

Stratified Populations: Multi-Session and Multi-Site Data

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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 . The modeling objectives in such cases are (1) to combine the data into a single, unified model for purposes of improved estimation of parameters that can be shared across groups and (2) to model variation in group-specific population sizes or, in the case of SCR models, density. 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 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).

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 (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., 2012b). 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 , conditional 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 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. The flexibility of model specification in **BUGS** is why we focus a whole chapter here on Bayesian analysis of stratified population models using data augmentation. However, we have noted previously that the **R** package `secr` fits a class of multi-session models which we applied to the ovenbird and possum data (Chapter 9), and models with sex-specific parameters in Chapters 7 and 8.

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, 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 we might still find them useful in cases where the strata are temporal periods or sessions.

14.1 Stratified data structure

We suppose that $g = 1, 2, \dots, G$ strata (or groups), having population 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.

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:

| | | | | | | | | | | |
|-----------------------|---|---|---|---|---|---|---|---|---|----|
| 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 that 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.

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 \mathbf{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

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.

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 . For example, it might be a covariate describing landuse, habitat or landscape structure, or a variable defining some treatment regime applied to a sample of small-mammal trapping arrays. 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 .

To develop a data augmentation scheme for this group-structured model, let's think about doing data augmentation separately for each population, by assuming that

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

where $\psi \sim \text{Uniform}(0, 1)$ as usual. We could do this multi-population data augmentation by just picking each M_g to be some large integer (as we always do when using data augmentation; see Section 5.7). However, we want to pick M_g in a way that induces the desired 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 Poisson with mean $\psi \exp(\beta_0 + \beta_1 C_g)$. 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 .

We cannot apply data augmentation directly to this stratified model, having Poisson augmented population sizes M_g , because the M_g values are not fixed (remember, the motivation for data augmentation is to fix the size of the data set). To resolve this problem, we remove the M_g variables from the model by conditioning on the “super-population” size $M_T = \sum_g M_g$. 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 $\pi_g = \lambda_g / \sum_g \lambda_g$. It will be easy to apply data augmentation to the larger super-population comprised of the populations from all G strata, having population size M_T . Given this multinomial super-population structure, we relate our stratum-specific population sizes N_g to each M_g by a binomial sampling (“random thinning”) model. ~~If we thin 14.2.3 with a binomial model having parameter ψ , then~~ the vector of N_g parameters has a multinomial distribution with cell probabilities $\psi \times \pi_g$.

When we apply data augmentation to the multinomial joint distribution, the ψ parameter of the binomial sampling model that relates each N_g to M_g 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 β_0 ¹ but this is recovered in the data augmentation parameter ψ . Thus, one of these parameters has to be fixed. We can set $\beta_0 = 0$ or else we can fix ψ (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

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

The linkage of β_0 and ψ was also discussed in Chapter 11 in the context of building spatial models for density. In that case, β_0 was the intercept of the intensity function and one could choose to estimate either β_0 or the data augmentation parameter ψ .

14.2.1 Implementation in BUGS

The **BUGS** implementation of data augmentation for stratified populations is straightforward. For each individual in the super-population we introduce a latent variable g_i to indicate which group or stratum the individual belongs too, and we introduce a

¹A technical argument is that the total N_T is the sufficient statistic for β_0 in the multinomial model and so, by conditioning on the total, β_0 is no longer a free parameter.

second variable z_i to indicate whether the individual is a “real” individual (augmented data are sampling zeros) or a structural zero. So, the multinomial 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 π_g and $z_i \sim \text{Bernoulli}(\psi)$. In other words, the multinomial assumption for the latent variables M_g is formulated in terms of “group membership” for each individual in the super-population of size M_T according to:

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

with $\boldsymbol{\pi} = (\pi_1, \dots, \pi_G)$ and $\pi_g = \lambda_g / (\sum_g \lambda_g)$ where $\{\lambda_g\}$ is the model describing the variation in population size among the G strata. The data augmentation is described by the binary variables z_1, \dots, z_{M_T} such that

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

where ψ is constrained as noted in the previous section. Specifying the multinomial model with data augmentation in terms of the 2 individual variables (g_i, z_i) takes just a couple of lines of **BUGS** code shown here:

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

The complete **BUGS** 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 ψ and β_0 as free parameters. The right panel shows the equivalent model but recognizing the constraint between ψ and β_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 β_0 appear to be draws from the prior distribution, uninformed by the data, supporting the point we made previously that ψ and β_0 are not uniquely informed by the data when we apply data augmentation to the super-population size across all strata.

14.2.2 Groups with no individuals observed

In practical settings, when the groups represent small populations, it will sometimes happen that some strata have no encountered individuals or even that $N_g = 0$. 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 from stratum g . You can try this out to verify for yourself.

| Implementation 1 | Implementation 2 |
|--|---|
| <pre> model { # This will show that psi and beta0 # 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]) <- beta0+beta1*C[j] gprobs[j]<-lam[j]/sum(lam[1:G]) } for(i in 1:M){ g[i] ~ dcat(gprobs[]) z[i] ~ dbern(psi) mu[i] <- z[i]*p y[i] ~ dbin(mu[i],K) } N <- 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 <- sum(lam[])/M for(j in 1:G){ log(lam[j]) <- beta0+beta1*C[j] gprobs[j]<-lam[j]/sum(lam[1:G]) } for(i in 1:M){ g[i] ~ dcat(gprobs[]) z[i] ~ dbern(psi) mu[i] <- z[i]*p y[i] ~ dbin(mu[i],K) } N <- sum(z[1:M]) } </pre> |

PANEL 14.1

BUGS model specification for a capture-recapture model with constant encounter probability and Poisson population 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 β_0 and DA parameter ψ , which are confounded. The required constraint is indicated in the specification under Implementation 2.

14.2.3 The group-means model

Under the Poisson model for group abundance N_g , even with a constant mean λ , 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 (λ or, equivalently, the data augmentation parameter ψ). However, the implied mean/variance relationship of the Poisson model may be inadequate in some applications.

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 λ_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 . However, some information might be borrowed from the different groups for estimating the encounter probability parameters ([Converse and Royle, 2012](#)). Under this model, we constrain one of the λ_g parameters to be 0, and N_g for that group is taken up by the data augmentation parameter ψ ; (2) Alternatively, we could identify specific

fixed covariates which might explain variation across groups, such as habitat or landscape composition, land use, or an experimental treatment. 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 λ and independent group-specific λ_g , is that in which we put a prior on λ_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.

14.2.4 Simulating stratified capture-recapture data

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 5×5 array of camera traps in each reserve. Here we will consider an ordinary closed population model, model M_0 , and we suppose there is some forest level covariate, say $\text{Dist} = \text{disturbance regime}$, perhaps measured by an index of trail density. 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 sizes and capture-recapture data for population inhabiting $G = 20$ forest patches (the “groups” in this situation). To fit this model, we need to augment the `g` and `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 analyzing the simulated data.

14.3 Other approaches to multi-session models

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 applying data augmentation independently for each population by itself. This is not any more or less difficult than the multinomial formulation described in this chapter 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 ψ as being variable for each individual in the augmented data set, 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

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

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 Λ_g , and then among-group structure is modeled in the parameter Λ_g (e.g., using a log-linear model that depends on a group-specific covariate). In our view, either model (binomial based on data augmentation, or the explicit Poisson assumption of `secr`) 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 treatment and stratum effects on abundance.

14.4 Application to spatial capture-recapture

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 center s_i , and the observation model has to be defined for each trap. With this in mind, we can see how the model described in Section 14.2 can be modified to accommodate a group-structured SCR situation. Specifically, we include the prior distribution for s_i and the observation model that relates s_i to the probability of encounter for individual i and trap j .

One practical consideration in developing models for stratified populations is constructing the state-space for the super-population, and describing it in the BUGS language. If the groups represent replicate samples in time made on a single population (as in the ovenbird data set), so that there is a single state-space and a consistent set of trap locations, then implementation proceeds as in the ordinary closed population situation of Section 14.2, but extending the model to include the individual activity center, as we have done so many times in previous chapters. On the other hand, when the groups represent distinct spatial units such as small mammal trapping grids (or the possum data), each group has its own state-space, and trap locations, and this has to be accommodated in the model specification. This can be slightly challenging to describe in the BUGS language if the trap arrays have different sizes or geometry, but it is not so difficult if the trap arrays are similar in structure, e.g., 7×7 grids of unit spacing (Royle and Converse, in review). If the groups are close together, then the different arrays can share a single, enlarged state-space (as we did in Section 9.3.2).

14.4.1 Multinomial (“multi-catch”) observations

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.² 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. In their analysis, they used the independent multinomial encounter model (“multi-catch”), recognizing that as a misspecification (see Section 9.3) of the true single-catch system. 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 in **JAGS**, as well as with a Poisson prior in *secr* using the multi-session models. We mimic the *secr* analysis here, by using the data augmentation and the multinomial distribution for N_g described above.

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

²It 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.

mist nets, an individual can be captured in at most one net during each occasion. 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 $J + 1$).

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:

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

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

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

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, where individuals often exhibit a trap-happy response due to baiting of traps, 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., $C_{ik} = 0$ until the occasion of first capture, and $C_{ik} = 1$ thereafter), then we include this covariate in our multinomial observation model as follows:

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

We note that, in this case, the multinomial probabilities depend not only on individual and trap, but also on sample occasion. The additional array dimension of the multinomial cell probability can lead to extremely slow MCMC sampling using the various BUGS engines, as we saw with similar models in Chapter 7.

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, and we model effects on the log-mean scale according to:

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

```

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),1)
    }
    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.

We considered two models: 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 of inclusion, 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 that distribute individuals among years, based on the year-specific mean λ_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

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 5,000 iterations (first 1,000 discarded), for a total of 12,000 iterations saved. Parameters are density (D_t), population size (N_t), parameters of the encounter probability model (α_0 and α_1) and year effect parameters of the log-linear model for population size ($\beta_{0,t}$). ψ is the data augmentation parameter and σ is the square root of the Gaussian encounter probability scale parameter.

| | 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 |
| α_0 | -3.465 | 0.159 | -3.779 | -3.465 | -3.155 | 1.004 |
| α_1 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 1.009 |
| $\beta_{0,1}$ | 4.250 | 0.244 | 3.754 | 4.257 | 4.710 | 1.001 |
| $\beta_{0,2}$ | 4.349 | 0.233 | 3.872 | 4.356 | 4.786 | 1.001 |
| $\beta_{0,3}$ | 4.516 | 0.220 | 4.059 | 4.522 | 4.930 | 1.001 |
| $\beta_{0,4}$ | 4.194 | 0.248 | 3.697 | 4.202 | 4.664 | 1.001 |
| $\beta_{0,5}$ | 4.013 | 0.275 | 3.456 | 4.022 | 4.524 | 1.001 |
| σ | 77.918 | 6.314 | 66.963 | 77.240 | 91.583 | 1.009 |
| ψ | 0.371 | 0.051 | 0.281 | 0.367 | 0.482 | 1.001 |

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`. To reproduce those results for a model that is similar to the one we just produced in **JAGS**, 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 σ (which has posterior mass up to near $\sigma = 100$). The `secr` results are shown in Table 14.2. There are, as always, slight differences between the MLEs shown in Table 14.2 and the posterior summaries shown in Table 14.1. The absolute differences between the MLEs and the Bayesian posterior means were .037, -.011, -.006, -.004, and -.004 for years 1–5, respectively.

Table 14.2 Estimates for the multi-session model fitted to the ovenbird data using *secr*. The model had a year-specific density parameter (D), and constant encounter probability parameters shared across all 5 years.

| | Link | Estimate | SE Estimate | LCL | UCL |
|-------------|-------|----------|-------------|--------|--------|
| 2005 | | | | | |
| D | log | 0.920 | 0.228 | 0.571 | 1.484 |
| g_0 | logit | 0.028 | 0.004 | 0.021 | 0.037 |
| σ | log | 78.567 | 6.379 | 67.025 | 92.095 |
| 2006 | | | | | |
| D | log | 0.963 | 0.238 | 0.598 | 1.553 |
| g_0 | logit | 0.028 | 0.004 | 0.021 | 0.037 |
| σ | log | 78.566 | 6.379 | 67.025 | 92.095 |
| 2007 | | | | | |
| D | log | 1.139 | 0.282 | 0.706 | 1.836 |
| g_0 | logit | 0.028 | 0.004 | 0.021 | 0.037 |
| σ | log | 78.566 | 6.379 | 67.025 | 92.095 |
| 2008 | | | | | |
| D | log | 0.832 | 0.206 | 0.516 | 1.341 |
| g_0 | logit | 0.028 | 0.004 | 0.021 | 0.037 |
| σ | log | 78.566 | 6.379 | 67.025 | 92.095 |
| 2009 | | | | | |
| D | log | 0.701 | 0.173 | 0.435 | 1.130 |
| g_0 | logit | 0.028 | 0.004 | 0.021 | 0.037 |
| σ | log | 78.566 | 6.379 | 67.025 | 92.095 |

14.5 Spatial or temporal dependence

The models described in previous sections of this chapter, and including the multi-session formulation used in *secr*, assume that the population sizes N_g are *independent* (in a limiting sense, under data 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 of non-independence is that in which the stratification variable is *spatial*, and the strata (e.g., trap arrays or other sampling mechanism) are in 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, so that we can preserve individual 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 the size of the augmented population, 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 the case of spatial dependency 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 .

14.6 Summary and outlook

Capture-recapture data are not always collected in single isolated studies but, instead, are often grouped or stratified in some natural way, either because a number of distinct trap arrays are used, or sampling occurs in several habitat patches, or repeatedly over time. Often this is motivated by specific objectives, e.g., the trap arrays or units represent experimental replicates, but sometimes replicate trap arrays are used 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., 2012b).

In this chapter, we outlined an approach to Bayesian analysis of multi-session models using data augmentation (Converse and Royle, 2012; Royle and Converse *in review*). This approach gives us one method for building explicit models for N_g and provides 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.

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, and are likely more appropriate when there is complete or near complete population turnover between replicate sessions (e.g., survival is low, immigration/emigration is high, etc.). We cover general open population models in Chapter 16.

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Non Print Items

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, or modeling the effect of explicit covariates related to landscape structure or management regime.

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.

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