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AU:1, page 370	Please check the citation of "Section [7.2.4]" in sentence "However, we have noted previously ...", and correct if necessary.

# Stratified Populations: Multi-Session and Multi-Site Data

# 14

p0005 In this chapter, we describe SCR models for situations when we have multiple distinct sample groups, strata, or “sessions” (the term used in `secr`) each with a population size parameter  $N_g$ , for group  $g$ . Such “stratified” populations are commonplace in capture-recapture studies, especially in the context where the strata represent distinct spatial regions, yet most SCR applications have been based on models that are distinctly single-population models. This is done either by analyzing separate data sets one-at-a-time, producing many, ~~if not dozens, of~~ independent estimates of abundance, or by pooling data from multiple study areas. A standard example that arises frequently is that in which multiple habitat patches (often refuges, parks, or reserves) are sampled independently with the goal of estimating the population size of some focal species in each reserve. If there are parameters that can be shared across sessions or groups, it makes sense to combine the data together into a single model that permits the sharing of information about some parameters, but provides individual estimates of abundance for each land unit. A similar situation is that in which a number of replicate trap arrays are located within a landscape, sometimes for purposes of evaluating the effects of management actions or landscape structure on populations. This is a common situation in studies of small mammals (Converse et al., 2006a,b; Converse and Royle, 2012), or in mist-netting of birds (DeSante et al., 1995), but there are examples of large-scale monitoring of carnivores and other species too, e.g., tigers (Jhala et al., 2011).

p0010 In previous chapters, we’ve analyzed data for a number of examples that have a natural stratification or group structure. In Chapter 9, we analyzed the ovenbird data as an example of a multi-catch (independent multinomial) model, where we used year as the stratification variable, and the possum data ~~set~~ (illustrating the single-catch situation) in which the group structure arose from the use of five distinct trap arrays. In Chapters 7 and 8 we fitted models with sex specificity of parameters using multi-session models, where the stratification variable in that case was sex. In this chapter, we focus on Bayesian analysis of stratified SCR models using data augmentation (Converse and Royle, 2012; Royle et al., 2012e). The technical modification of data augmentation to deal with such models is that it is based on a model for the joint distribution of the stratum-specific population sizes,  $N_g$ , **conditioned** on their total. This results in a multinomial distribution for all  $N_g$ , which we can analyze in some generality using data augmentation. As a practical matter, specification of this

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multinomial distribution for the  $N_g$  parameters **induces** a distribution for an individual covariate, say  $g_i$ , which is “group membership.” This is extremely handy to analyze by MCMC in the various **BUGS** engines that you are familiar with by now, ~~and the~~ flexibility of model specification in **BUGS** is why we focus a whole chapter here on Bayesian analysis ~~by~~ data augmentation. However, we have noted previously that the **R** package `secr` fits a class of multi-session models which we ~~have already seen~~ (Section 6.5.4), ~~and we used `secr` to analyze several case studies using the multi-session models including the ovenbird (Section 9.2.4) and the possum data (Section 7.2.4), and models with sex-specific parameters in Chapters 7 and 8.~~

**AU:1**

In the stratified population models considered here, an individual is assumed to be a member of a single stratum, so that the population sizes  $N_g$  for the  $g$  strata are independent of one another. However, stratified or multi-session SCR models are also directly relevant when the stratification index is time, either involving distinct periods within a biological season, or even across years. In this case, individuals might belong to multiple of the strata, but, the models discussed in this chapter do not acknowledge that explicitly. Unlike the case in which the strata represent spatial units, with temporally defined strata, we imagine a fully dynamic, or demographically open model for  $N$  might be appropriate—one that involves survival and recruitment. We deal with those models specifically in Chapter 16. However, the stratified models covered here can be thought of as a primitive type of model for open systems in which the population sizes are assumed to be **independent** across temporal strata, and so we might still find them useful in cases where the strata are temporal periods or sessions.

p0015

### 14.1 Stratified data structure

s0005

We suppose that  $g = 1, 2, \dots, G$  strata (or groups), having sizes  $N_g$ , and state-spaces  $S_g$ , are sampled using some capture-recapture method producing sample sizes of  $n_g$  unique individuals and encounters  $y_{ijk}$  for individual  $i = 1, 2, \dots, \sum_{g=1}^G n_g$ . Right now we won’t be concerned with the details of every type of capture-recapture observation model so, for context, and to develop some technical notions, we consider a Bernoulli encounter model in which individual ~~and~~ trap-specific encounter frequencies are binomial counts:  $y_{ij} \sim \text{Binomial}(K, p_{ij})$ . Let  $g_i$  be a covariate (integer-valued,  $1, \dots, G$ ) indicating the group membership of individual  $i$ . This covariate is **observed** for the sample of captured individuals but not for individuals that are never captured.

p0020

To illustrate the prototypical data structure for stratified SCR data, we suppose that a population comprised of four groups is sampled  $K = 5$  times. Then, a plausible data set has the following structure:

p0025

individual (i):	1	2	3	4	5	6	7	8	9	10
total encounters (y):	1	1	3	1	1	2	2	4	1	1
group (g):	1	1	1	2	3	3	3	3	4	4

This data set indicates three individuals were captured in group 1 (captured 1, 1, and 3 times), a single individual was captured in group 2, four individuals were captured in group 3, and two individuals were captured in group 4.

p0030 A key idea discussed shortly is that the assumption of certain models for the collection of abundance variables  $N_g$  implies a specific model for the group membership variable  $g_i$ . Then, the data from all groups can be pooled, and analyzed as data from a single population with the appropriate model on  $g_i$ , without having to deal with the  $N_g$  parameters in the model directly. In this way, we can easily build hierarchical models for stratified populations, using an *individual*-level parameterization of the model. Obviously, this is important for SCR models as they all possess at least one individual-level random effect in the form of the activity center  $s$ . In the context of stratified or multi-session type models, the “population membership” variable  $g_i$  is a *categorical* type of individual covariate (Huggins, 1989; Alho, 1990; Royle, 2009b). Before considering SCR models specifically, in the next section we talk a little bit about the technical formulation of data augmentation for stratified populations in the context of ordinary closed population models.

## 14.2 Multinomial abundance models

s0010  
p0035 One of the key ideas to Bayesian analysis of stratified population models is that we make use of multinomial models for allocating individuals into strata or sessions. We do this because it allows us to analyze the models by data augmentation (Converse and Royle, 2012; Royle and Converse, in review), and it has a natural linkage to the Poisson model, which is commonly used throughout ecology to model variation in abundance.

p0040 To motivate the technical framework, consider sampling  $g = 1, 2, \dots, G$  groups having unknown sizes  $N_g$ , and we wish to impose model structure on the group-specific population size variables using a Poisson distribution:

$$N_g \sim \text{Poisson}(\lambda_g) \quad (14.2.1)$$

with

$$\log(\lambda_g) = \beta_0 + \beta_1 C_g, \quad (14.2.2)$$

where  $C_g$  is some measured attribute for group  $g$ . We could generalize this a bit by considering a random effect in Eq. (14.2.2), producing overdispersed population sizes  $N_g$ . For the special case of adding log-gamma noise, this results in negative binomial models for  $N_g$ .

p0045 To develop a data augmentation scheme for this group-structured model, let’s think about doing data augmentation on each population *individually*, by assuming that

$$N_g \sim \text{Binomial}(M_g, \psi),$$

where  $\psi \sim \text{Uniform}(0, 1)$  as usual. ~~A key point is that we allow  $M_g$  to be population specific but  $\psi$  is constant.~~ We could do this multi-population data augmentation by

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just picking each  $M_g$  to be some large integer (as we always do by data augmentation; see Section 9.2.4). However, we want to pick  $M_g$  in a way that induces the correct structure on  $N_g$ . If we want to enforce our Poisson model on  $N_g$  from above, we naturally choose  $M_g$  to be Poisson also, in which case the marginal distribution of  $N_g$  is also Poisson, but with mean  $\psi \exp(\beta_0 + \beta_1 C_g)$ . Here, clearly  $\psi$  and  $\beta_0$  are confounded (see below for more discussion). Regardless, for multiple groups that we want to model jointly, the key point is that we impose the structure that we desire for  $N_g$ , on the super-population parameters  $M_g$ . To implement this model at the individual level we need to get rid of the  $M_g$  parameters (which is the entire motivation of data augmentation in the first place). So we condition on the “total super-population” size  $M_T = \sum_g M_g$  (in a sense, this is the super-super-population!). Then, the vector  $\mathbf{M} = (M_1, \dots, M_G)$  has a multinomial distribution:

$$\mathbf{M} | M_T \sim \text{Multinomial}(M_T; \boldsymbol{\pi}), \quad (14.2.3)$$

where  $\pi_g = \lambda_g / \sum_g \lambda_g$ . This is handy because we can implement this model, e.g., in **BUGS**, by introducing a variable  $g_i$  for each  $i = 1, 2, \dots, M_T$  which is the “group membership” of each individual in the super-super-population. Then, conditional on  $g_i$ , an individual is either “real,” or a pseudo-individual, according to the binary data augmentation variable  $z_i$ . As specified in **BUGS** pseudo-code, the model is:

```
psi ~ dunif (0,1)                                o0005
for (g in 1:G){                                    o0010
  pi[g] <- lambda[g]/sum(lambda[])                 o0015
}                                                    o0020
g[i] ~ dcat(pi[1:G])                               o0025
z[i] ~ dbern(psi)                                   o0030
```

This produces a vector of population size parameters  $\mathbf{N} = (N_1, \dots, N_G)$  which are approximately, for large  $M_T$ , independent Poisson random variables.

When we apply data augmentation to the multinomial joint distribution, the  $\psi$  parameter takes the place of  $N_T$ , the total population size (across all groups or strata). In addition, by constructing the model conditional on the total,  $N_T$ , we lose information about the intercept  $\beta_0$ <sup>1</sup> but this is recovered in the data augmentation parameter  $\psi$ . Thus, one of these parameters has to be fixed. We can set  $\beta_0 = 0$  or else we can fix  $\psi$  (see Chapter 11). The constraint can be specified by noting that, under the binomial data augmentation model,  $\mathbb{E}(N_T) = \psi M_T$  and, under the Poisson model,  $\mathbb{E}(N_T) = \sum_g \exp(\beta_0 + \beta_1 C_g)$  and so we can set

$$\psi = \frac{1}{M_T} \sum_g \exp(\beta_0 + \beta_1 C_g).$$

<sup>1</sup>A technical argument is that the total  $N_T$  is the sufficient statistic for  $\beta_0$  in the multinomial model and so, by conditioning on the total,  $\beta_0$  is no longer a free parameter. np005

The linkage of  $\beta_0$  and  $\psi$  was also discussed in Chapter 11 in the context of building spatial models for density. In that case,  $\beta_0$  was the intercept of the intensity function and one could choose to estimate either  $\beta_0$  or the data augmentation parameter  $\psi$ .

### s0015 14.2.1 Implementation in BUGS

p0055 The **BUGS** implementation of data augmentation for structured populations is straightforward. For each individual in the ~~super~~-super-population we introduce a latent variable  $g_i$  to indicate which *population* the individual belongs too, and we introduce a second variable  $z_i$  to indicate whether the individual is ~~alive or not~~. So, the latent structure for the  $M_g$  variables and the binomial sampling of those super-population sizes is equivalently represented by the latent variable pair  $(g_i, z_i)$  where  $g_i$  is categorical with prior probabilities  $\pi_g$  and  $z_i \sim \text{Bernoulli}(\psi)$ . In particular, the multinomial assumption for the latent variables  $M_g$  is formulated in terms of “group membership” for each individual in the ~~super~~-super-population of size  $M_T$  according to:

$$g_i \sim \text{Categorical}(\boldsymbol{\pi})$$

with  $\boldsymbol{\pi} = (\pi_1, \dots, \pi_G)$  and  $\pi_g = \lambda_g / (\sum_g \lambda_g)$ . The binomial sampling is described by the binary variables  $z_1, \dots, z_{M_T}$  such that

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

where  $\psi$  is constrained as noted in the previous section. The **BUGS** model specification for this individual-level formulation of the model is shown in Panel 14.1 for an ordinary closed population model (model  $M_0$ ). This actually shows two equivalent formulations. In the left panel we have  $\psi$  and  $\beta_0$  as free parameters. The right panel shows the equivalent model but recognizing the constraint between  $\psi$  and  $\beta_0$ . Running these models using the `multisession.sim` function, you can verify that the two parameters are not uniquely estimable. In particular, using the model (representation 1) in the left-hand side of Panel 14.1, you will see that draws of  $\beta_0$  appear to be draws from the prior distribution, uninformed by the data, supporting the point we made previously that  $\psi$  and  $\beta_0$  are not uniquely informed by the data.

### s0020 14.2.2 Groups with no individuals observed

p0060 In practical settings, when the groups represent small populations, it will sometimes happen that some ~~groups~~ have no encountered individuals or even that  $N_g = 0$  ~~for some groups~~. This is dealt with implicitly in the development of the model shown in Panel 14.1 in the sense that the *prior* for  $N_g$  has the proper dimension (namely,  $G$  multinomial cells of non-zero probability) and thus some posterior mass may occur on non-zero values of  $N_g$  even if the *data* contain no representatives of group  $g$ . You can try this out to verify for yourself.

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Implementation 1	Implementation 2
<pre> model { # This will show that psi and b0 # are confounded. p ~ dunif(0,1) beta0 ~ dnorm(0,.1) beta1 ~ dnorm(0,.1) psi ~ dunif(0,1) for(j in 1:G){   log(lam[j]) &lt;- beta0+beta1*C[j]   gprobs[j]&lt;-lam[j]/sum(lam[1:G]) } for(i in 1:M){   g[i] ~ dcat(gprobs[])   z[i] ~ dbern(psi)   mu[i] &lt;- z[i]*p   y[i] ~ dbin(mu[i],K) } N &lt;- sum(z[1:M]) } </pre>	<pre> model { # This version constrains psi with # the intercept parameter p ~ dunif(0,1) beta0 ~ dnorm(0,.1) beta1 ~ dnorm(0,.1) psi &lt;- sum(lam[])/M for(j in 1:G){   log(lam[j]) &lt;- beta0+beta1*C[j]   gprobs[j]&lt;-lam[j]/sum(lam[1:G]) } for(i in 1:M){   g[i] ~ dcat(gprobs[])   z[i] ~ dbern(psi)   mu[i] &lt;- z[i]*p   y[i] ~ dbin(mu[i],K) } N &lt;- sum(z[1:M]) } </pre>

### PANEL 14.1

BUGS model specification for a capture-recapture model with constant encounter probability and Poisson subpopulation sizes,  $N_g$ , with mean depending on a single covariate  $C[j]$ . Two versions of the model: The first one describes the model in terms of the intercept  $\beta_0$  and DA parameter  $\psi$ , which are confounded. The required constraint is indicated in the specification under Implementation 2.

### 14.2.3 The group-means model

s0025

Under the Poisson model for group abundance  $N_g$ , even with a constant mean  $\lambda$ , each stratum or group may have a different realized population size, and this comes at the low price of a single parameter in the model ( $\lambda$  or, equivalently, the data augmentation parameter  $\psi$ ). ~~Thus, for a single parameter in this group-structured model, we are able to realize variation in the  $N_g$  parameters. In a sense, this is a benefit of the group structure in which  $N_g$  are regarded as random variables.~~

p0065

To accommodate more flexibility than afforded by the single-parameter Poisson model, there are a couple of choices: (1) We could allow the mean to be group specific such as:  $N_g \sim \text{Poisson}(\lambda_g)$  where each  $\lambda_g$  is its own free parameter, independent of each other. This produces a model with  $G$  distinct “fixed” parameters, and effectively renders the Poisson assumption irrelevant as it doesn’t induce any “Bayesian shrinkage” (Sauer and Link, 2002) or impose any group structure on the population sizes  $N_g$ . It should provide estimates that are effectively the same as analyzing each data set independently, or using the independent binomial prior that we introduced in Chapter 9, where some information might be borrowed from the different groups

p0070

for estimating the encounter probability parameters. Under this model, we constrain one of the  $\lambda_g$  parameters to be 0, and  $N_g$  for that group is taken up by the data augmentation parameter  $\psi$ ; (2) Alternatively, we could identify specific fixed covariates which might explain variation across groups. Each additional covariate adds only one additional fixed parameter to the model; (3) A flexible formulation that provides something of an intermediate model, between that of a constant  $\lambda$  and independent group-specific  $\lambda_g$ s, is that in which we put a prior on  $\lambda_g$ . For example, if we assume

$$\lambda_g \sim \text{Gamma}(a, b)$$

this corresponds to imposing a Dirichlet compound-multinomial model on the population size vector, or, marginally, a negative binomial model on  $N_g$ . See [Takemura \(1999\)](#) for some discussion of such models relevant to data augmentation. For this model, we impose the constraint  $b = 1$  to account for conditioning on the total population size  $N_T$  to use data augmentation.

#### s0030 14.2.4 Simulating stratified capture-recapture data

p0075 It is helpful, as always, to simulate some data in order to understand the model. Suppose we cracked the conservation lotto jackpot and obtained funding to carry out a camera trapping study of some flashy carnivore in 20 forest patches or reserves, using a  $5 \times 5$  array of traps. Here we will consider an ordinary closed population model, model  $M_0$ , and we suppose there is some forest level covariate, say  $\text{Dist}_g =$  disturbance regime, perhaps measured by an index of trail density or something. We imagine a model for patch-level population size such as the following:

$$N_g \sim \text{Poisson}(\lambda_g),$$

$$\log(\lambda_g) = \beta_0 + \beta_1 \text{Dist}_g.$$

We simulate some population sizes and encounter data under this model as follows:

```
> set.seed(2013)
> G <- 20                                # G = 20 groups or strata
> beta0 <- 3                             # Abundance model parameters
> beta1 <- .6
> p <- .3                                 # Encounter probability
> K <- 5                                  # Sample occasions for capture-recapture
> Dist <- rnorm(G)                       # Simulate covariate
> lambda <- exp(beta0+beta1*Dist)         # Simulate population sizes
> N <- rpois(G,lambda=lambda)

> y <- NULL                               # Simulate model M0 data
> for(g in 1:G){
+   if(N[g]>0)
+     y <- c(y, rbinom(N[g],K,p))
+ }
> g<- rep(1:G,N)

> ## Now keep the group id and encounter frequency only for
> ## individuals that are captured
> g<-g[y>0]
> y<-y[y>0]
```



That's it! We just simulated a population size model and capture-recapture data for the populations inhabiting  $G = 20$  forest patches (the "groups" in this situation). To fit this model, we need to augment the  $\mathbf{g}$  and  $\mathbf{y}$  data objects, and then we can run the model in **JAGS** or **WinBUGS** using the code given in Panel 14.1. See the help file `?multisession.sim` for doing this analysis with these simulated data.

### 14.3 Other approaches to multi-session models

s0035

The multinomial super-population model allows for the joint modeling of a collection of population sizes using data augmentation. However, as we demonstrated in Section 9.2.4, we can analyze the models by putting independent binomial priors on each  $N_g$  and doing the data augmentation independently for each population by itself. This is not any more or less difficult than the multinomial formulation but, we imagine, it could be slightly less efficient computationally. In this case we could build in among-group structure by modeling the DA parameter  $\psi$  as being variable for each subject, as a function of group-specific variables (see [Hendriks et al., 2013](#), for an example). For example, if  $C_g$  is the value of some covariate for group  $g$ , then we could have  $z_i \sim \text{Bernoulli}(\psi_i)$  with

p0080

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 C_{g_i}.$$

This implies a binomial model for the stratum population sizes:

$$N_g \sim \text{Binomial}(M, \psi_g).$$

If  $M$  is large then the  $N_g$  are approximately independent Poisson random variables with means  $\psi_g M$ .

As we noted in Chapter 6, the multi-session models in `secr` are based on a Poisson prior for  $N_g$  with mean  $\Lambda_g$ , and then among-group structure is modeled in the parameter  $\Lambda_{g_i}$ . In our view, either model (binomial based on data augmentation, or Poisson) is satisfactory for any application of capture-recapture to stratified populations. The main advantage of the formulation we provided here over that implemented in `secr` is we have quite a bit more flexibility in specifying models of all sorts, either in the population size model for  $N_g$ , or for the capture-recapture model. For example, [Royle and Converse \(in review\)](#) fitted a model having random group effects on encounter probability and abundance (i.e., extra-Poisson variation).

p0085

### 14.4 Application to spatial capture-recapture

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Although we developed the implementation of Bayesian models for stratified populations using ordinary closed population models, the underlying ideas are completely general and can be applied equally to spatial capture-recapture models without any novel considerations. We already discussed (Chapter 4) that SCR models are ordinary closed population models but with an individual covariate which is the activity

p0090

center  $\mathbf{s}_i$ , and the observation model has to be defined for each trap. With this in mind, it should be obvious how the **BUGS** specification in Panel 14.1 can be modified to accommodate a group-structured SCR situation. Specifically, we include the prior distribution for  $\mathbf{s}_i$  and the observation model that relates  $\mathbf{s}_i$  to the probability of encounter for individual  $i$  and trap  $j$ , as we've done so many times in previous chapters.

#### s0045 14.4.1 Multinomial (“multi-catch”) observations

p0095 We discuss Bayesian analysis of the multi-session model using data augmentation in the context of a multinomial observation model such as for a multi-catch sampling situation.<sup>2</sup> For context, we return to the ovenbird data set, from the **R** package `secr`, which we introduced in Chapter 9. Another example can be found in Royle and Converse (in review), who applied the model to a small-mammal trapping problem which involved replicate “single-catch” arrays of traps, in a study of the effects of forest management practices on small-mammal densities. The ovenbird data is a type of multi-catch observation model where the group index variable is “year” and, in our earlier analyses, we analyzed the data set using independent binomial priors for  $N_g$  within data augmentation in **JAGS**, as well as with a Poisson prior in `secr` using the multi-session models. We mirror the `secr` analysis here, but using the data augmentation formulation leading to a multinomial distribution for  $N_g$  we introduced above.

p0100 To refresh your memory about the multinomial observation model, let  $\mathbf{y}_{ik} = (y_{i1k}, y_{i2k}, \dots, y_{iJk}, y_{i,J+1,k})$  be the spatial encounter history for individual  $i$ , during sample occasion  $k$  where the last element  $y_{i,J+1,k}$  corresponds to “not captured.” For mist nets, an individual can be captured in at most one trap. Then, the vector  $(y_{i1k}, y_{i2k}, \dots, y_{iJk}, y_{i,J+1,k})$ , contains a single 1 and the remaining values are 0. This  $(J + 1) \times 1$  vector  $\mathbf{y}_{ik}$  is a multinomial trial:

$$\mathbf{y}_{ik} \sim \text{Multinomial}(n = 1; \boldsymbol{\pi}_{ik}),$$

where  $\boldsymbol{\pi}_{ik}$  is a  $(J + 1) \times 1$  vector where each element represents the probability of being encountered in a trap (for elements  $1, \dots, J$ ) or not captured at all (element  $J + 1$ ).

p0105 For the multinomial observation model, the encounter probability vector is a function of distance between trap locations and individual activity centers, modeled on the multinomial logit scale. The Gaussian encounter probability model is:

$$\text{mlogit}(\pi_{ij}) = \eta_{ij} = \alpha_0 - \alpha_1 \text{dist}(\mathbf{x}_j, \mathbf{s}_i)^2, \quad (14.4.1)$$

where  $\alpha_1 = 1/(2\sigma^2)$  and  $\sigma$  is the scale parameter of the Gaussian model. Then,

$$\pi_{ij} = \exp(\eta_{ij}) / [1 + \sum_j \exp(\eta_{ij})]$$

np010 <sup>2</sup>This might be slightly confusing that we are considering multinomial observation models and multinomial models for group-specific abundance parameters  $N_g$ , but we will take care to be clear about this along the way.

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for each  $j = 1, 2, \dots, J$ , and the last cell corresponding to the event “not captured” is:

$$\pi_{i,J+1} = 1 - \sum_{j=1}^J \pi_{ij}.$$

There are no novel technical considerations in order to model covariates of any kind. For example, in many studies we are concerned with a behavioral response to physical capture. This is typical in small-mammal trapping studies, and in mist-net studies of birds where individuals exhibit net avoidance after first capture. For this, let  $C_{ik}$  be a covariate of previous encounter (i.e.,  $C_{ik} = 0$  before the occasion of first capture, and  $C_{ik} = 1$  thereafter), then we include this covariate in our multinomial observation model as follows:

$$\text{mlogit}(\pi_{ijk}) = \eta_{ijk} = \alpha_0 - \alpha_1 \text{dist}(\mathbf{x}_j, \mathbf{s}_i)^2 + \alpha_2 C_{ik}.$$

We note that, in this case, the multinomial probabilities depend not only on individual and trap, but also on sample occasion.

### 14.4.2 Reanalysis of the ovenbird data

Here we use Bayesian analysis by data augmentation to fit a model that approximates the Poisson model with expected value  $\mathbb{E}(N_g) = \lambda_g$  where we model effects on the log-mean scale according to:

$$\log(\lambda_g) = \beta_0 + \beta_1 C_g.$$

We considered only two models here: A model with year-specific abundance, and a model with a linear trend in density over time, so  $C_g \equiv \text{Year}$ . However, using the Kuo and Mallick (1998) indicator variable selection idea (see Chapter 8), the linear trend term was found to have little or no posterior probability, so we do not reproduce analyses of that here (but see the `ovenbird.ms` function for the **R** script). We show the **BUGS** model specification for the year-specific abundance model in Panel 14.2. Note the construction of the multinomial cell probabilities which distribute individuals among years, based on the year-specific mean  $\lambda_t$ . On the log scale, each of these parameters has a diffuse normal prior: `beta0[t] ~ dnorm(0, 0.01)`. A few lines of model specification that compute the derived population size parameters and density are not shown, but you can look at the **R** script `ovenbird.ms` in `scrbook` to run this analysis, and produce the posterior summaries shown in Table 14.1.

We previously analyzed these data in Section 9.2.4 using `secr` and the “one-at-a-time” data augmentation approach (independent binomial priors for  $N_t$ ). To reproduce those results from `secr` for the equivalent model, we execute this command:

```
> ovenbird.model.DT<-secr.fit (ovenCH,model=list (D~session),buffer=300)
```

Note, small values of `buffer` can produce a warning that it is too small relative to the indicated value of  $\sigma$  (which has posterior mass up to near  $\sigma = 100$ ). The

```

model {
  alpha0 ~ dnorm(0,.01)                # Prior distributions
  sigma ~ dunif(0,200)
  alpha1 <- 1/(2*sigma*sigma)
  psi <- sum(lambda[])/bigM
  for(t in 1:5){
    beta0[t] ~ dnorm(0,0.01)           # Year-specific abundances
    log(lambda[t]) <- beta0[t]
    pi[t] <- lambda[t]/sum(lambda[])    # Calculate multinomial probs
  }
  for(i in 1:bigM){
    z[i] ~ dbern(psi)
    yrid[i] ~ dcat(pi[])
    S[i,1] ~ dunif(xlim[1],xlim[2])    # Activity centers
    S[i,2] ~ dunif(ylim[1],ylim[2])
    for(j in 1:ntraps){
      d2[i,j] <- pow(pow(S[i,1]-X[j,1],2) + pow(S[i,2]-X[j,2],2),.5)
    }
    for(k in 1:K){
      Ycat[i,k] ~ dcat(cp[i,k,])
      for(j in 1:ntraps){
        # Construct trap enc. probs.
        lp[i,k,j] <- exp(alpha0 - alpha1*d2[i,j])*z[i]*(1-died[i,k])
        cp[i,k,j] <- lp[i,k,j]/(1+sum(lp[i,k,1:ntraps]))
      }
      cp[i,k,ntraps+1] <- 1-sum(cp[i,k,1:ntraps]) # last cell = not captured
    }
  }
}

```

#### PANEL 14.2

BUGS model specification for a stratified (multi-session) SCR model using data augmentation. This shows a multinomial (“multi-catch”) type of observation model, used to analyze the ovenbird data. Some code to tally up the derived population sizes and density parameters is omitted. See ovenbird.ms script.

seccr results are as follows shown in Table 14.2. There are, as always, slight differences between the MLEs shown here and the posterior summaries shown Table 14.1. The absolute difference between the MLEs and the Bayesian posterior means was .037, −.011, −.006, −.004, and −.004 for years 1–5, respectively.

## 14.5 Spatial or temporal dependence

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The models described here, and including the multi-session formulation used in seccr, assume that the population sizes  $N_g$  are *independent* (in a limiting sense, under data

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**Table 14.1** Posterior summaries for the Bayesian stratified population (“multi-session”) model fitted to the ovenbird data. Results are based on three chains, each with 5000 iterations (first 1000 discarded), for a total of 12,000 iterations saved.

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	Mean	SD	2.5%	50%	97.5%	Rhat
D[1]	0.883	0.191	0.562	0.868	1.308	1.002
D[2]	0.972	0.200	0.624	0.954	1.418	1.001
D[3]	1.146	0.224	0.758	1.125	1.638	1.001
D[4]	0.836	0.183	0.538	0.819	1.247	1.001
D[5]	0.705	0.167	0.428	0.685	1.088	1.001
N[1]	72.208	15.596	46.000	71.000	107.000	1.002
N[2]	79.478	16.367	51.000	78.000	116.000	1.001
N[3]	93.725	18.327	62.000	92.000	134.000	1.001
N[4]	68.399	14.952	44.000	67.000	102.000	1.001
N[5]	57.665	13.659	35.000	56.000	89.000	1.001
alpha0	-3.465	0.159	-3.779	-3.465	-3.155	1.004
alpha1	0.000	0.000	0.000	0.000	0.000	1.009
beta0[1]	4.250	0.244	3.754	4.257	4.710	1.001
beta0[2]	4.349	0.233	3.872	4.356	4.786	1.001
beta0[3]	4.516	0.220	4.059	4.522	4.930	1.001
beta0[4]	4.194	0.248	3.697	4.202	4.664	1.001
beta0[5]	4.013	0.275	3.456	4.022	4.524	1.001
psi	0.371	0.051	0.281	0.367	0.482	1.001
sigma	77.918	6.314	66.963	77.240	91.583	1.009

augmentation). As a practical matter, this precludes the sharing of individuals among populations (i.e., the same individual cannot be captured in multiple groups) which can be violated in a number of situations. First, when the groups represent sampling in distinct time periods (seasons, years) but of the same functional population (a standard “robust design” situation), it is possible that some individuals remain in the population from one time period to the next. In this situation, by disregarding individual identity across groups, the models ignore a slight bit of dependence of  $N_g$  which may entail some incremental loss of efficiency. We imagine this should have little practical effect unless survival probability is extremely high between the periods. Estimators of parameters obtained by assuming independence should be conservative in their statement of precision, but they should be unbiased (or, rather, ignoring the dependence should not affect the bias of the estimator much if at all).

A second distinct situation is that in which the stratification variable is *spatial*, and the strata (e.g., trap arrays or other sampling mechanism) are in relatively close spatial proximity to one another so that individuals can sometimes be encountered by more than one array (e.g., the possum data, see Figure 9.2). This case is somewhat easier to deal with in the analysis because we can build a model in which the state-space is the joint state-space enclosing all of the trapping arrays, and we preserve individual

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Table 14.2 Estimates for the multi-session model fitted to the ovenbird data using <code>seccr</code> . The model had a year-specific density parameter, and constant encounter probability parameters.					
	Link	Estimate	SE Estimate	LCL	UCL
2005					
D	log	0.920	0.228	0.571	1.484
g0	logit	0.028	0.004	0.021	0.037
sigma	log	78.567	6.379	67.025	92.095
2006					
D	log	0.963	0.238	0.598	1.553
g0	logit	0.028	0.004	0.021	0.037
sigma	log	78.566	6.379	67.025	92.095
2007					
D	log	1.139	0.282	0.706	1.836
g0	logit	0.028	0.004	0.021	0.037
sigma	log	78.566	6.379	67.025	92.095
2008					
D	log	0.832	0.206	0.516	1.341
g0	logit	0.028	0.004	0.021	0.037
sigma	log	78.566	6.379	67.025	92.095
2009					
D	log	0.701	0.173	0.435	1.130
g0	logit	0.028	0.004	0.021	0.037
sigma	log	78.566	6.379	67.025	92.095

identity in an ordinary SCR model, just with a larger array of traps that is the union of the trap arrays of all sample groups. This may be impractical when the trap arrays are far apart creating only a slight bit of overlap of populations, because, in that case, the combined state-space may contain a huge population that one has to deal with in the MCMC (remember that increasing  $M$  increases computation time). Royle et al. (2011a) had this problem in an analysis of data from a sample of 1 km quadrats using a search-encounter type model (discussed in the following chapter). Even in this case the independent  $N_g$  model is probably not too detrimental to inferences that apply to explaining marginal variation in  $N_g$ , such as habitat or landscape effects that are modeled on the expected value of  $N_g$ .

s0060

## 14.6 Summary and outlook

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Capture-recapture data are not always collected as single isolated studies but, instead, data are often grouped or stratified in some natural way, either because a number of

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distinct trap arrays are used, or sampling occurs in several forest patches, or over time. Often this is motivated by specific objectives, e.g., the trap arrays or units represent experimental replicates, or sometimes just to derive more valid estimates of density by obtaining a representative (ideally, random) sample of space within some region. The fact that data are grouped in such a way raises the obvious technical problem of having to combine data from multiple arrays, sites, or otherwise defined groups in a single unified model that accommodates explicit sources of variation in density among these groups. This is naturally accomplished by developing an explicit model for variation in  $N$ , e.g., a Poisson GLM or similar (Converse and Royle, 2012; Royle et al., 2012c).

In this chapter, we outlined an approach to Bayesian analysis of multi-session models using data augmentation (Converse and Royle (2012) and Royle and Converse (in review)). This approach gives us one method for building explicit models for  $N_g$  and gives us great flexibility in specifying the encounter model using standard or novel capture-recapture modeling considerations. Certain types of multi-session models can be fitted easily in `secr` (see Chapter 9) and we suspect that platform will be satisfactory for many problems you encounter. However, as always, we believe the flexible model-building platform of the **BUGS** language can be beneficial in many situations. p0140

A common applied context of these multi-session models is when replicate arrays are used to address explicit hypotheses about the effects of landscape variation or modification on abundance. For example, in studies of forestry practices and their effects on local fauna, small-mammal grids are used as experimental units, and the “dependent variable” is  $N$  (or density) of small mammals (or some small-mammal focal species) for each trap array, which is not observable. Thus, hierarchical models are needed to directly address the basic hypotheses of such studies. Another distinct context for the application of multi-session models is when the populations are temporally structured (e.g., the ovenbird data), such as when sampling occurs in distinct seasons or years. In these applications, we view multi-session models as a simplified type of open population model, an open model *without* explicit Markovian dynamics. They are analogous to what is usually referred to as models of random temporary emigration (Kendall et al., 1997; Chandler et al., 2011). The models are not incorrect, just simplified, reduced versions of more general Markovian models, and with fewer parameters to estimate. We cover general Markovian models in Chapter 16. p0145

## Non Print Items

sp005 **Abstract:** In this chapter, we describe SCR models for situations when we have multiple distinct sample groups, strata or “sessions” (the term used in secr), and our interest is in modeling variation in population size or density among the different strata. Such stratified populations are commonplace in capture-recaptures studies, especially in the context where the strata represent distinct spatial regions. A standard example that arises frequently is that in which multiple habitat patches (often refuges, parks or reserves) are sampled independently with the goal of estimating the population size of some focal species in each reserve.

We present a Bayesian framework for inference for stratified SCR models using data augmentation, and also demonstrate the use of multi-session models in the R package **secr**. We apply the stratified models to the ovenbird data, in which the strata are not spatially indexed but, instead, represent temporally defined strata (years). For such cases, we imagine a fully dynamic, or demographically open model might be appropriate—one that involves survival and recruitment (covered in Chapter 16). However, the stratified SCR models can be thought of as a primitive type of model for open systems in which the population sizes are assumed to be independent, and so we might still find them useful as simplified models for open populations.

st075 **Keywords:** Group structure, Multiple sites, Multiple years, Multi-session models, Open populations, Sex effects, Stratified populations, Temporary emigration