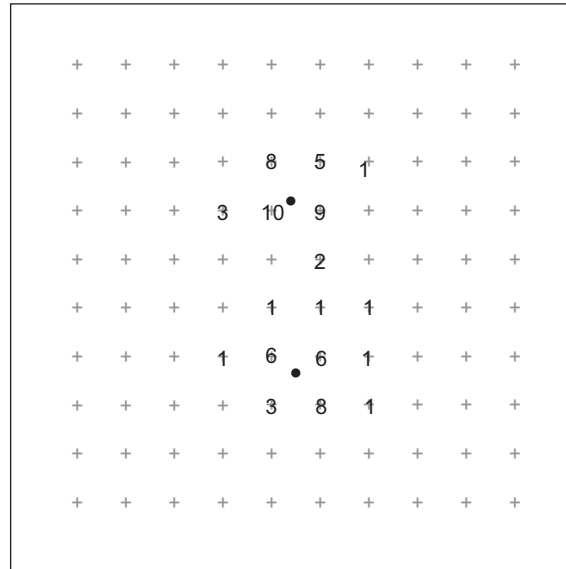
FIGURE 18.1

Simulated count data at each of 100 camera traps (crosses) after $K = 10$ sampling occasions. The black dots are the locations of two animal activity centers. The spatial count model estimates both the location and number of activity centers exposed to sampling using such spatially referenced count data.

Furthermore, the degree to which the counts dissipate from the two areas of highest intensity is information about the parameter governing home range size. These two pieces of information are enough to estimate the number of individuals exposed to sampling, given that a bivariate normal home range is a valid assumption. Of course, the data could just as well have been generated by a single individual whose home range is bimodal, and thus *as always* the assumptions of our model need to be carefully examined using our biological knowledge of the system. If the assumptions do not hold, it is almost always possible to relax them, for instance by allowing for non-stationary home ranges as we demonstrated in Chapters 12 and 13.

18.2.2 **Types of spatial correlation**

The spatial correlation allowed by the SC model is assumed to arise from animal movement; however, this is just one type of spatial correlation that may exist in ecological count data. Another common type of spatial correlation results from the spatial correlation of environmental covariates. Habitat variables, such as, the percent cover of deciduous forest in North America, will often be patchy rather than randomly distributed, and this can result in spatial correlation in abundance, and hence in count data. Often, this type of spatial correlation can be dealt with by simply including the

habitat covariate in the model. For example, a simple, non-spatial species distribution model with only a few habitat variables can result in a distribution map that reflects the spatial correlation in abundance (Sillett et al., 2012; Royle et al., 2012). The point is that the relevant assumption of non-spatial models (e.g., GLMs) is that no spatial correlation exists in the *residuals*, and often, any spatial correlation apparent in the counts can be accounted for using covariates. This may be obvious, but it is a point that seems to be frequently misunderstood.

Of course, sometimes spatial correlation exists in residuals even after including covariate effects. This may be due to unobserved covariates or unmodeled processes such as dispersal. When mechanistic models cannot be developed to describe these processes, several options exist for handling spatial correlation as a nuisance (Besag and Kooperberg, 1995; Zuur et al., 2009; Wikle, 2010). In the context of SCR models, including the SC model dealt with in this chapter, movement-induced spatial correlation is always explicitly modeled, and other sources of spatial correlation can be accounted for as well. For instance, environmentally induced spatial correlation can be modeled by adopting an inhomogeneous point process model for the activity centers. That is, the point process intensity can be modeled as a function of observed covariates, and theoretically, it should be possible to allow for spatially correlated random effects to deal with unobserved covariates. See Chapter 11 for details.

18.3 Spatial count model

18.3.1 Data

Whereas traditional SCR models require spatially referenced individual encounter histories, the SC model requires simple, spatially reference count data. Let n_{jk} be the count data at sampling location j on occasion k. The entire $J \times K$ matrix of counts will be denoted **n**. A sampling location in this context could be any device capable of recording count data, such as a human observer or a camera trap, and one of the benefits of the SC model is that it can be applied to data collected using many different survey methods. For ease of presentation, we will refer to sampling devices as traps, but remember that a trap is just something capable of recording count data. As in all SCR models, we also require the coordinates of the J traps, and we denote the location of trap j by $\mathbf{x}_j$. In some instances, additional data might be available such as trap-specific covariates, state-space covariates, information on the identities of a subset of individuals, or perhaps even distance data. We consider some of these model extensions in Section 18.6, but for the time being we ignore these possibilities so that we can focus on the basic model.

18.3.2 Model

The state model is exactly the same as the one we have dealt with throughout this book. It is a point process describing the number and distribution of activity centers in the state-space $\mathcal{S}$. Although it might be possible to fit inhomogeneous point process

models using the methods described in Chapter 11, given the simplicity of the data, we concentrate on a homogeneous point process $\{\mathbf{s}_i, \ldots, \mathbf{s}_N\} \sim \text{Uniform}(\mathcal{S})$ where $\mathbf{s}_i$ is the activity center of individual i in the population of size N. For the moment, we will assume that N is known.

The observation model is the same as in other SCR models in the sense that it describes the probability of encountering individual i at trap j, conditional on the location of the individual's activity center. The specific encounter process will depend on the sampling method, and here we consider the standard camera trapping situation in which an individual can be encountered at multiple traps during a single occasion—e.g., one night during a camera-trapping study—and it can be detected multiple times at a single trap during an occasion. This is the Poisson encounter model (a.k.a. the count detector case) described in Chapter 9. Our experience with alternative observation models such as the Bernoulli and multinomial models suggests that the parameters of the model may not be identifiable in these cases, at least when no additional information is available. This is a subject of ongoing research.

As before, we define y_{ijk} as the encounter data for individual i at trap j on occasion k, which we model as:

$$y_{ijk} \sim \text{Poisson}(\lambda_{ij}), \tag{18.3.1}$$

where λ_{ij} is the encounter rate. A common encounter rate model is the Gaussian, or half-normal, model:

$$\lambda_{ij} = \lambda_0 \exp(-\|\mathbf{x}_j - \mathbf{s}_i\|^2/2\sigma^2)$$

in which λ_0 is the baseline encounter rate, $\|\mathbf{x}_j - \mathbf{s}_i\|$ is the Euclidean distance between the trap and activity center, and σ is the scale parameter determining the rate at which encounter rate decreases with distance. In this context, σ also determines the amount of correlation among the counts because if σ is low relative to the trap spacing then it is unlikely that an individual will be detected at multiple traps.

When individuals cannot be uniquely identified, the encounter histories cannot be directly observed, which seems like a massively insurmountable problem of epic proportions. The solution of Chandler and Royle (2013) is the same one we routinely apply when we cannot directly observe the process of interest—we regard the encounter histories as latent variables. This leaves the remaining task of specifying the relationship between the count data and the encounter histories, i.e., we need a model of $[\mathbf{n}|\mathbf{y}]$ where $\mathbf{y}$ represents the entire collection of encounter histories. In this case, there is only one possibility because, by definition, the count data are simply a reduced-information summary of the latent encounter histories. That is, they are the sample- and trap-specific totals, aggregated over all individuals:

$$n_{jk} = \sum_{i=1}^{N} y_{ijk}. \tag{18.3.2}$$

So, unlike most model-development problems faced in this book, we don't have to consider competing probability models for $[\mathbf{n}|\mathbf{y}]$, but instead, we recognize the fact that the relationship between the counts and the latent encounter histories is

deterministic. This deterministic constraint poses some computational challenges, which we discuss below. But first we present some alternative formulations of the model.

Recall from Chapter 2 that the sum of two or more Poisson random variables is also a Poisson random variable. Specifically, if $x_1 \sim \text{Poisson}(\lambda_1)$ and $x_2 \sim \text{Poisson}(\lambda_2)$, then $(x_1 + x_2) \sim \text{Poisson}(\lambda_1 + \lambda_2)$. Thus, under this Poisson model for the latent encounter histories, the count data can be modeled as Poisson:

$$n_{jk} \sim \text{Poisson}(\Lambda_j), \qquad (18.3.3)$$

where

$$\Lambda_j = \lambda_0 \sum_i \exp(\|\mathbf{x}_j - \mathbf{s}_i\|^2 / 2\sigma^2),$$

and because Λ_j does not depend on k, we can aggregate the replicated counts, defining $n_{j.} = \sum_k n_{jk}$ and then

$$n_{j.} \sim \text{Poisson}(K\Lambda_j).$$

As such, K and λ_0 serve equivalent roles as affecting baseline encounter rate. Formulating the model in terms of the aggregated count data demonstrates that the model can be applied to data from a single sampling occasion ($J \equiv 1$) as has been noted elsewhere for standard SCR models (Efford et al., 2009b). In the context of studying marked populations, the model parameters will only be identifiable in the $J \equiv 1$ case if an animal can be captured at multiple traps during a single occasion. The SC model essentially requires the same thing, which is to say that it requires correlation in the count data resulting from an individual being captured in multiple, closely spaced traps.

This formulation of the model in terms of the aggregate count also simplifies computations as the latent encounter histories do not need to be updated in the MCMC estimation scheme; however, retaining them in the formulation of the model is important if some individuals are uniquely marked. This is because uniquely identifiable individuals produce observations of some of the y_{ijk} variables, which we elaborate on in the next chapter.

18.3.3 On *N* being unknown

Even though there are no observed encounter histories in the situation we consider here, we can still use data augmentation (Tanner and Wong, 1987; Liu and Wu, 1999) to resolve the problem that N is unknown. In fact, we are actually using two different types of data augmentation since we first augment the observed data with latent encounter histories, and then we augment this latent data array with a set of all-zero encounter histories. This approach turns out to be very similar to other data augmentation schemes used to model spatial dependence in other contexts (Wolpert and Ickstadt, 1998; Best et al., 2000).

Although the process of data augmentation should be familiar by now, we briefly review the basics. For homogeneous point process models, N is typically modeled

as $N \sim \text{Binomial}(M, \psi)$, which is equivalent (marginally) to a discrete uniform prior on N if $\psi \sim \text{Uniform}(0, 1)$. Since a binomial model is equivalent to a series of M independent Bernoulli trials, we can rewrite $N \sim \text{Binomial}(M, \psi)$ as $z_i \sim \text{Bernoulli}(\psi)$ where z_i is an auxiliary variable indicating if individual i is a member of the population, such that $N = \sum_{i=1}^{M} z_i$. Having expanded the model to include a prior on N, we can summarize the SC model, with a Gaussian observation model, as follows:

$$z_i \sim \text{Bernoulli}(\psi),$$

$$y_{ijk} \sim \text{Poisson}(\lambda_{ijk} z_i),$$

$$\lambda_{ijk} = \lambda_0 \exp(-\|\mathbf{x}_j - \mathbf{s}_i\|^2)/(2\sigma^2),$$

$$n_{jk} = \sum_{i=1}^{M} y_{ijk}.$$

18.3.4 Inference

Bayesian analysis can proceed once suitable priors have been put on the hyperparameters ψ, σ, and λ_0. Chandler and Royle (2013) provided **R** code for fitting the model using MCMC, and they evaluated the model's performance with uniform priors on the three hyperparameters. They also discussed the possibilities and effects of including prior knowledge about σ into the model. In Section 18.5, we explain how the model can be implemented using **JAGS**, but first we briefly contemplate the viability of classical analysis of this model.

   The obvious challenge faced when conducting a classical analysis of this model is that the number of latent variables is huge. In all SCR models, the activity centers are latent, but now, even the encounter histories are latent. Maximizing likelihoods with latent variables (random effects) involves integrating (or summing) over all possible values of the latent variables. For the activity centers, this is typically accomplished by integrating the conditional-on-**s** likelihood $[\mathbf{y}_i|\mathbf{s}_i]$ over the two-dimensional state-space $\mathcal{S}$ (Chapter 6). However, with the SC model, we have to sum over all possible encounter histories meeting the constraint of Eq. (18.3.2). The number of possible encounter histories will, in general, be too high to make the likelihood tractable, and thus we do not think that maximum-likelihood is a viable option for analyzing this model. However, one might be able to obtain approximate maximum-likelihood estimates using simulation-based methods (Lele et al., 2010), which will typically be more computationally challenging than the Bayesian analysis.

18.4 How much correlation is enough?

In Chapter 10, we noted that if trap spacing is too wide relative to the encounter rate parameter σ, then few spatial recaptures will be realized and the model parameters will be estimated poorly. The same principle applies here—σ shouldn't be too small or too large relative to trap spacing or else the counts will be *iid* Poisson random variables. So how much correlation is enough? Phrased differently, what is the ideal ratio of σ to trap spacing to ensure correlation and minimize the variance of the posterior

distributions? We see two options for answering this questions, both of which are topics in need of additional research. The first approach is to use the methods described in Chapter 10, i.e., by either conducting simulation studies with various trap spacing to σ ratios, or to analytically minimize a variance criterion for a given set of sampling conditions and effort. The former approach was used by Chandler and Royle (2013) whose limited simulation study indicated that an ideal ratio is approximately 2. This agrees with findings from previous research on the optimal design of SCR studies (Chapter 10), as it should.

A second approach that may be of use if a data set has already been collected is to use standard techniques from spatial statistics to determine if adequate correlation exists in the counts. For example, one might compute Ripley's K-statistic or generate (semi-) variograms (Illian et al., 2008). We have not studied the utility of such approaches, but they seem worthy of investigation.

18.5   Applications

18.5.1   Simulation example

Simulating data under the SC model proceeds by first simulating standard SCR encounter history data and then collapsing it into count data. The following blocks of **R** code generate data from the model, with parameters $\sigma = 5$, $\lambda_0 = 0.4$, and $N = 50$. The state-space is a $[0, 100] \times [0, 100]$ square, and a grid of 100 traps is centered in the middle. The first block of code generates the trap coordinates X and the $N = 50$ activity centers:

```
> tr <- seq(15, 85, length=10)
> X <- cbind(rep(tr, each=length(tr)),
+            rep(tr, times=length(tr)))   # 100 trap coords
> set.seed(10)
> xlim <- c(0, 100); ylim <- c(0, 100)    # S is [0,100]x[0,100] square
> A <- (xlim[2]-xlim[1])*(ylim[2]-ylim[1])/1e4 # Area of S
> mu <- 50                                # Density(animals/unit area)
> N <- rpois(1, mu*A)                     # Generate N=50 as Poisson deviate
[1] 50
> s <- cbind(runif(N, xlim[1], xlim[2]), runif(N, ylim[1], ylim[2]))
```

We could have set $N = 50$ directly, but instead we treated density as a fixed parameter ($\mu = 50$) and generated N as a random variable—it just so happens that with the specified random seed, N equals 50.

Now we can generate the encounter histories under the Poisson observation model. Let's suppose that sampling is conducted over $K = 5$ nights:

```
> sigma <- 5
> lam0 <- 0.4
> J <- nrow(X)
> K <- 5
> y <- array(NA, c(N, J, K))
> for(j in 1:J) {
```

```
+     dist <- sqrt((X[j,1]-s[,1])^2 + (X[j,2] - s[,2])^2)
+     lambda <- lam0*exp(-dist^2/(2*sigma^2))
+     for(k in 1:K) {
+         y[,j,k] <- rpois(N, lambda)
+     }
+ }
```

The object y is the $N \times J \times K$ array of encounter data, which cannot be directly observed if the animals are unmarked. Converting the encounter data to count data can be accomplished using a single apply command:

```
> n <- apply(y, c(2,3), sum)
> dimnames(n) <- list(paste("trap", 1:J, sep=""),
+                      paste("night", 1:K, sep=""))
> n[1:4,]
       night1  night2  night3  night4  night5
trap1       1       0       0       0       0
trap2       1       2       2       0       1
trap3       1       0       0       1       0
trap4       0       0       0       0       0
```

This displays the first four rows of n, the $J \times K$ matrix of counts.

The question now is: Is it possible to estimate the parameters? In our simulated dataset we have $J \times K = 500$ data points, but how many parameters do we need to estimate? A frequentist might say that there are only three parameters: λ_0, σ, and N (or density μ) because inference about the latent parameters is carried out using prediction methods after the three hyperparameters have been estimated. However, a Bayesian would probably say that each **s** and each element of the latent encounter array **y** is a parameter in need of a posterior. From this perspective there are far more parameters than data points, and thus it would appear as though the situation is dire. Whether or not the parameters are actually estimable is a rather difficult question to answer. One simplistic, but not definitive, approach for addressing the question is to conduct a simulation study and evaluate the frequentist performance of the model by asking how often the data-generating values are included in confidence/credible intervals, and how biased are point estimates. Chandler and Royle (2013) conducted such a simulation study and found that, while the variance of the posterior distribution was high by most standards, the bias of the posterior mode of N was small and the coverage of the credible intervals was close to nominal. Moreover, they found no evidence that the posterior distributions were dominated by the priors, further supporting the conclusion that spatial correlation in the count data is sufficient for estimating density and encounter probability parameters.

At this point in time the SC model can only be fit using one of the **BUGS** engines, or using custom software like the **R** code accompanying Chandler and Royle (2013). Although **BUGS** might provide the most flexible option for fitting the model, it is not straightforward because of the constraints in the model. **JAGS** has a distribution called dsum that was designed for this type of situation in which the observed data are a sum of random variables. Panel 18.1 shows the **JAGS** code, but we abbreviated the

```
model{
sigma ~ dunif(0, 200) # Tailor this to your state-space
lam0 ~ dunif(0, 5)     # consider dgamma() as an alternative
psi ~ dbeta(1,1)
for(i in 1:M) {
   z[i] ~ dbern(psi)
   s[i,1] ~ dunif(xlim[1], xlim[2])
   s[i,2] ~ dunif(ylim[1], ylim[2])
   for(j in 1:J) { # Number of traps
       distsq[i,j] <- (s[i,1] - X[j,1])^2 + (s[i,2] - X[j,2])^2
       lam[i,j] <- lam0 * exp(-distsq[i,j] / (2*sigma^2))
       for(k in 1:K) { # Number of occasions
           y[i,j,k] ~ dpois(lam[i,j]*z[i])
           }
       }
   }
for(j in 1:J) {
   for(k in 1:K) {
       n[j,k] ~ dsum(y[1,j,k], y[2,j,k], ..., y[200,j,k])
       }
   }
N <- sum(z[])   # Realized population size
A <- (xlim[2]-xlim[1])*(ylim[2]-ylim[1]) # Area of state-space
D <- N / A      # Realized density
ED <- (M*psi)/A # Expected density
}
```

PANEL 18.1

JAGS code defining the spatial count model. This version includes the latent encounter histories. Note the abbreviated arguments to dsum().

arguments to dsum because in practice you need to provide all M of them. The code looks slightly unwieldy if M is large, but you can easily create it using the paste function in **R**. Here is an example, with an unrealistically small value of $M = 10$:

```
> paste("y[", 1:10, ",j,k]", sep="", collapse=", ")
[1] "y[1,j,k], y[2,j,k], y[3,j,k], y[4,j,k], y[5,j,k], y[6,j,k],
y[7,j,k], y[8,j,k], y[9,j,k], y[10,j,k]"
```

The **JAGS** model in Panel 18.1 can be used to fit the version of the model in which the latent encounters are updated at each Monte Carlo iteration. One challenge faced when using this version of the model is that **JAGS** cannot autogenerate initial values that honor the constraints in the model, so it is necessary to provide them. The following code presents one fairly general way of creating acceptable starting values and formatting the data for analysis using the rjags package:

```
> library(rjags)
> dat1 <- list (n=n, X=X, J=J, K=K, M=200, xlim=xlim, ylim=ylim)
> init1 <- function() {
+    yi <- array(0, c(dat1$M, dat1$J, dat1$K))
+    for(j in 1:dat1$J) {
+        for(k in 1:dat1$K) {
+            yi[sample(1:dat1$M, dat1$n[j,k]),j,k] <- 1
+        }
+    }
+    list(sigma=runif(1, 1, 2), lam0=runif(1),
+        y=yi, z=rep(1, dat1$M))
+ }
> pars1 <- c("lam0", "sigma", "N", "mu")
```

The code in Panel 18.1 is useful because it shows how closely this model is related to standard SCR models, and it provides the basis for including data on both marked and unmarked individuals, as will be discussed in the next chapter. However, this model runs very slowly, even when using a fast 64 bit machine with chains run in

```
model{
sigma ~ dunif(0, 200)
lam0 ~ dunif(0, 5)
psi ~ dbeta(1,1)
for(i in 1:M) {
   z[i] ~ dbern(psi)
   s[i,1] ~ dunif(xlim[1], xlim[2])
   s[i,2] ~ dunif(ylim[1], ylim[2])
   for(j in 1:J) { # Number of traps
       distsq[i,j] <- (s[i,1] - X[j,1])^2 + (s[i,2] - X[j,2])^2
       lam[i,j] <- lam0 * exp(-distsq[i,j] / (2*sigma^2)) * z[i]
       }
   }
for(j in 1:J) {
   bigLambda[j] <- sum(lam[,j])
   for(k in 1:K) {
       n[j,k] ~ dpois(bigLambda[j])
       }
   }
N <- sum(z[])
}
```

PANEL 18.2

JAGS code defining the spatial count model. This version does not include the latent encounter histories, and thus runs much faster than the code in Panel 18.1.

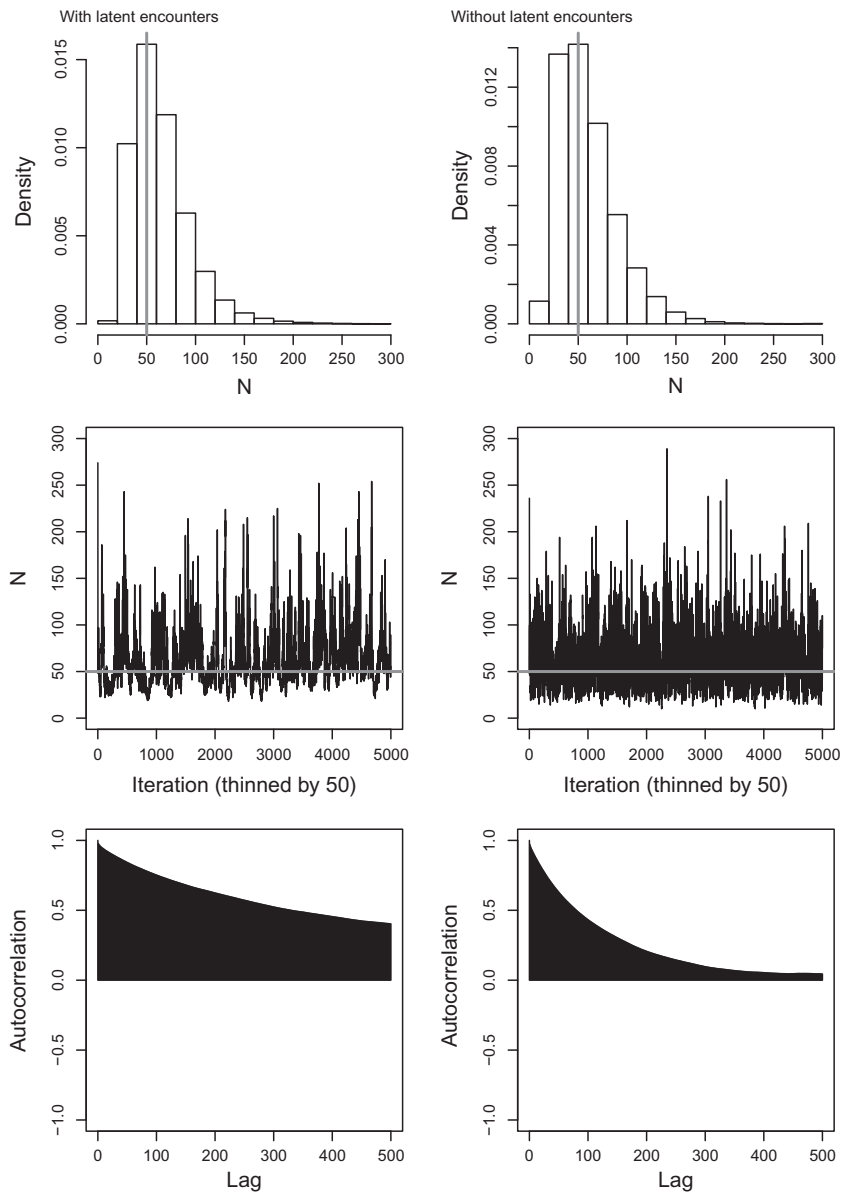parallel. The code in Panel 18.2 runs much faster because it does not include the latent encounter histories.

An even faster (but perhaps less efficient) alternative is to use the scrUN function in scrbook. The usage is as follows:

```
> out1 <- scrUN(n=n, X=X, M=300, niter=25000, xlims=xlim, ylims=ylim,
                inits=list(lam0=0.3, sigma=rnorm(1, 5, 0.1)), updateY=TRUE,
                tune=c(0.004, 0.09, 0.35))
```

where n is the matrix of counts, X is the trap coordinate matrix, M sets the size of the data-augmented latent data, xlims and ylims define the rectangular state-space, inits is a list of starting values, and updateY determines if the latent encounter histories are updated as part of the MCMC algorithm. In general, we recommend using the option updateY=FALSE because the Markov chains tend to mix better. Even so, it can be important to fiddle with the tuning parameters until the acceptance rates are between 40% and 60%. Otherwise, the Markov chains will exhibit extremely high autocorrelation. This is one reason to favor **JAGS** over our implementation in scrbook since **JAGS** finds suitable tuning parameters automatically during the adaptive phase (when using Metropolis updates).

We fit the model to the simulated data using both formulations—with and without the latent encounter histories—using both **JAGS** and scrUN. Table 18.1 shows summaries of 25,000 posterior draws, and suggests that while the true parameter values are easily covered by the 95% credible intervals, the intervals are rather wide. This low precision is not just a peculiarity of this particular data set—it will generally be

Table 18.1 Posterior summaries from the spatial count ("SC") model applied to simulated data using scrbook and **JAGS**. Twenty-five thousand samples were generated, but substantial Monte Carlo error is still evident. All parameters were given uniform priors.

Parameter	Mean	SD	2.5%	50%	97.5%
scrUN (..., updateY=FALSE)					
$\sigma = 5$	4.718	0.922	3.239	4.615	6.833
$\lambda_0 = 0.4$	0.500	0.136	0.268	0.489	0.793
$N = 50$	60.653	31.067	21.000	54.000	137.000
scrUN (..., updateY=TRUE)					
σ	4.554	0.784	3.216	4.486	6.264
λ_0	0.489	0.131	0.262	0.479	0.775
N	64.772	30.162	26.000	59.000	140.000
JAGS (without latent encounter histories)					
σ	4.70	0.88	3.24	4.66	6.63
λ_0	0.52	0.14	0.27	0.52	0.80
N	58.55	30.30	20.00	52.00	135.00

FIGURE 18.2

MCMC results for the parameter N from the two algorithms (with and without the latent encounter histories). The first row contains the histograms of the posterior distributions, the second row contains the history (or trace) plots, the third row shows the autocorrelation plots.

low unless the sample size is very large, as noted by Chandler and Royle (2013). Furthermore, autocorrelation of the samples will typically be high (Figure 18.2), and thus it may take many iterations to achieve convergence. The results shown in Figure 18.2 also indicate that the algorithm that includes the latent encounter histories seems to have a hard time exploring the region of the posterior in which N is low. Given these technical difficulties, we recommend using the **JAGS** implementation (based on Panel 18.2), and it is always a good idea to use MCMC diagnostic tools such as those available in the `coda` package (Chapter 17).

The take-home message is that, even with simulated data, the precision of the posterior distributions is low and mixing is poor. This should be expected given that we are asking so much from so little data. In essence, we are trying to fit a point process model while being twice removed from the actual point (activity center) locations. These difficulties may warrant the investigation of simpler models at the expense of the mechanistic description of the system. Another option is to figure out ways of improving model precision—options we discuss in Section 18.6. Before doing so, we re-analyze the northern parula (*Parula americana*) data described in Chandler and Royle (2013).

18.5.2 Northern parula in Maryland

The parula data are standard avian point count data, with one exception. Typically, when studying passerines, points are spaced by > 200m in order to maintain statistical independence. In contrast, the parula data were collected at 105 points located on a 50 m grid, which virtually ensures spatial correlation since the parula song can be
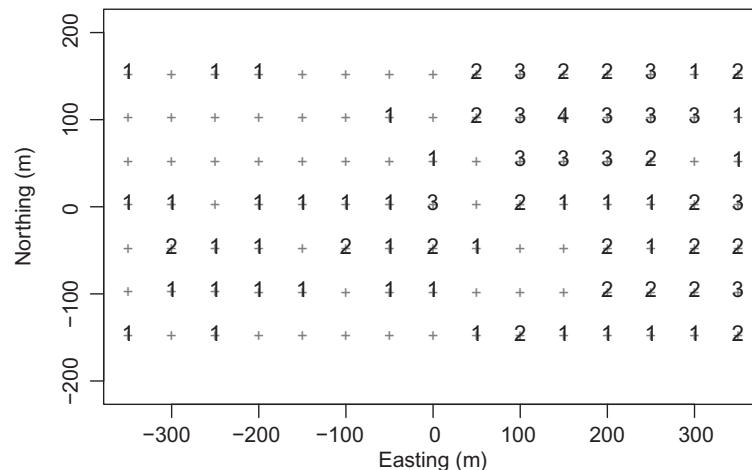

FIGURE 18.3

Spatially correlated counts of northern parula. Gray crosses are the locations of the 105 point count stations. Superimposed are the number of detections after three survey occasions.

heard from distances > 50m. Each point was surveyed three times during June 2006, and Figure 18.3 depicts the resulting spatially correlated counts ($n_{j.}$). A total of 226 detections were made with a maximum count of 4 during a single survey. At 38 points, no birds were detected. All but one of the detections were of singing males, and this one observation was not included in the analysis.

We fit the model using **JAGS** and the code from Panel 18.2, which does not include the latent encounter histories. For comparative purposes, we used two sets of priors: (1) the improper uniform priors considered by Chandler and Royle (2013) and (2) proper Gamma(0.001, 0.001) priors for σ and λ_0 as well as an approximate $N \propto 1/N$ prior, which is (almost) the Jeffreys prior (see Link (in review) and Link and Barker (2010) for details on Jeffreys prior). The state-space created by buffering the grid of point count locations by 250 m. M was set to 300. To reduce computation time, we used the parallel package and distributed three chains to three separate cores. The entire example can be reproduced using the code on the help page for nopa in our **R** package scrbook. The following code illustrates the essential elements:

```
> library(scrbook)
> library(rjags)
> dat2 <- list(n = nopa$n, X = nopa$X, M=300, J=nrow(nopa$n), K=ncol(nopa$n),
+              xlim=c(-600, 600), ylim=c(-400, 400))
> init2 <- function() {
+    list(sigma=rnorm(1, 100), lam0=runif(1), z=rep(1, dat2$M))
+ }
> cl2 <- makeCluster(3) # Open 3 parallel R instances
> clusterExport(cl2, c("dat2", "init2", "pars1")) # send objects to 3 cores
> out2 <- clusterEvalQ(cl2, {# executes the folowing commands on each core
+    library(rjags)
+    jm <- jags.model("nopa2.jag", dat2, init2, n.chains=1, n.adapt=1000)
+    jc <- coda.samples(jm, pars1, n.iter=150000)
+    return(as.mcmc (jc))
+ })
> mc2 <- mcmc.list(out2) # put the 3 chains together
> plot(mc2)
> summary(mc2)
```

18.6 Extensions of the spatial count model

18.6.1 Improving precision

The results of the parula analysis are presented in (Table 18.2). Once again, we see wide credible intervals for N and high sensitivity to the priors. These limitations support the conclusions of Chandler and Royle (2013) that researchers should: (1) elicit prior information from the published literature and/or (2) mark a subset of individuals when applying the SC model. Both of these options should be readily accomplished in many studies, especially the first option because extensive information on home range size has been compiled for many species in diverse habitats (e.g., DeGraaf and Yamasaki, 2001), which can be embodied as a prior distribution for

Table 18.2 Posterior summary statistics for spatial count model applied to the northern parula data. Note the sensitivity of the posterior to the two different prior distributions.

Par	Prior	Mean	SD	2.5%	50%	97.5%
N	DUnif(0,300)	38.474	37.275	1.000	29.000	138.000
λ_0	Unif(0,∞)	0.310	0.183	0.082	0.269	0.817
σ	Unif(0,∞)	127.935	99.303	44.760	87.291	438.374
N	$\propto 1/N$	29.591	32.555	1.000	19.000	119.000
λ_0	Gamma(0.001,0.001)	0.309	0.194	0.078	0.261	0.843
σ	Gamma(0.001,0.001)	150.183	105.044	48.735	117.069	447.616

the encounter rate parameter σ in a Bayesian analysis (Chandler and Royle (2013), Chapter 5).

In some cases, it may not be possible to mark any individuals, and no prior information may exist about encounter parameters; however, it may be possible to improve precision by collecting auxiliary data, such as distance measurements. In fact, in the parula study, detections were classified as either within or beyond 150 m, and it seems sensible to expand the model to accommodate this rudimentary distance sampling data. But if auxiliary data such as distance measurements exist, why bother with the SC model at all since density can be estimated using the distance data alone? This is a good point, and in general, the simplest model that does the job should be preferred. The reasons why one might prefer an expanded SC model over a simple distance sampling model include the ability to model spatial correlation and the ability to model movement. But how exactly can the SC model be extended to accommodate such auxiliary data?

The basic extension that we consider here is to use a type of search-encounter model (Chapter 15) that includes the activity centers (**s**) and the actual locations of individuals (**u**). By including both activity centers and actual locations in the model, abundance in any region $\mathcal{B}$ is given by

$$N(\mathcal{B}) = \sum_i I(\mathbf{u}_i \in \mathcal{B}). \tag{18.6.1}$$

Thus, in the context of distance sampling studies in which the distance data are recorded in discrete intervals, the region $\mathcal{B}$ would be the area corresponding to a particular distance interval. The probability of detecting the individuals $N(\mathcal{B})$ would be the average detection probability $\bar{p}$, which is computed by integrating a distance-based detection function over the distance interval.

In other contexts, such as when conducting removal surveys, the region $\mathcal{B}$ could be a fixed-area plot, such as a stream segment. Again, Eq. (18.6.1) could be used to model local abundance ($N(\mathcal{B})$), and detection probability within the region could be modeled conditional on $N(\mathcal{B})$. A reasonably general description of this model is as

follows:

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

$$\mathbf{u}_{ik} \sim \text{BVN}(\mathbf{s}_i, \boldsymbol{\Sigma}),$$

$$N(\mathcal{B}_{jk}) = \sum_{i=1}^{M} I(\mathbf{u}_{ik} \in \mathcal{B}_{jk}),$$

$$n_{jkl} \sim \text{Binomial}(N(\mathcal{B}_{jkl}), p),$$

where $\boldsymbol{\Sigma} = \begin{pmatrix} \tau & 0 \\ 0 & \tau \end{pmatrix}$, with τ governing the size of the bivariate normal home range. The interpretation of the parameter p will depend upon the survey protocol (Nichols et al., 2009).

When plots are far enough apart that individuals cannot move between them, the counts will be uncorrelated and the model can be approximated using a non-spatial N-mixture model allowing for temporary emigration (Chandler et al., 2011). In the next example, we consider data in which the plots are obviously not independent.

18.6.2 Dusky salamanders in Maryland

The independence assumption of the Chandler et al. (2011) model will not always hold. A prime example is in studies of aquatic species in stream networks. For example, consider the data depicted in Figure 18.4. The figure shows counts of northern dusky salamanders (*Desmognathus fuscus*) in 25 m stretches on a small stream in the Chesapeake and Ohio National Historic Park. The data were collected by E.H.C. Grant and colleagues with the objective of understanding the spatial and temporal dynamics of salamander populations in response to seasonal and annual variations in stream hydrology.

To sample the population, the stream networks were divided into 25 m stretches, and in each stretch, "temporary" removal sampling was conducted, which involves capturing and removing salamanders on three consecutive passes. The salamanders are placed in individual plastic baggies for the brief 30–60 min duration of sampling and then they are released at the location of capture. The entire process is repeated 3–4 times per season (May–August). In a subset of streams and years, individuals are marked, but in general it is too expensive to mark all of the captured individuals, and the data considered here consists entirely of unmarked individuals.

The sampling protocol may be thought of as a "robust design" (Pollock, 1982), with "occasions" (typically 1 day) being the primary period, and secondary samples being the removal passes within the primary periods. An obvious feature of these data is that the neighboring counts are spatially correlated. In this case, we have reason to believe that this correlation is the result of habitat preferences, with individuals actively selecting habitat in the upper reaches of the streams. This could be modeled as a function of a covariate describing the distance from the mouth of the stream. Another obvious feature of this data is that the pattern of spatial correlation remains consistent between occasions, but the overall counts decline markedly over the course of the season. These phenomena can be explained by the fact that the salamanders have
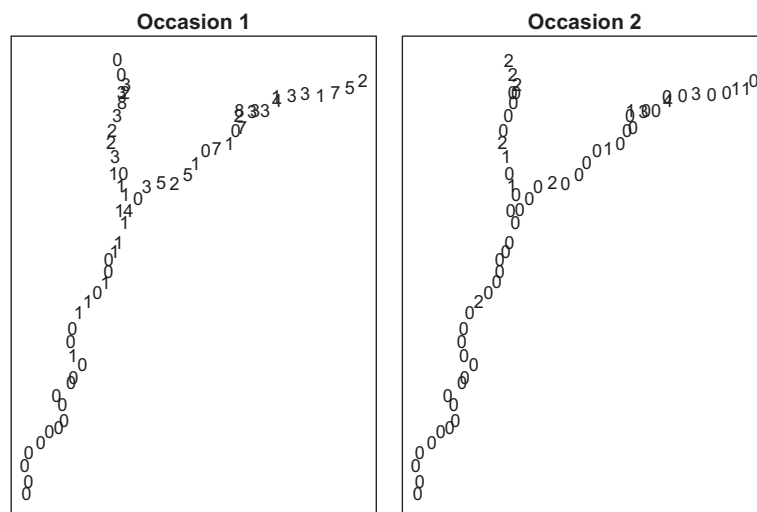
FIGURE 18.4

Stream segment counts of northern dusky salamanders in the Chesapeake and Ohio National Historic Park, VA/MD. Each number is the count associated with a 25 m stretch in which three removal passes were made on three occasions each summer (only two occasions are shown here). Notice the consistency of the spatial correlation between occasions and the temporal decline in the counts.

relatively small home ranges, and this results in the consistent pattern of correlation among occasions. Furthermore, as the season progresses, the streams dry out, and many individuals move underground.

Given the importance of movement within home ranges, which determines the correlation among occasions, and movement underground, which results in a decreasing number of individuals being available for sampling, it would be helpful to have a model that describes both processes and allows for evaluation of hypotheses regarding the effects of environmental variables. For example, one might ask how stream flow is related to the probability that an individual remains active, i.e., aboveground. A model describing this process could be used to predict activity levels under future conditions. Although we do not investigate covariate effects in this section, we do present a general model allowing for movement among occasions, and for decreasing availability over the season.

This expanded model is founded on the one described in the previous section, but it also includes a removal model for the observation process, and it includes a basic "open" population model to allow for a decline in abundance over time (Chapter 16). Actually, the population is not thought to decline substantially during the season, but rather, the number of individuals *available* for detection declines because many

```
model {
phi ~ dbeta(1,1)      # "availability" parameter
tau ~ dunif(0, 1000)  # "movement parameter" of Gaussian kernel model
p ~ dbeta(1,1)        # detection prob
psi ~ dbeta(1,1)      # data augmentation parameter
for(i in 1:M) {
  z[i,1] ~ dbern(psi)       # is the individual real?
  z[i,2] ~ dbern(z[i,1]*phi) # and still aboveground?
  z[i,3] ~ dbern(z[i,2]*phi) # ...
  s[i] ~ dcat(PrSeg[]) # location (stream segment) of activity center
  for(g in 1:G) {
    PrU[i,g] <- exp(-distmat[s[i],g]^2/(2*tau^2)) # Pr(u | s)
    }
  for(k in 1:K) {
    u[i,k] ~ dcat(PrU[i,]) # location of guy i at time k
    for(g in 1:G) {
      y[i,g,k] <- (u[i,k] == g)*z[i,k] # was individual at u==g?
      }
    }
  }
for(j in 1:J) {
  for(k in 1:K) {
    NB[j,k] <- sum(y[,seg[j],k]) # Number in seg j at time k
    # removal model:
    n[j,1,k] ~ dbin(p, NB[j,k])
    NB2[j,k] <- NB[j,k] - n[j,1,k]
    n[j,2,k] ~ dbin(p, NB2[j,k])
    NB3[j,k] <- NB2[j,k] - n[j,2,k]
    n[j,3,k] ~ dbin(p, NB3[j,k])
    }
  }
N[1] <- sum(z[,1]) # Total abundance, occasion 1
N[2] <- sum(z[,2]) # Total abundance, occasion 2
N[3] <- sum(z[,3]) # Total abundance, occasion 3
}
```

PANEL 18.3

BUGS description of model for the data shown in Figure 18.4. The model allows for spatially-explicit temporary emigration, and for a decrease in abundance as individuals move underground throughout the course of the season.

individuals move underground as the streams dry. Each of these components is included in the **BUGS** description of the model presented in Panel 18.3.

We fit this model to the data and obtained the posterior distributions summarized in Table 18.3. The results indicate that the population size available for detection did decrease rapidly during the season, the rate of which is determined by the ϕ parameter. Modeling this parameter as a function of water flow or volume would allow one to

Table 18.3 Posterior summarizes from removal model of salamander counts allowing for movement and decreasing population size over the course of a breeding season.

Parameter	Mean	SD	2.5%	50%	97.5%
N_1	178.393	16.346	151.000	177.000	214.000
N_2	62.322	6.884	51.000	62.000	77.000
N_3	21.202	3.695	15.000	21.000	29.000
ϕ	0.348	0.038	0.275	0.348	0.425
τ	27.427	3.200	21.293	27.173	33.706
p	0.396	0.053	0.294	0.394	0.502

predict salamander activity under future environmental conditions. Another result of the analysis is that the movement parameter, τ, was relatively low, indicating that adult salamanders rarely move more than 100 m from their home range center during a season. This explains why the distribution of individuals within the stream remains relatively constant over time.

18.7 Summary and outlook

Unlike traditional models of count data used in ecology, the SC model is parameterized in terms of *individuals*—individuals that just so happen not to be marked. Although developing the model in terms of latent encounters increases model complexity, several reasons exist for accommodating this latent structure. First, it allows for individual-level covariates, including the location of each individual in the population. Second, by including an underlying point process specific to individual activity centers (and possibly locations in time), the model allows for modeling continuous variation in density, which, if ignored, may result in bias in conventional models of count data. Third, accommodating the latent structure provides a more mechanistic description of ecological systems, for example by attaching a mechanism (movement) to the widely observed phenomenon of spatial correlation in count data.

The SC model is a conceptually simple extension of standard SCR models, but in terms of computational requirements and latent structure, it is perhaps at the extreme end of what is possible to do with count data. As is always true, the harder we try to mirror reality with our models, the harder it becomes to estimate the parameters of the system. In this chapter, we tried to emphasize that as conceptually appealing as the SC model may be, it is unlikely to produce satisfying results in the absence of additional information. However, additional information such as home range size estimates will often be available for many species, and if not, we have provided an alternative method of accommodating additional data in the form of distance measurements or removal counts. This can greatly increase precision of estimates from studies designed to make spatially explicit inferences about population processes.

Although we focused on the situation in which all individuals are unmarked, one of the reasons for developing this class of models was to handle the problem of estimating population size or density when only a subset of individuals are marked. This topic is the subject of the next chapter, which builds on a rich literature of combining data from marked and unmarked individuals for purposes of designing efficient studies Bartmann et al. (1987), Neal et al. (1993), Conroy et al. (2008) and McClintock and White (2009).

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Abstract: All SCR models described in previous chapters address the classical situation (of all capture-recapture studies) in which individuals in the population can be uniquely identified when captured. This is not always possible using common methods of sampling. In this chapter, we investigate spatially explicit alternatives for estimating density of unmarked populations. That is, when individual identity is not possible or not available. We develop a framework for inference in these cases by specifying a model for observed trap-specific counts that is conditional on an underlying SCR model. The encounter histories are completely latent and the observed counts are aggregations of the latent encounter histories. Because the model is formulated in terms of the data we wish we had, i.e., the typical encounter history data observed in standard capture-recapture studies of marked animals, the model for counts is just a SCR model with a single extension to account for the fact that the encounter history data are unobserved. Using the methods in this chapter, we find that SCR models can be applied to data collected using methods like points counts in which observers record simple counts of animals at an array of survey locations. The model can also be fitted to camera trapping data collected on unmarked animals, representing one of the first formal method for estimating density from such data. To demonstrate the model, we begin by applying it in its most basic form to simulated data. Then we proceed, by way of a few examples, to consider extensions of the model in which ancillary information can be used to increase precision. Extensions of the method to improve precision include obtaining informative priors based on information from the literature, or using a subsample of marked individuals (covered in detail in Chapter 19). The method can also be extended to include other sampling protocols or model structures, and we provide an application to sampling salamanders along a stream which involves a removal type of sampling protocol. The model for the salamander data also includes a spatially explicit submodel for temporary emigration, allowing for movement-induced correlation in the count data from neighboring stream segments.

Keywords: Spatial correlation, Spatial model, Process convolution, Data augmentation, N-mixture model