Open Population Models

<div style="text-align:right">

16

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16.1   Introduction

In the previous chapters we focused mostly on closed population models for estimating density and for inference about spatial variation in density and space usage. However, a thorough understanding of population dynamics requires information about both spatial *and* temporal variation in population density and demographic parameters. In this chapter, we discuss modeling the processes governing spatial and temporal population dynamics, namely survival, recruitment, and movement over larger temporal scales (e.g., migration, dispersal, etc.). The ability to estimate these parameters is critical to both basic and applied ecological research (Knape et al., 2012). For example, testing hypotheses about life history trade-offs requires accurate estimates of both survival and fecundity (Caswell, 1989; Nichols et al., 1994). Inference about density-dependent population regulation, which has fascinated theoretical ecologists for well over a century, is likewise best accomplished by directly studying the factors affecting survival and fecundity, rather than the more common approach of modeling time series data (Nichols et al., 2000b). A mechanistic understanding of population changes, which is essential to address ecological and conservation related questions, requires useful models of vital rates. Furthermore, if we know how environmental variables affect demographic parameters, we can make predictions about population changes under different future scenarios. We can also assess the sensitivity of parameters such as population growth rate to variation in survival or fecundity. Although matrix population models are often used for these purposes (Caswell, 1989; Stther and Bakke, 2000), the same objectives can be accomplished by computing posterior predictive distributions of projected population sizes as part of an MCMC algorithm.

The modeling framework we will develop in this chapter is based on a formulation of the classical Cormack-Jolly-Seber (CJS) and Jolly-Seber (JS) type models (Cormack, 1964; Jolly, 1965; Seber, 1965) which is amenable to modeling individual effects, including individual covariates. There is a long history of use of these models in fisheries, wildlife, and ecology studies (Pollock et al., 1990; Lebreton et al., 1992; Pradel, 1996; Williams et al., 2002; Schwarz and Arnason, 2005; Gimenez et al., 2007). Additionally, there have been many modifications and developments of the

CJS and JS models including dealing with individuals that do not have a well-defined home range but instead are moving through the sampled area (transients), dealing with more than one site or state (multi-state models, where states may be geographic units, reproductive stage, etc.), and addressing individual movement through spatially implicit models.

For the first time, these models can fully integrate the movement of individuals in the vicinity of the trap array with their encounter histories to simultaneously estimate density, survival, and recruitment in a spatial model. For many species, such as those that are rare or not often observed by researchers, this allows inferences to be made about survival and recruitment without having to physically capture individuals. Additionally, another reason for extending SCR models to open populations arises purely from a sampling perspective. Longer time periods are often needed to sample rare or elusive species to ensure that enough captures and recaptures are produced. This prolonged sampling can quickly lead to violations in the assumption of population closure (see also Chapter 10). For example, the European wildcat study that was mentioned in Chapter 7 (see Kéry et al. (2011) for details) was conducted over a year-long period. While the researchers in that study used a closed population model, they did model variation in detection as a function of time to account for seasonal variation in behavior. Another approach would have been to use an open population model to account for possible changes in the population over time (however, the spatial capture-recapture open models had not been developed at the time of the wildcat study, so we'll forgive the authors for not having used this more appropriate model).

In this chapter, we present the traditional JS model and the spatial version, demonstrating both with an example of mist-netting of ovenbirds, which was also analyzed in Chapter 9. Then we review the traditional CJS, multi-state CJS, and then describe the spatial model. To demonstrate the CJS models, we will use an example of American shad. Finally, we end by discussing some of the new approaches to modeling temporal dynamics including correlated movement and dispersal.

16.1.1 Brief overview of population dynamics

The most basic formulation of models for population growth stems from an idea originally used in accounting, the balance sheet (see Conroy and Carroll (2009, Chapter 3) for a more complete description). To gain a mechanistic understanding of population dynamics, it is important to understand four fundamental processes that drive population size: births and immigrants (i.e., population "credits") and deaths and emigrants (i.e., population "debits"). The population at time $t + 1$ is a function of these four components:

$$N(t + 1) = N(t) + B(t) + I(t) - D(t) - E(t),$$

where $N(t)$ is the population size at time t, $B(t)$ and $I(t)$ are the credits (additions) from births and immigrants at time t, and $D(t)$ and $E(t)$ are the debits (losses) due to deaths and emigration. This balance equation model is known as the "BIDE model." A simple population growth model under density independence, assuming

no immigration or emigration, can be derived as:

$$N(t + 1) = N(t) + N(t)r(t),$$

where $r(t) = b(t) - d(t)$. Here, $b(t)$ and $d(t)$ are the per capita birth and death rates and thus $r(t)$ is the per capita growth rate. Models which are based only on the intrinsic population growth rate, "r," however, do not retain much information about the underlying drivers of the population dynamics. Density-dependent, age structured, stochastic effects on growth, spatially structured, and competition models (e.g., Lotka-Volterra) all are derivations of the basic BIDE model.

In closed population models, we focus on estimating the population size, N, but in open population models we are interested in the dynamics that arise between years or seasons and thus we focus not only on $N(t)$ but on the processes that drive population changes. By taking the basic parameters in the BIDE model and reconceptualizing them, they can then be related to the commonly used parameters in JS and CJS models, described in more detail throughout this chapter. In the absence of movement, survival can be estimated in the CJS model and both survival and recruitment can be estimated in the JS model. However, in considering movement, it becomes difficult to distinguish births from immigrants in recruitment and deaths from emigrants in survival rate, because data are usually only collected in one area and when an animal leaves that area we cannot determine its fate.

For example, survival ($\phi(t)$) is defined as the probability of an individual surviving from time t to $t + 1$, and often this is called "*apparent* survival" because deaths and emigration cannot be separated. Mortality, the probability of dying from time t to $t + 1$ is $1 - \phi(t)$. Recruitment (γ) is the probability of a new individual entering the population between t to $t + 1$, which includes both those born into the population and immigrants. This inability to distinguish between the different forms of losses and gains does not allow researchers to test specific hypotheses about population dynamics. To address this, Nichols and Pollock (1990) applied the robust design to a two age class situation in order to separate estimates of recruitment into immigration and *in situ* reproduction. While models that focus on the population growth rate tend to lose important information on population dynamics, more recent work has been done to estimate the contributions of survival and recruitment to the per capita growth rate, "r," using capture-recapture data and a reverse-time modeling approach (Pradel, 1996; Nichols et al., 2000a). All of these model improvements have provided invaluable information in the study of population dynamics, but none explicitly incorporate animal movement.

16.1.2 Animal movement related to population demography

One issue that arises frequently in traditional open population models is that movement can make it difficult to distinguish survival from emigration. For example, we know that movement of transients and temporary emigration will affect the estimates of survival, causing us to refer to estimates as "apparent survival" (Lebreton et al., 1992). This is because an animal that appears in the population for a short period of time

and then leaves is going to appear as though it has died. Due to this problem, there has been a significant amount of work developing models to deal with temporary emigration and transients in both closed and open capture-recapture models (Kendall et al., 1997; Pradel et al., 1997; Hines et al., 2003; Clavel et al., 2008; Gilroy et al., 2012; Chandler et al., 2011). Because movement is modeled directly within the SCR framework, we can better understand the impact of animals moving onto and off of the trap array and hence we can improve our estimates of survival by combining the traditional CJS and JS models with the SCR model.

While demographic parameters such as survival rates, population growth, etc., are influenced by density (Fowler, 1981; Murdoch, 1994; Saether et al., 2002), it is also likely that movement of individuals can influence these parameters. It is generally accepted that population structure (i.e., age, stage, or size distribution) can affect both population size and growth over time (Caswell and Werner, 1978). We also know that how animals distribute themselves in space can directly influence the age or stage structure of a population—this can be behavioral, habitat related, or some combination of factors. For example, if habitat is limited, some younger members of the population might have trouble finding and/or defending a territory. Ultimately, this may lower survival for a certain age class in the population directly impacting the population structure.

Dispersal can also affect population structure. In population ecology, dispersal can be related to access to reproduction, population regulation, habitat quality, as well as the linking of local populations in metapopulation ecology (Clobert et al., 2001; Ovaskainen, 2004; Ovaskainen et al., 2008). It is known that dispersal ~~may~~ be influenced by density dependence (Matthysen, 2005); for example, competition may cause individuals to be more likely to emigrate from an area, or individuals may leave an area in search of a mate. We discuss modeling dispersal with capture-recapture data a bit further in Section 16.4 at the end of the chapter.

16.2 Jolly-Seber models

16.2.1 Traditional Jolly-Seber models

The JS model was developed as a way to estimate not only detection and abundance, but survival and recruitment (new individuals coming into the population) based on capture-recapture data (Jolly, 1965; Seber, 1965). There are a number of ways that researchers have formulated the JS model (Cooch and White, 2006) and while all are slightly different, the resulting estimates of abundance and the driving parameters such as survival and some form of recruitment are consistent. Commonly used formulations are the Link-Barker (Link and Barker, 2005), Pradel-recruitment (Pradel, 1996), Burnham JS (Burnham, 1997), and the super-population formulation of Schwarz and Arnason (1996). In all of these models, the parameter of interest is recruitment, or how new individuals arrive into the population. Therefore one of the main differences between the various models is how new entrants into the population are parameterized.

Traditionally, sampling for the JS model included only one data collection event per primary occasion and this allowed for the estimation of survival and recruitment. However, without repeated visits within a primary occasion, there is not enough data to allow for variation in detection and this leads to potentially inaccurate estimates of population size. This led Pollock (1982) to devise the robust design in order to allow for heterogeneity in capture probability (by sex, age, social status, etc.) and trap response under the JS model. We present the robust design approach as it is more flexible and generalizing to the spatial version of the JS model will be ~~much~~ simpler. The basic idea is that there are primary occasions (e.g., years, seasons) and we allow the population to be "open" between the primary occasions. This means that individuals can enter and leave the population (i.e., births, deaths, immigration, emigration can occur) between the primary occasions; however, within a primary occasion, the population is assumed to be closed to these processes. The standard JS model does not allow for variation in detection probability between individuals or within a primary occasion because only one sample is collected per primary period. However, when multiple samples are taken within a primary occasion (we call these "secondary occasions"), then variation in detection probability can be modeled and thus our estimates of N can be improved. To that extent, we can envision the data as arising from repeated sampling over seasons or years (or *primary* periods) within which one or more samples (e.g., trap nights) might be taken (*secondary* periods). Figure 16.1 demonstrates the sampling process graphically. Comparing this with all of our previous work, the sample occasions (e.g., trap nights, weeks, etc.) described in the closed population chapters are called *secondary* sampling occasions in the context of open population models.

We can easily formulate a non-spatial JS model using the robust design. We define y_{ikt} as the encounter history for individual i at secondary occasion k during primary occasion t. If we have a Bernoulli encounter process then we can describe the observation model, specified conditional on the "alive state," $z(i, t)$, for individual i
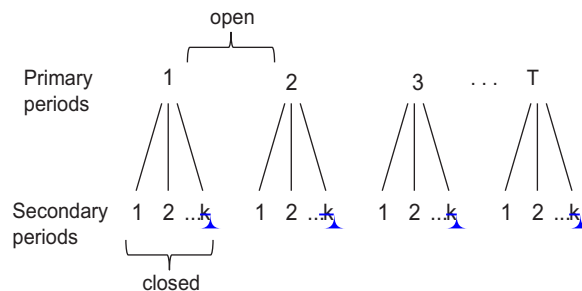

FIGURE 16.1

Schematic of the robust design with T primary sampling periods and K secondary periods. The populations are considered open between primary periods and closed within each.

at primary time t, as:

$$y_{ikt}|z(i, t) \sim Bernoulli(p_t z(i, t)).$$

(Note: throughout this chapter we will focus on changes in the alive state, so we will index z using parentheses in order to make the notation easier to read, where $z(i, t)$ is equivalent to z_{it}.) Thus, if individual i is alive at time t ($z(i, t) = 1$), then the observations are Bernoulli with detection probability p as before. Conversely, if the individual is not alive ($z(i, t) = 0$), then the observations must be fixed zeros with probability 1. Note our distinct use of the variable z here as representing the state of individuals (alive/dead) instead of our previous use of z as the data augmentation variable.

Survival and recruitment in the open population are manifest in a model for the latent state variables $z(i, t)$ describing individual mortality and recruitment events. An important aspect of the hierarchical formulation of the model that we adopt here is that the model for the state variables is described conditional on the total number of individuals ever alive during the study (a parameter which we label N) based on T periods, as in Schwarz and Arnason (1996). Data augmentation induces a special interpretation on the latent state variables $z(i, t)$. In particular, "not alive" includes individuals that have died, or individuals that have not yet been recruited. Royle and Dorazio (2008) showed that using this formulation simplifies the state model and allows it to be implemented directly in the **BUGS** language. For example, considering the case $T = 2$, the state model is composed of the following two components: First, the initial state is described by:

$$z(i, 1) \sim Bernoulli(\psi),$$

and then a model describing the transition of individual states from $t = 1$ to $t = 2$:

$$z(i, 2) \sim Bernoulli(\phi z(i, 1) + \gamma (1 - z(i, 1))).$$

If $z(i, 1) = 1$, then the individual may survive to time $t = 2$ with probability ϕ whereas, if $z(i, 1) = 0$, then the "pseudo-individual" may be recruited with probability γ.

We can then generalize this model for $T > 2$ time periods and allow survival and recruitment to be time dependent. Initialize the model for time $T = 1$ as we have done above and then the model describing the transition of individual states from t to $t + 1$ is:

$$z(i, t + 1) \sim Bernoulli(\phi_t z(i, t) + \gamma_t (1 - z(i, t))).$$

This parameterization results in $T - 1$ survival and recruitment parameters. The main difference here from the CJS model, described below, is that we include recruitment and are interested in estimating N for each t. Since this state model described above is conditional-on-N, we must deal with the fact that N is unknown, which is done through data augmentation similar to how we used it in the closed population models.

16.2.2 **Data augmentation for the Jolly-Seber model**

The fundamental challenge in carrying out a Bayesian analysis of this model is that the parameter N (the total number of individuals alive during the study) is not known. We have discussed and demonstrated data augmentation in many previous chapters; however, with the open population model, we have to take care that two issues are addressed: (1) the data augmentation is large enough to accommodate all potential individuals alive in the population during the entire study and (2) that individuals cannot die and then re-enter the population. Royle and Dorazio (2008) (see also Kéry and Schaub 2012) describe this formulation for open population models, including the non-spatial JS and robust design models.

To begin, let's consider the role of recruitment, γ, in the model when we use data augmentation to estimate N. Data augmentation formally reparameterizes the model, replacing N, the number of individuals ever alive with M, where we assume $N \sim \text{Binomial}(M, \psi)$. That is, the expected value of N under the model is equal to ψM. As a result of this reparameterization, the recruitment parameters, γ_t, are also relative to the number of "available recruits" on the data augmented list of size M, and not directly related to the population size. We can derive N_t and R_t, the population size and number of recruits in year t, as a function of the latent state variables $z(i, t)$. For example, the total number of individuals alive at time t is

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

and the number of recruits is

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

which is the number of individuals *not* alive at time $t - 1$ but alive at time t.

In the case of just two primary periods, this process is straightforward. When the number of primary sample occasions is greater than 2, we must formulate the model for recruitment by introducing another latent variable, in order to ensure that an individual can only be recruited once into the population. Here, this formulation of the model uses a set of indicator variables, labeled $A(i, t)$. Let $A(i, t) = 1$ if individual i is available to be recruited in time interval $(t-1, t)$ otherwise $A(i, t) = 0$. We define $A(i, t)$ for $i = 1, 2 \ldots, N$ and $t > 1$ as

$$A(i, t) = \left(1 - I \left(\sum (z(i, \tau)) > 0 \right) \right).$$

Each recruitment indicator is conditional on whether the individual was ever previously alive. This ensures that an individual cannot be recruited again after initial recruitment. Then, we can describe the state variables $z(i, t)$ by a first-order

Markov process. For $t = 1$, the initial states are fixed:

$$A(i, 1) \equiv z(i, 1)$$

and, for subsequent states, we have

$$z(i, t) | z(i, t - 1), A(i, t) \sim \text{Bernoulli}(\phi_t z(i, t - 1) + \gamma_t A(i, t)).$$

Thus, if an individual is in the population at time t (i.e., $z(i, t) = 1$), then that individual's status at time $t + 1$ is the outcome of a Bernoulli random variable with parameter (survival probability), ϕ_t. If the individual, however, is not in the population at time t (i.e., $z(i, t) = 0$), then the outcome is a Bernoulli random variable with probability γ_t, a parameter that is related to recruitment. We define this model in **JAGS** by using the sum() and step() functions together to ascertain if a particular individual i was ever previously alive. The step() function is a logical test in **JAGS** for $x \geq 0$ such that step($x \geq 0$) returns a 1, otherwise 0. Individuals that were ever previously alive are no longer eligible to be "recruited" into the population. The implementation of this model in **JAGS** is shown in Panel 16.1.

16.2.2.1 *Ovenbird mist-netting study*

We now return to the ovenbird data collected using mistnets at Patuxent Wildlife Research Center. We introduced these data in Chapters 9 and 14, and they are provided with the secr package (see, Efford et al. 2004, Borchers and Efford 2008). To refresh your memory: 44 mist nets spaced 30 m apart on the perimeter of a 600 m × 100 m rectangle (see Figure 16.2) were operated on 9 or 10 non-consecutive days in late May and June for 5 years from 2005 to 2009.

In Chapters 9 and 14, we dealt with this dataset as a type of spatial "multi-session" model where abundances in each year, N_t, were regarded as independent random variables either with a Poisson prior (as implemented in secr) or a binomial prior if analyzed using **BUGS** with data augmentation. This is the simplest approach for modeling data collected over multiple years, but it does not allow for inference about demographic processes, as does the JS model.

In the spatial multi-session model (S-MS) we did not use individual identity across years; however, we need to maintain the order of individuals across years to estimate the survival and recruitment of individuals into the population. We organize the data set so that each row in the array represents just one individual across all primary periods. For the ovenbird data set, we can organize the data by creating a master list of all individuals captured during the entire study. From this list, we can assign each individual a unique row in our data set (in the **R** commands, we do this by using the unique() function on the row names for each year of our three-dimensional array and use pmatch() to associate the data to the correct column). The resulting array is individual by secondary occasion by primary occasion, $M \times K \times T$. The **R** commands to organize the data in a way suitable for fitting a Jolly-Seber type model are included in the scrbook package using the function ovenbirds.js() and are not shown here. The key difference between our model and organization of the data here and

```
model{

psi ~ dunif(0,1)
phi ~ dunif(0,1)
p.mean ~ dunif(0,1)

for(t in 1:T){
    N[t] <- sum(z[1:M,t])
    gamma[t] ~ dunif(0,1)
}

for(i in 1:M){
  z[i,1] ~ dbern(psi)            # Alive state for the first year
 cp[i,1] <- z[i,1]*p.mean
  Y[i,1] ~ dbinom(cp[i,1], K)     # Y are the number of encounters
  A[i,1] <- (1-z[i,1])

  for(t in 2:T){                   # For loop for years 2 to T
      a1[i,t] <- sum(z[i, 1:t])    # Sum over the alive states from 1 to t
       A[i,t] <- 1-step(a1[i,t] - 1)
  # A is the indicator if an individual is available to be recruited
      mu[i,t] <- (phi*z[i,t-1]) + (gamma[t]*A[i,t-1])
  # Alive state at t is dependent on phi and gamma
       z[i,t] ~ dbern(mu[i,t])
       cp[i,t] <- z[i,t]*p.mean
        Y[i,t] ~ dbinom(cp[i,t], K)
           }
        }
}
```

PANEL 16.1

JAGS model specification for the non-spatial Jolly-Seber model using data augmentation.

that in Chapter 9 is that, here, we have to preserve individual identity across years (in the model and data structure).

The data augmentation must be large enough to include individuals alive during any of the time periods and to account for that, we set $M = 200$. There were 70 unique individuals captured over the 5-year period. For this example, we hold survival constant but allow recruitment to be time dependent (since γ is essentially a function of the data augmentation process as described above, it does not make sense to hold recruitment constant).

To implement the model in Panel 16.1, the following commands are used:

```
 # Set initial values for the alive state, z
> zst <- c(rep(1,M/2),rep(0,M/2))
> zst <- cbind(zst,zst,zst,zst,zst)
```
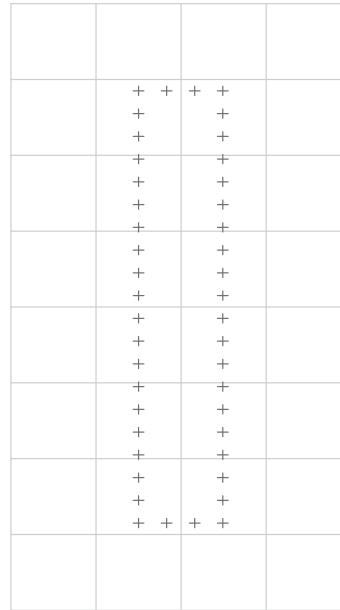
FIGURE 16.2

Arrangement of the mist nets in the ovenbird study. The nets are arranged in a 600 m by 100 m rectangle, spaced 30 m apart.

```
> inits <-function()list(z=zst,sigma=runif(1,25,100),gamma=runif(5,0,1))
> parameters <- c("psi","N","phi", "p.mean", "gamma")
> data <- list (K=10,Y=Ybin,M=M)

> library("rjags")
> out1 <- jags.model("modelNSJS.txt",data,inits,n.chains=3,n.adapt=500)
> out2NSJS <- coda.samples(out1,parameters,n.iter=20000)
```

In this non-spatial JS model, N_t is estimated to be between about 22 and 33 for each of the 5 years (see Table 16.1 for results). The posterior mean for detection (p.mean in the model) was 0.14. We did not include p.mean in the table because the SCR models do not have a parameter that directly corresponds to it. Instead, SCR models have a detection function that is related to distance.

16.2.2.2 *Shortcomings of the traditional JS models*

One of the biggest shortcomings of the non-spatial JS model is that we estimate N but have no explicit spatial area associated with it (so, in Table 16.1, the density estimate from the non-spatial JS model is listed as NA). Ignoring the spatial information in the data makes the estimation of density an informal process. As we saw in the closed models, the incorporation of spatial information in the model will allow us to make

Table 16.1   Posterior mean of model parameters for the non-spatial Jolly-Seber model (NS-JS), the spatial Jolly-Seber model (S-JS), and the spatial multi-session model (S-MS) fitted to the ovenbird data set. Density shown in individuals per hectare.

	NS-JS	S-JS	S-MS
D[1]	–	0.96	0.93
D[2]	–	1.00	1.00
D[3]	–	1.10	1.20
D[4]	–	1.10	0.89
D[5]	–	0.79	0.76
N[1]	26.5	33	32.4
N[2]	30.2	36	35.8
N[3]	33.1	39	42.1
N[4]	29.5	37	30.8
N[5]	21.7	28	26.2
alpha0	–	−2.9	−2.88
alpha1	–	1.2e-04	1.22e-04
sigma	–	6.4	6.44
gamma[1]	0.50	0.50	–
gamma[2]	0.09	0.09	–
gamma[3]	0.11	0.13	–
gamma[4]	0.13	0.16	–
gamma[5]	0.07	0.08	–
phi	0.48	0.53	–
psi	0.14	0.17	–
R2	–	15	–
R3	–	19	–
R4	–	8.3	–
R5	–	8.3	–

an explicit estimate of density. This improvement should also carry through to our estimation of other demographic parameters such as survival and recruitment as the movement of individuals is directly accounted for in the model.

16.2.3 **Spatial Jolly-Seber models**

To parameterize the spatial JS models, we follow all of the same steps as the non-spatial model but also include the trap location information into our detection function. Basically, we are using the closed population SCR model to estimate the detection parameters and initial population size, and the open component is carried out in the process of how we model the transition of $z(i, t)$ to $z(i, t + 1)$ which is the same as in the non-spatial JS model. To do so, we describe the Bernoulli observation model, specified conditional on $z(i, t)$, as has been done throughout the book:

$$y_{ijkt} | z(i, t) \sim \text{Bernoulli}(p_{ijk} z(i, t))$$

with

$$p_{ijk} = p_0 \exp(-\alpha_1 d_{ij}^2), \tag{16.2.1}$$

where $d_{ij} = ||\mathbf{x}_j - \mathbf{s}_i||$, the distance between activity center $\mathbf{s}_i$ and trap $\mathbf{x}_j$. As before, p_0 is the baseline encounter probability, for an individual with home range center located precisely at a trap, and $\alpha_1 = 1/(2\sigma^2)$ where σ is the scale parameter in this Gaussian encounter probability model.

If individual i is alive at time t ($z(i, t) = 1$), then the observations are Bernoulli. Conversely, if the individual is not alive ($z(i, t) = 0$), then the observations must be fixed zeros with probability 1. As always, other observation models can be considered in the context of a fully open JS-type model, such as the Poisson or multinomial models described in Chapter 9, and we can consider many alternative models of encounter probability.

We initialize the model for time $T = 1$ and then model the transition of individual states from t to $t + 1$ as:

$$z(i, t + 1) \sim \text{Bernoulli}(\phi_t z(i, t) + \gamma_t (1 - z(i, t))).$$

Previously, in Section 16.2.2, we described how this formulation of the model uses a set of latent indicator variables $A(i, t)$ which describes if an individual is available to be recruited into the population during time interval $(t - 1, t)$. We apply the same approach here, so that, as before, $A(i, t) = 1$ if individual i is recruited in time interval $(t - 1, t)$; otherwise $A(i, t) = 0$.

The number of recruits into the population is calculated based on the alive state of the previous time steps $(1, 2, \ldots, t - 1)$ and the current time step (t). For example, to estimate the number of recruits from time period 1 to 2, we count those individuals not in the population at time 1 ($z(i, 1) = 0$) but alive at time 2 ($z(i, 2) = 1$). We can determine if individual i has entered the population at time $t = 2$ by using the formula: $R_{i,2} = (1 - z(i, 1))z(i, 2)$ and then sum $R_{i,2}$ over M to get the total number of recruits. We can do this for all the primary periods in our study, as shown in the **JAGS** code in Panel 16.2. For this example, we model the activity centers as independent for each primary period, such that $s(i, t) \sim \text{Uniform}(S)$. However, we discuss alternative models for the activity centers in Section 16.4.

16.2.3.1 *Ovenbird mist-netting study*

In the previous analysis of the ovenbird data, we did not make use of the spatial location for each net the ovenbirds were captured in. However, there were 44 mist nets operational during each of the sampling occasions. We already organized the data so that the 3-D encounter histories are set up (see Section 16.2.2.1). The data set is then $M = 200$ individuals by $K = 10$ secondary occasions by $T = 5$ primary occasions. In the non-spatial version, we reduced the data to captured or not-captured; however, the encounter history array, `Yarr`, contains the number of the net that each individual was captured in and contains a 45 if the individual was not captured. The code above describes how the encounter history array is created, so we do not reproduce this piece of code here. To fit the model, use the following **R** code which sets the initial values

```
model {
psi ~ dunif(0,1)        # Prior distributions
phi ~ dunif(0,1)
alpha0 ~ dnorm(0,10)
sigma ~ dunif(0,200)
alpha1 <- 1/(2*sigma*sigma)
A <- ((xlim[2]-xlim[1]))*((ylim[2]-ylim[1]))  # Area of state-space

for(t in 1:T){
  N[t] <- sum(z[1:M,t])  # Calculate abundance for each year
  D[t] <- N[t]/A         # Calculate density for each year
  R[t] <- sum(R[1:M,t])    # Calculate the recruits for each year
  gamma[t] ~ dunif(0,1)  # Prior for time specific recruitment parameter
}

for(i in 1:M){
  z[i,1] ~ dbern(psi)
  R[i,1] <- z[i,1]        # To estimate the number of recruits
  R[i,2] <- (1-z[i,1])*z[i,2]
  R[i,3] <- (1-z[i,1])*(1-z[i,2])*z[i,3]
  R[i,4] <- (1-z[i,1])*(1-z[i,2])*(1-z[i,3])*z[i,4]
  R[i,5] <- (1-z[i,1])*(1-z[i,2])*(1-z[i,3])*(1-z[i,4])*z[i,5]

  for(t in 1:T){
     # Independent activity centers for each year
     S[i,1,t] ~ dunif(xlim[1],xlim[2])
     S[i,2,t] ~ dunif(ylim[1],ylim[2])
  for(j in 1:ntraps){
      d[i,j,t] <- pow(pow(S[i,1,t]-X[j,1],2) + pow(S[i,2,t]-X[j,2],2),1)
      }
  for(k in 1:K){
     for(j in 1:ntraps){
        lp[i,k,j,t] <- exp(alpha0 - alpha1*d[i,j,t])*z[i,t]
        cp[i,k,j,t] <- lp[i,k,j,t]/(1+sum(lp[i,k,,t]))
     }
    cp[i,k,ntraps+1,t] <- 1-sum(cp[i,k,1:ntraps,t])
    # Here, the last cell indicates not captured
    Ycat[i,k,t] ~ dcat(cp[i,k,,t])
  }
}
  A[i,1]<-(1-z[i,1])
for(t in 2:T){                       # For loop for years 2 to T
     a1[i,t] <- sum(z[i, 1:t])  # Sum over alive states from 1 to t
      A[i,t] <- 1-step(a1[i,t] - 1)
  # A indicates if individual is available to be recruited at time t
     mu[i,t] <- (phi*z[i,t-1]) + (gamma[t]*A[i,t-1])
  # Alive state at t is dependent on phi and gamma
      z[i,t] ~ dbern(mu[i,t])
         }
     }
}
```

PANEL 16.2

JAGS model specification for the fully spatial Jolly-Seber model. This extends the ordinary Jolly-Seber model by the inclusion of a spatial component to the encounter probability model.

for z[i,t], the parameters to monitor, and calls **JAGS**. The code is also available in the ovenbirds.js() function:

```
> zst <- c(rep(1,n),rep(0,M-n))
> zst <- cbind(zst,zst,zst,zst,zst)

> inits <- function(){list(z=zst,sigma=runif(1,25,100),
        gamma=runif(5,0,1), S=Sst,alpha0=runif(1,-2,-1))}
> parameters <- c("psi", "alpha0", "alpha1", "sigma", "N",
                    "D", "phi", "gamma", "R")
> data <- list(X=as.matrix(X[[1]]), K=10, Ycat=Yarr,
              M=M, ntraps=ntraps, ylim=ylim, xlim=xlim)
> library("rjags")
> out1 <- jags.model("modelJS.txt", data, inits, n.chains=3,
            n.adapt=500)
> out2JS <- coda.samples(out1,parameters,n.iter=10000)
```

Our results for density, α_0, and α_1 are similar to those found in the multi-season analysis from Chapter 9. Since all of the parameters including α_0 and α_1 are shared between seasons, we would expect these results to be similar between the multi-season model and the JS model (see Table 16.1). There are some slight differences in the parameter estimates, for example, the density is lower in year 4 in the multi-season model than in the JS model. This may be due to a smaller sample size in that year; due to the Markovian relationship between abundances, the JS model is able to make use of the data more efficiently. This may also be due to the implied prior on N_t (see Royle and Dorazio 2008, Chapt. 10). Because we have defined the same state-space for the spatial JS model and multi-season, our estimates of N_t are directly comparable. However, the estimates of N_t under the non-spatial JS model are not directly comparable as we do not have a well-defined effective trapping area. We see from Table 16.1 that N_t is smallest for the non-spatial JS model across all years. This suggests that the actual effective trapping area is smaller than our state-space, but we cannot estimate the effective trapping area in a formal manner and thus we cannot to make useful comparisons between the N_ts.

In the JS formulation of the model, we also estimate the recruitment for each year, and we can look at our derived values for recruitment (R2, R3, R4, and R5). R2 is the number of new recruits from primary period 1 to 2; R3 is the number of new recruits from primary period 2 to 3; and so forth. R2 and R3 are almost double that of R4 and R5, suggesting that less animals were recruited into the population in the latter years of the study. The density in the last year of the study was lower than previous years. It is good to check your results when you see a pattern like this—the number of recruits declining each year—because this could be an indication that the data augmentation was not large enough. In this example, we checked to make sure that $M = 200$ was sufficiently large by examining the recruitment parameter, γ. If γ is close to 1 during any of the time periods, then there are not enough augmented individuals in the overall data set. In this case, the 97.5% quantile of γ_5, the recruitment probability in the final
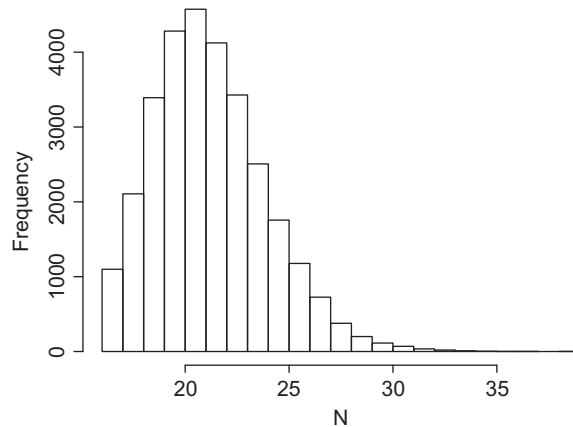
FIGURE 16.3

Posterior distribution of N_5 from the spatial JS model for the ovenbird dataset. This figure suggests that there is no truncation of the posterior of N_5 by M.

year of the study, was 0.14 and none of the other γs were close to 1 either. You can also look at the posterior distributions of the total N or each N_t to make sure they are not truncated, Figure 16.3 shows that the posterior distribution of N_5 is not truncated. The posterior mean for survival, ϕ, was 0.53. Although we did not do that in this example, it should be easy to see that we could allow survival to vary by time, as we did with recruitment. Our estimates of survival seem reasonable when compared with the ovenbird literature. Some studies have found annual male ovenbird survival to be around 0.62 (Porneluzi and Faaborg, 1999; Bayne and Hobson, 2002), whereas female ovenbird survival is much lower (0.21, Bayne and Hobson, 2002). With more individuals, we could run this model with survival estimated for each sex separately. However, researchers should be careful not to overparameterize models. The results indicate that the posterior mean estimate of ϕ was greater in the SCR model (0.53) than the non-spatial model (0.48) which suggests that the SCR model is partitioning some movement from survival this produces an estimate of true rather than apparent survival.

16.3 Cormack-Jolly-Seber models

16.3.1 Traditional CJS models

Cormack-Jolly-Seber (CJS) models are used extensively to model animal survival. There are two common ways to fit these models, using either a multinomial likelihood approach (Lebreton et al., 1992) or a state-space formulation of the model (Gimenez et al., 2007; Royle, 2008). The multinomial likelihood approach is based on summarizing the data to counts of unique encounter histories, which have a multi-

nomial distribution. The data are summarized over individuals and so it is not feasible to build general models that contain individual covariates. On the other hand, the state-space formulation of the model preserves individual identity and, therefore, parameters can be modeled at the individual level, and individual effects (covariates or heterogeneity) can be included. In the present context of spatial capture-recapture models, we naturally think about including individual locations, or activity centers, as individual covariates.

We can adopt a state-space parameterization of the single-state, non-spatial CJS model in which the observation model is described conditional on the latent state variables $z(i, t)$ – the "alive state," which indicates whether individual i is alive ($z(i, t) = 1$) or not ($z(i, t) = 0$) during each of $t = 1, 2, \ldots, T$ *primary* periods. Let y_{it} indicate the observed encounter data of individual i in primary period t. The model, specified conditional on $z(i, t)$, is:

$$y_{it}|z(i, t) \sim \text{Bernoulli}(p_t z(i, t)).$$

Analogous to the JS model, if individual i is alive at time t ($z(i, t) = 1$), then the observations are Bernoulli with probability of detection p_t.

If the individual is not alive ($z(i, t) = 0$), then the observations are fixed zeros with probability 1. Contrary to the JS model, in the CJS model we condition on first capture, which means that $z(i, t)$ will be 1, with probability 1, when t is the primary period individual i is first captured in. We denote this $z(i, f_i)$, where f_i indicates the primary occasion in which individual i is first captured, which can vary from $1 \ldots T$. This ensures that each individual is alive upon entering the data set.

The "alive state" at time t for each individual is a function of the state at the previous time step $t - 1$. Because we condition on the first capture, the initial state is set to one:

$$z(i, f_i) = 1.$$

The model for the transition of individual states from t to $t + 1$ for all $t > f_i$ is

$$z(i, t) \sim \text{Bernoulli}(\phi z(i, t - 1)).$$

The individual survives with probability ϕ to time $f_i + 1$ and so forth. Once an individual leaves the population (i.e., $z(i, t) = 0$), there is no mechanism for the individual to return. In the CJS model we are not estimating N_t, so we do not need to make use of data augmentation here in order to account for uncaptured individuals (remember: we explicitly condition on first capture). This version of the model is easy to construct in ~~the~~ **BUGS** (or **JAGS**) ~~language~~ which is shown in Panel 16.3. Variations on this basic model and associated code for fitting the model in **BUGS** are described in detail in Kéry and Schaub (2012, Chapters 7–9).

16.3.1.1 *Movement and survival of American shad in the Little River*
As an example for the CJS model, we use data collected on American shad (*Alosa sapidissima*) in the Little River in North Carolina, USA (see photo in Figure 16.4).

```
model{
  phi ~ dunif(0,1)  # Survival (constant over time)

  for(t in 1:T){
    p[t] ~ dunif(0, 1)  # Detection (varies with time)
  }

 for(i in 1:M){
    z[i,first[i]] ~ dbern(1)
    for (t in (first[i]+1):T){
        tmp[i,t] <- z[i,t]*p[t]
          y[i,t] ~ dbern(tmp[i,t])
      phiUP[i,t] <- z[i,t-1]*phi
          z[i,t] ~ dbern(phiUP[i,t])
    }
  }
}
```

PANEL 16.3

JAGS model specification for the non-spatial basic Cormack-Jolly-Seber (CJS) model. Note that the first alive state of each individual, `z[i,first[i]]`, is not stochastic. It is equal to 1 with probability 1.

The Little River is a tributary to the Neuse River and the confluence is near Goldsboro, North Carolina, about 212 river kilometers from the Pamlico Sound. The motivation for this example stems from an interest in better understanding survival and movement of migratory fish. American shad are an anadromous fish that use rivers for spawning. The data were collected and analyzed as described in Raabe (2012). Using a resistance board weir near the river mouth, 315 fish were tagged with passive integrated transponders (PIT) in the spring of 2010. An array of seven upstream PIT antennas passively recaptured individuals during upstream and downstream migrations. Each time a fish passed over the antenna, it was recorded and the data were summarized weekly for 12 weeks. The fish do not necessarily move past all antennas and may remain in the river between antennas for more than a week, thus they are not all detected at each time period. The antennas do not always operate perfectly either and fish that pass may not be recorded at some times.

To apply the CJS model, we create the encounter history for each individual for the 12 weeks and we also create a vector to indicate the period (week) of first capture. The code is not shown here but is availabe in the `scrbook` package within the function `shad.cjs()`. This function contains all of the code to fit the non-spatial, multi-state, and spatial CJS models to the American shad data set.

FIGURE 16.4

American shad caught in North Carolina, USA. *Credit*: Joshua Raabe, North Carolina State University.

Table 16.2 shows the estimated detection probabilities for each of the 12 primary periods in the study. The posterior mean for detection probabilities ranges from 0.126 to 0.880, which could potentially be due to variation in water flow, stream depth, storms, timing of migration, etc. The weekly survival probability, ϕ, had a posterior mean estimate of 0.824. This estimate could be considered low for a weekly probability, but is likely due to the fact that the migration upstream can be quite energetically taxing and the fish are likely to only feed minimally in rivers (Leggett and Carscadden, 1978; Leonard and McCormick, 1999). Additionally, the CJS model is only estimating apparent survival and some fish may have left the stream temporarily or permanently heading back to the ocean or possibly to other tributaries that are not monitored. We demonstrate in Panel 16.3 how to allow p to vary by time, but we could also allow survival, ϕ, to vary by time by implementing it exactly as we do for p. As we move into the multi-state model, we can test for movement and survival by state, which allows more specific biological questions to be addressed.

16.3.2 Multi-state ~~CJS~~ models

The standard CJS model only allows for estimation of survival and detection probabilities. However, researchers are often interested in addressing other ecological questions such as age-dependent survival rates, habitat-specific movements, etc. Multi-state models allow researchers to directly address such questions by incorporating more than one state that an individual may be in (Arnason (1972, 1973) and Brownie et al. (1993)). These possible states can be geographic location, age class, or reproductive status among many others. Instead of just having an encounter history for an individual, we will also have auxiliary information on the state of that individual at capture (e.g., breeder or non-breeder, or geographic location). Since our interest, in

Table 16.2 Posterior summaries of model parameters for the non-spatial CJS model fitted to the American shad data set.

	Mean	SD	2.5%	50%	97.5%
p[1]	0.499	0.289	0.026	0.499	0.975
p[2]	0.627	0.058	0.511	0.628	0.738
p[3]	0.762	0.036	0.689	0.763	0.829
p[4]	0.880	0.025	0.828	0.882	0.925
p[5]	0.548	0.043	0.465	0.548	0.633
p[6]	0.259	0.038	0.190	0.258	0.337
p[7]	0.126	0.031	0.072	0.124	0.194
p[8]	0.236	0.045	0.155	0.234	0.332
p[9]	0.237	0.049	0.148	0.234	0.341
p[10]	0.589	0.072	0.447	0.590	0.728
p[11]	0.834	0.063	0.700	0.839	0.942
p[12]	0.468	0.072	0.330	0.466	0.614
ϕ	0.824	0.011	0.802	0.825	0.846

the context of spatial modeling, is in movement of individuals, we will consider states that represent spatial units or geographic locations. For example, we might think that the movement rates between locations (or, in the present context, state transition rates) could be due to habitat features (or quality) and we can use multi-state models to help us address such a question. In addressing movement through a multi-state modeling approach, the movement is often parameterized as random or Markovian between patches (Arnason, 1972, 1973; Schwarz et al., 1993).

In the simplest version of the multi-state model we have just two states. Thus, individuals can be marked and recaptured in one of two states (we'll call them A and B here). We will assume that the two "states" are different geographic regions. In the single-state model above, an individual i was either alive ($z(i, t) = 1$) at time t or dead ($z(i, t) = 0$). Now, we must consider that the individual could be alive in a given state or dead and that individuals can transition between states. An easy way to think about this is to look at the state-transition matrix in Table 16.3. Here, ϕ^A is the probability of surviving in state A from time t to $t + 1$ and ϕ^B is the analogous parameter for state B. The movement (i.e., state-transition) parameters are ψ^{AB} and ψ^{BA}, where ψ^{AB} is the probability that an individual, which survived from t to $t + 1$, moves to state B just before $t + 1$, and vice versa for ψ^{BA}. The movement could also be defined as occurring before the survival; i.e., ψ^{AB} is the probability that an individual moves from state A to state B shortly after time t.

Because individuals are not necessarily observed and the observation probability may depend on the state, detection probability should be estimated separately for each of the states. Hence, we also have p^A and p^B, the probability of detecting an individual in state A and state B, respectively. Also, at this point, we assume that there

Table 16.3 Transition matrix for a multi-state model with two states.

	State A	**State B**	**Dead**
State A	$\phi^A(1 - \psi^{AB})$	$\phi^A\psi^{AB}$	$1 - \phi^A$
State B	$\phi^B\psi^{BA}$	$\phi^B(1 - \psi^{BA})$	$1 - \phi^B$
Dead	0	0	1

is no error in observed state (i.e., if the animal is observed, then the state is recorded correctly).

Classical multi-state models are closely related to closed population SCR models. In particular, keeping with the notion of having a discrete state variable and going back to the shad example from Section 16.3.1.1, instead of having a Markovian state-transition model, we imagine that each fish has a "home area", and the observation state is conditioned on that (constant) home area, **s**. We can express that model as

$$u_{it} \sim dcat(\psi(s_i))$$

where u_{it} (a discrete state) is the current location of fish i, and **s** (also a discrete state) is its home area. We could imagine that the state-transition probability vector, $\psi(\mathbf{s})$, is related in some fashion to distance between possible observation states and home area. In this model, the current state, u_{it}, is not Markovian as it is in classical multi-state models but, rather, an independent sample from a distribution indexed by s. We see that, by letting the number of possible states increase to infinity, the model morphs into a continuous space SCR model, except u_{it} can take on any value in the state-space (this type of "search-encounter" model was discussed in Chapter 15)). If we restrict the potential observation locations to some prescribed subset of the state-variable **s**, e.g., trap locations, then the model is precisely an SCR model for a fixed trap array. Therefore, SCR models can be viewed as multi-state models, but with a continuous state-variable (instead of discrete) - "space" - and with independent transitions between states in successive times (instead of Markovian).

To describe the two state model for **JAGS**, we define the observation as $y_{it} = 1, 2$, or 3 where 3 indicates "not observed." Additionally, we use $z(i, t)$ to indicate the true state of individual i such that $z(i, t) = 1, 2$, or 3 where 1 indicates alive and in state 1, 2 indicates alive and in state 2, 3 indicates "not alive." Using these definitions, we just need to set up the transition matrix based on Table 16.3 and define each item within the model specification, shown in Panel 16.4. Note that this can become quite cumbersome when dealing with models that have many states.

16.3.2.1 *Movement and survival of American shad in the Little River*

Previously, we analyzed the American shad data using a basic (i.e., non-spatial) CJS model. To demonstrate the two-state version of the multi-state CJS model, we will reanalyze the American shad data set, now defining two regions of the river

```
model{

# r is an index for state (excluding the 'not alive' state)
for(r in 1:2){
    phi[r] ~ dunif(0,1)
    psi[r] ~ dunif(0,1)
    p[r] ~ dunif(0,1)
}

for (i in 1:M){
    z[i,first[i]] <- y[i, first[i]]
for (t in (first[i]+1):T){
    z[i,t] ~ dcat(ps[z[i,t-1], i, ])
    y[i,t] ~ dcat(po[z[i,t], i, ])
    }
    ps[1, i, 1] <- phi[1] * (1-psi[1])
    ps[1, i, 2] <- phi[1] * psi[1]
    ps[1, i, 3] <- 1-phi[1]
    ps[2, i, 1] <- phi[2] * (1-psi[2])
    ps[2, i, 2] <- phi[2] * psi[2]
    ps[2, i, 3] <- 1-phi[2]
    ps[3, i, 1] <- 0
    ps[3, i, 2] <- 0
    ps[3, i, 3] <- 1

    po[1, i, 1] <- p[1]
    po[1, i, 2] <- 0
    po[1, i, 3] <- 1-p[1]
    po[2, i, 1] <- 0
    po[2, i, 2] <- p[2]
    po[2, i, 3] <- 1-p[2]
    po[3, i, 1] <- 0
    po[3, i, 2] <- 0
    po[3, i, 3] <- 1
 }
}
```

PANEL 16.4

JAGS model specification for a two-state version of the multi-state CJS model. Code modified from Kéry and Schaub (2012, Chapter 9).

("downstream" and "upstream"). Any number of states could be selected for this example, and a logical choice might be 7, the number of antenna used in the study. However, here we will simplify problem by using just two states in order to demonstrate how to set up and run the model described in the previous section. Defining

Table 16.4 Results of the multi-state ~~CJS~~ model for ~~the migratory fish~~ example. p^A is the detection probability in the first state (A), which in this case is the downstream area. ϕ^A is the weekly survival probability in state A and ψ^{AB} is the probability that an individual, which survived from t to $t + 1$ in Site A, moves to State B just before $t + 1$.

	Mean	SD	2.5%	50%	97.5%
p^A	0.777	0.045	0.689	0.777	0.866
p^B	0.434	0.027	0.382	0.434	0.489
ϕ^A	0.850	0.022	0.807	0.851	0.893
ϕ^B	0.782	0.019	0.743	0.782	0.820
ψ^{AB}	0.421	0.034	0.356	0.421	0.489
ψ^{BA}	0.927	0.014	0.897	0.937	0.952

two states, downstream and upstream, allows us to explore potential differences in survival based on the location of the fish in the stream. To set up the model, we first assigned each antenna to a state based on its location: those below 20 river kilometers were considered in the downstream state, all others considered upstream. Each fish has an encounter history including whether or not the fish was detected during each week of the 12-week study, but also the "state" of capture ("downstream" or "upstream"). A vector to indicate the period of first capture was also created. Fish captured in more than one state during the week were assigned the state in which they were captured most during that week. And the model assumes that individuals observed in a state at consecutive primary periods did not move from that state within the primary period. The data manipulation and model specification for the multi-state CJS model are provided in the `scrbook` package under the function `shad.cjs()`.

Survival between the two areas was quite different (see Table 16.4). This might suggest that fish moving further upstream are expending more energy and are more likely to die. While survival in the two states was different, it is intuitive that the average of the survival probabilities for A and B is essentially the same as that from the basic non-spatial CJS ($\phi = 0.82$, see Table 16.2). Also, it should be noted that ψ^{BA} was very high, indicating that fish in this study are returning downstream after spawning in the upstream area. These results highlight the utility in using a multi-state model to understand movement between states; here, we used spatial states, but age, class, breeding status, etc., are all possibilities.

16.3.3 Spatial CJS models

In the above example on American shad, we lost a lot of information (about movement) by using a two-state model. As already mentioned, we could have used a seven-state model that would have allowed us to use the encounters at each antenna. However, as the number of states increases, so does the number of parameters, particularly the number of transition parameters. It stands that highly parameterized transition

probability matrices require huge amounts of data, which are often not available. Information is also lost in that we must reduce the encounter histories to be binary ("captured" or not during each sample occasion). In our shad example, fish can pass an antenna multiple times within a sample occasion but this information is typically not used in multi-state models. And finally, one other issue that multi-state models have not rectified is being in more than one state at a time. Again, in our shad example, we must decide what to do with a fish that is detected at more than one antenna. By reducing our example to two states of upstream and downstream, we reduced this problem to just a few cases. However, within the dataset, many fish are detected at two or more antenna during a week. This can be addressed sometimes by creating additional "states", but again, the number of states can grow quickly.

These issues are directly resolved by using a fully spatial CJS model in continuous space. We've established many times that various observation models allow for multiple detections in a given occasion, analogous to closed SCR models, so that information is not lost by reducing the data to binary encounter histories. Additionally, by not defining a distinct state, spatial CJS models directly address the issue of individuals only being able to be in one state at a time. The formulation as an SCR model also resolves the problem of estimating large transition probability matrices, by allowing us to essentially parameterize the whole matrix by "distance" and therefore reduce the dimensionality of the problem to just 1 or a few parameters.

To achieve a fully spatial CJS model, we build on the state-space and multi-state CJS models, but explicitly incorporate individual movement as an individual covariate ((Royle, 2009a). With this in mind, we need only make a few changes to the model. We will not have discrete states and thus the biggest difference is that individuals do not "transition" between a finite set of states, but instead are allowed to move in continuous space.

We may consider the same basic encounter models as described previously (i.e., Poisson, Bernoulli, or multinomial). In particular, let y_{ijkt} indicate the observed encounter data of individual i in trap j, during interval (secondary period or subsample) $k = 1, 2, \ldots, K$ and primary period t. We note that in some cases we may have only one interval ($K = 1$), which correspond to the design underlying a standard CJS or JS models, whereas the case $K > 1$ corresponds to the "robust design" (Pollock, 1982). The Poisson observation model, specified conditional on $z(i, t)$, is:

$$y_{ijkt}|z(i, t) \sim \text{Poisson}(\lambda_0 g_{ij} z(i, t)),$$

where λ_0 is the baseline encounter rate and g_{ij} is the detection model as a function of distance. If the individual is not alive ($z(i, t) = 0$), then the observations must be fixed zeros with probability 1. Remember that in the CJS formulation, we condition on first capture which means that $z(i, t)$ will be 1 when t is the first primary period of capture. As before in the non-spatial CJS model, we can denote this as $z(i, f_i)$ where f_i indicates the primary occasion in which individual i is first captured. Modeling time-effects either within or across primary periods is straightforward. For that, we define $\lambda_0 \equiv \lambda_0(k, t)$ and then develop models for $\lambda_0(k, t)$, as in our closed SCR models (we note that trap-specific effects could be modeled analogously).

To model survival, we follow the same description as that of the non-spatial version of the CJS (Section 16.3.1). In that version, we did not allow for survival to be time specific. However, it is easy to do so by allowing ϕ to vary with each time step:

$$z(i, t) \sim \text{Bernoulli}(\phi_t z(i, t-1)).$$

Under this model, or the one in Section 16.3.1, recruitment is not modeled and therefore once an individual leaves the population (i.e., $z(i, t) = 0$), it cannot return.

16.3.3.1   *Movement and survival of American shad in the Little River*

Going back to our American shad example, we can consider that this is exactly a spatial capture-recapture problem. In stream networks, the placement of PIT antennas along the stream mimics the type of spatial data collected in terrestrial passive detector arrays such as camera traps, hair snares, acoustic recording devices, etc. The difference is that for fish and aquatic species, the stream constrains the movement of individuals to a linear network. Using the data from the array of seven PIT antennas and the number of times each fish passed over the antenna, we can apply the spatial CJS model to evaluate movement up and downstream of these fish. When we look at the individuals encountered at each antenna for each of the primary periods, the dimensions of the data are 315 individuals by 7 antennas by 12 sample occasions. Individuals can encounter any antenna any number of times during the week, which means we just sum the encounters over the week and eliminate any need for explicit secondary occasions in the model. The result is a three-dimensional array instead of a four-dimensional array. Given the structure of the encounters, we use a Poisson encounter model in this example shown in 16.5. The code to carry out this model is provided in the `scrbook` package using the function `shad.cjs()`.

The baseline encounter rate, λ_0, was allowed to vary by week and ranged from 0.188 to 5.555. We use the Poisson encounter model in this spatial CJS example rendering λ_0 not directly comparable to p_0 from the non-spatial and multi-state versions, which arises as the detection probability under the binomial encounter model. The posterior mean for ϕ was 0.784 (see Table 16.5), again showing that the weekly survival probability is rather low, just as we saw in the two previous example analyses of these data. Here, we are modeling survival probability as constant, but there is reason to believe that it might vary by time (similar to detection) and we might consider this additional parameterization in a more complete analysis of the data set. The other parameter of interest is σ, the movement parameter, which had a posterior mean of 13.954. Stream locations are recorded in river kilometers (~~RKM~~), so σ is in units of km. Our system here is linear, so we do not think of fish as having a home range radius, which would imply a circular home range. This example demonstrates how to carry out a spatial CJS model making use of all the data collected. However, in this version of the model, we have specified the activity centers as being independent across each primary period ($s(i, t) \sim \text{Uniform}(S)$). While this may be a useful model in many applications and a good starting place for demonstrating the model, here, we were hoping to gain more information about the movement of shad up

```
model {
# Priors
sigma ~ dunif(0,80)
sigma2 <- sigma*sigma
lam0 ~ dgamma(0.1, 0.1)
phi ~ dunif(0, 1)    # Survival (constant across time)
tauv~dunif(0, 30)
tau<-1/(tauv*tauv)

for (i in 1:M){
  z[i,first[i]] <- 1
  S[i,first[i]] ~ dunif(0,50)    #Fish enter the stream at 0, thus the
                 #first AC is set to the lower stream end

for(j in 1:nantenna) {
  D2[i,j,first[i]] <- pow(S[i,first[i]]-antenna.loc[j], 2)
      lam[i,j,first[i]] <- lam0*exp(- D2[i,j,first[i]]/(2*sigma2))
      tmp[i,j,first[i]] <- lam[i,j,first[i]]
        y[i,j,first[i]] ~ dpois(tmp[i,j,first[i]])
      }

   for (t in first[i]+1:T) {
          S[i,t] ~ dunif(xl, xu)#xl and xu are the upper and lower
                   limits of the stream
         for(j in 1:nantenna) {
             D2[i,j,t] <- pow(S[i,t]-antenna.loc[j], 2)
             lam[i,j,t] <- lam0 * exp(-D2[i,j,t]/(2*sigma2))
             tmp[i,j,t] <- z[i,t]*lam[i,j,t]
             y[i,j,t] ~ dpois(tmp[i,j,t])
 }
     phiUP[i,t] <-  z[i,t-1]*phi
       z[i,t] ~ dbern(phiUP[i,t])
}
}
}
```

PANEL 16.5

JAGS model specification for the spatial Cormack-Jolly-Seber (CJS) model for the American shad data set. Note that the first alive state of each individual, z[i,first[i]], is not stochastic. It is equal to 1 with probability 1.

and downstream. When an individual is not captured during a primary period, there is no data to inform the activity center and thus the posterior for the estimate is the prior. This is unsatisfying and we recognize that one could use the information from the preceding time period (or other variations, such as the following time period or

Table 16.5 Posterior summary statistics of model parameters from the spatial Cormack-Jolly-Seber model fitted to the American shad data set.

	Mean	SD	2.5%	50%	97.5%
lam0[1]	5.555	0.224	5.125	5.553	6.003
lam0[2]	4.442	0.155	4.143	4.437	4.752
lam0[3]	1.892	0.068	1.763	1.891	2.031
lam0[4]	1.126	0.055	1.021	1.125	1.238
lam0[5]	0.949	0.058	0.838	0.948	1.067
lam0[6]	0.359	0.040	0.284	0.357	0.443
lam0[7]	0.188	0.031	0.133	0.186	0.254
lam0[8]	0.309	0.044	0.230	0.307	0.402
lam0[9]	0.363	0.052	0.269	0.361	0.471
lam0[10]	0.627	0.072	0.493	0.625	0.777
lam0[11]	1.611	0.109	1.408	1.607	1.835
lam0[12]	0.939	0.139	0.697	0.929	1.241
ϕ	0.784	0.012	0.760	0.785	0.807
σ	13.954	0.197	13.573	13.950	14.350

combinations of the two) to inform the location information when the fish is not observed. In addition to providing information on the fish activity centers, this also holds promise for improving estimates of "true" ϕ as we can better separate emigration from mortality (see Section 20.1.7 for a short discussion). In the following section, we discuss further models for the movement dynamics that can be implemented and postulate a few models specifically related to the shad example.

16.4 Modeling movement and dispersal dynamics

Animal movement is both a nuisance and a fascinating process of interest in its own right. It can be a nuisance in the sense that ignoring it can bias estimators of density and survival. Numerous models (including SCR!) have been developed to deal with movement simply as a way of eliminating bias. However, movement is a key determinant of population viability, age structure, and distribution (Clobert et al., 2001), and rather than simply accounting for movement, we often want to develop explicit models for inference about processes such as dispersal and migration.

At this point, very little work has been done to model movement using SCR models; however, we expect that in the near future this will be one of the most exciting areas of research. While many sophisticated movement models exist, few of them are embedded within a framework that allows for estimation of density and other demographic parameters. This is one of the most important unrealized promises of SCR models, and in this section we will outline some possible avenues for moving forward. To begin, we will focus on the movement of activity centers among primary periods, which might result from dispersal or other large scale movements.

A primitive movement model might assume that activity centers change over time but are independent from year to year for a given individual such $\mathbf{s}(i, t) \sim$ Uniform($\mathcal{S}$). This is also how the spatial versions of the JS and CJS models were formulated above and this might be a reasonable model when there are large time lags between surveys, or if the individuals redistribute themselves frequently in the study population.

A more realistic model includes a movement (or dispersal) kernel of the form $[\mathbf{s}_t | \mathbf{s}_{t-1}]$. The bivariate normal distribution is one possibility, which represent as $\mathbf{s}_t \sim$ BVN($\mathbf{s}_{t-1}, \boldsymbol{\Sigma}$). A symmetric kernel could be specified as $\boldsymbol{\Sigma} = \left(\begin{smallmatrix} \tau & 0 \\ 0 & \tau \end{smallmatrix} \right)$ where the scale parameter τ determines how far an individual is likely to disperse. For example, many adult passerines exhibit high site fidelity, and thus τ is likely to be very small for these individuals. However, juvenile passerines can disperse hundreds of kilometers and so τ might be much larger for these individuals.

Other approaches to analyzing movement in a mark-recapture framework focus on modeling individual locations rather than activity centers (Ovaskainen, 2004; Ovaskainen et al., 2008; Grimm et al., 2005; Hooten et al., 2010). The same could be done in SCR models by including a model component $[\mathbf{u}|\mathbf{s}]$ where $\mathbf{u}$ is location of an individual at some point in time. We could further allow the observed locations to follow an auto-regressive model such that $\mathbf{u}_{ikt} \sim$ Normal($\rho(\mathbf{u}_{i,k,t-1} - \mathbf{s}(i, t-1)), \Sigma_t^*$). These are just a few simple examples; as more information becomes available and data are collected over longer time periods, we will be able to use more complex movement models in open SCR models.

16.4.1 Cautionary note

Under the Markovian movement models described above, activity centers can leave the state-space. This is a problem because it will result in an unjustified decrease in density over time. Several solutions exist, but the easiest one to implement is to truncate the dispersal kernel such that activity centers are not allowed to leave $\mathcal{S}$. In **JAGS**, this can be accomplished using the truncation function `T()`. For example: `s[i,1,t] ~ dnorm(s[i,1,t-1], tau)T(xl, xu)` constrains the variable to lie within the range specified by `xl` and `xu`.

Another issue related to the state-space is that it should be large enough such that an individual whose activity center is located near a boundary during the initial time period should have a negligible probability of being captured. Thus, for individuals that move long distances, the state-space should be very large. Alternatively, the state-space may be designated based on knowledge of suitable habitat, thereby constraining the region within which individuals can move.

16.4.2 Thoughts on movement of American shad

In our American shad example above, we had reason to believe that individual movement is directly related to stream flow. When the stream flow is low, we might expect that the fish move very little, and when the stream flow is high, they might move more within the stream. In this case, we could model the effect of stream flow in two ways.

First, we might allow σ to be a function of flow and to vary for each primary occasion, according to:

$$\log(\sigma_t) = \mu_\sigma + \alpha_2 \text{Flow}_t.$$

This model would only relate the movement of fish about their activity center with the flow, essentially only affecting the encounter probability. But if we think that the change in activity centers between primary periods might be related to the general pattern of fish migrating upstream more during high flow or staying closer to the same location in low flow, then we could allow the activity center locations to be a function of flow. For example, we might assume the activity centers move from the previous value with ~~variance~~ that depends on flow (i.e., larger movements in response to flow),

$$\mathbf{s}(i, t) \sim \text{Normal}(\mathbf{s}(i, t - 1) + \beta \text{Flow}_t, \tau^2 \mathbf{I}),$$

We could extend this model too so that individuals might move at different rates upstream versus downstream based on their migration patterns. These are just a few thoughts on simple ways to model movement as a function of habitat variables which we have only started exploring on these data.

16.4.3   Modeling dispersal

Dispersal is widely studied in population ecology and is often of heightened interest because it relates directly to population regulation, habitat quality, and linking of local populations. However, studying dispersal with capture-recapture data can be difficult for a few reasons. One common issue with using capture-recapture data for dispersal estimation is that short distances are sampled more frequently than long distances. This is particularly true if we consider that most trap arrays are not large relative the potential dispersal distances of animals. In some cases, such as with small mammals, we may be able to capture both short and long distance dispersals in one trap array; in other cases, we may have discrete study sites set up across a larger area which capture individuals within and between sites. Either way, data are likely to be sparse for long distance dispersal events and this is particularly true if there are different habitat types which are sampled with different levels of effort (Ovaskainen et al., 2008), thus causing more difficulty in fitting models to data where much information is missing. In addition to that, determining if an individual has left an area or died can be difficult if the sampling does not cover the area an individual has moved to or if the sampling method has failed (e.g., a band or tag falls off or a mark is lost). As a result of this, dispersal biases estimates of survival probability obtained using standard JS or CJS models, and it is therefore important to model dispersal and survival explicitly (Schaub and Royle, 2013).

Regardless of these common sampling limitations, let's look at an ideal situation where we have the trap array large enough to observe some dispersal events (or possibly multiple trap arrays on the landscape where an individual is observed in different arrays). We sketch out a possible dispersal model but note that this is a simple example. In this case, each individual could have some probability of dispersing, say

η where $pd_{i,t} \sim$ Bernoulli(η) indicates if an individual disperses at time t and then

$$s_{i,t+1,1} = s_{i,t,1} + pd_{i,t}(ds_{i,t}\cos(\theta_{i,t})),$$
$$s_{i,t+1,2} = s_{i,t,2} + pd_{i,t}(ds_{i,t}\sin(\theta_{i,t})),$$

where ds_i is the dispersal distance for individual i and θ is the dispersal direction. Thus when $pd_i = 0$, then the activity centers remain the same as the previous time step and if $pd_i = 1$ then the individual disperses to a new activity center. For this specification, we have to provide a model for dispersal distance. One option is to let $ds_{i,t} \sim$ exponential(L) where L is the mean dispersal distance for individuals dispersing and let $\theta_{i,t} \sim$ Uniform($-\pi, \pi$) where π is not a parameter in this case, but the mathematical constant (i.e., $\pi = 3.14159\ldots$). If all individuals are expected to move some distance between periods, then the pd indicator could be removed. More complex models involving non-Euclidean distance (Graves et al., 2013), weighted directional movement and different movement states could be fit (see Jonsen et al., 2005; Johnson et al., 2008a; McClintock et al., 2012).

16.5 **Summary and outlook**

In this chapter we have described a framework for making inference not only about spatial and temporal variation in population density, but also demographic parameters including survival, recruitment, and movement. The ability to model population vital rates is essential for ecology, management, and conservation; and the models described here allow researchers to examine the spatial and temporal dynamics governing those population parameters. While we have covered a lot of ground in this chapter, there are many variations of the basic JS and CJS models, such as dead recovery models or models that address transiency that we have not explicitly "converted" to a spatial framework. These areas provide a broad field of further model development. As open models are further developed, mechanisms for dealing directly with dispersal and transients will provide improved inference frameworks for understanding movement as well as the potential to estimate *true* survival instead of only *apparent survival*. This is a function of explicitly modeling movement, which means we can separate movement from mortality, as we sketched out in the model above for dispersal, providing a huge advantage over traditional models. Also, models of individual dispersal can be used to examine variation in population dynamics relative to habitat, density dependence, or climatic events.

Birth and death processes, as well as movement, all have the potential to be related to the space usage of animals in the landscape. Understanding the impact of spatially varying density on survival and recruitment will provide insights into the basic ecology of species. With the advent of non-invasive techniques, like camera trapping and genetic analysis of tissue, we can start to understand the population dynamics of species that are rarely observed in the wild. As more and more data are collected, we can use the models to explore the spatio-temporal patterns of survival, recruitment, density, and movement of species, providing incredibly useful biological

and ecological information as we face broad changes in climate, land use, habitat fragmentation, etc. Rathbun and Cressie (1994) articulate a model for marked point processes where they separate out the spatial birth, growth, and survival processes for longleaf pine trees. Because of the application, these demographic parameters are slightly different than how they are often considered in wildlife and ecology, but still, there are analogies. Allowing birth, growth, and survival as well as density to arise from different spatially varying processes is the next stage in development of the open SCR models.

Abstract: In this chapter, we discuss spatial capture-recapture models in the context of populations that are open to demographic processes such as mortality and birth, and movement dynamics such as dispersal or migration. First, we provide an introduction to the ordinary (non-spatial) Jolly-Seber (JS) model, which estimates both abundance and demographic rates. We address how to carry out Bayesian analysis of this model using a data augmentation framework, as well as a few of the technical issues related to this formulation of the model. Using data augmentation, it is easy to provide an individual capture-history formulation of the model, and this facilitates the inclusion of individual covariates. Based on this individual capture-history formulation of the model, it is straight forward to extend the non-spatial to a spatial JS model.

We reanalyze the ovenbird mist-netting data from Efford et al. (2004), which we previously analyzed using the multi-session modeling framework, using a spatial Jolly-Seber type of model. We further discuss the classical Cormack-Jolly-Seber (CJS) model, which is a restricted version of the JS model that conditions on entry into the sample, and therefore does not model the recruitment process. We provide an example of modeling movement and survival using a spatial CJS model fitted to data from a study of American shad in spawning migration. Finally, we discuss other types of spatial capture-recapture models that involve more complex movement dynamics such as dispersal, encorporating, for example, a model for how individual activity centers move throughout time.

Keywords: Open population, Jolly-Seber model, Cormack-Jolly-Seber model, Multi-state model, Survival, Recruitment, Movement, Dispersal, Migration