Chapter 1

Open Population Models

1.1 Introduction

All of the previous chapters focused on closed population models for estimating density and for inference about spatial variation in density. 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 develop a framework for inference about the processes governing spatial and temporal dynamics, namely survival, recruitment, and movement (migration, dispersal, etc...). The ability to estimate these parameters is critical to both basic and applied ecological research. For example, testing hypotheses about life history trade-offs requires accurate estimates of both survival and fecundity (citations). Inference about density-dependent population regulation, which has fascinated theoretical ecologists for well over a century, is likewise best accomplished by studying the factors affecting survival and fecundity, rather than the more common approach of modeling time series data (Nichols et al., 2000). Modeling vital rates is important for applied ecologists and conservation biologists, because a mechanistic understanding of population decline requires it. 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; Sæther and Bakke, 2000), the same objectives can be accomplished by computing posterior predictive distributions as part of the MCMC algorithm.

For the first time, we can fully integrate the movement of individuals onto and off 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 us to make inference about survival and recruitment without having to physically capture individuals. Additionally, another reason extending our SCR models

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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 extended time frame can quickly lead to violations in the assumption of population closure. For example, the European wildcat study that was mentioned in Chapt **??** (see Kéry et al. (2011) for details) was conducted over a year long period. While the researchers in that study used a closed population, they did model variation in detection as a function of time. Another approach would have been to use an open population model (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).

The modeling framework we will develop in this chapter is based on a formulation of Cormack-Jolly-Seber (CJS) and Jolly-Seber (JS) type models (Cormack, 1964; Jolly, 1965; Seber, 1965) that are 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 transients, multi-state, and spatially implicit model.

1.1.1   Brief overview of population dynamics

The most basic formulation of models for population growth stem from an idea originally used in accounting, the balance she

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. Density-dependent, age structured, stochastic effects on growth, spatially structured, and competition models (e.g., Lotka-Volterra) all are basic derivations of the BIDE model. 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.

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 the 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, deaths (D) can be estimated in the CJS model and both D and B (births) can be estimated in the JS model. However, in considering movement, it becomes difficult to distinguish births from immigrants and deaths from emigrants. 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 those 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 'using capture-recapture data and a reverse-time modeling approach ((Pradel, 1996; Nichols, 2000)). All of these model improvements have provided invaluable information in the study of population dynamics, but none explicitly incorporate animal movement.

1.1.2 Animal movement related to population demography

Density may influence demographic parameters such as survival rates, population growth, etc., it is also likely that movement of individuals can influence these parameters. For example, we know that movement of transients will affect our estimates of survival, causing us to typically refer to estimates as "apparent survival". 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 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). Because we estimate movement 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.

But what if movement and space usage of individuals directly influences the survival rates or recruitment? It is generally accepted that population structure (i.e., age, stage, or size distribution) can affect both population size and growth

over time. 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 many animal populations, dispersal is linked with reproduction and population regulation. Thus, movement including spatial arrangement of activity centers and dispersal are key components to population dynamics. We start here by showing how to extend the SCR models to open populations, but this chapter opens the door for how we would go about incorporating space usage into models of demographic dynamics. For example, we could incorporate space and movement into age-dependent multistate capture-recapture models to address the impact of dispersal on recruitment or survival.

1.1.3 Basic assumptions of JS and CJS models

Before extending the classic open models to our SCR framework, let's first look at the basic assumptions of both models. No tag (or mark) loss is assumed in both models. If a marked animal losses it's tag or mark, then that animal cannot be recaptured and this could appear as though the animal has died. Hence, to maintain unbiased estimates of survival, no tag or mark loss is important. Additionally, capture and release should be instantaneous (or as close as possible), otherwise the time interval between capture occasions could differ for individuals and that would result in individual heterogeneity of survival. Individuals must also be recorded accurately.

In the standard CJS models, it is also assumed that all emigration from the study area is permanent and that capture and survival probabilities are constant within each sample occasion and group. A group can be created based on sex, age, area, etc. In the CJS model, we condition on the captured individuals, and therefore we estimate only the probability of recapture and the survival rates. Here, survival is considered the "apparent" survival because emigration and mortality are confounded within the model, thus apparent survival is always estimated lower than true survival when emigration is not zero. The JS version of the model does not condition on marked individuals. Thus we can estimate survival like we do in the CJS, but now we can also model recruitment (new individuals coming into the population) and the total abundance/density of the population. Estimating more parameters does require a few more assumptions including that all individuals in the population have the same probability of capture. Under a "robust design" (Pollock, 1982), which we will demonstrate in this chapter, we can estimate heterogeneity in capture probabilities

1.2 Jolly-Seber Models

1.2.1 Traditional Jolly-Seber models

There are a number of ways that researchers have formulated the JS model and while all are slightly different, the resulting estimates of abundance and the driving parameters such as survival and some form of recruitment should be the same. The most commonly used formulations are the Link-Barker ((Link and Barker, 2005), Pradel-recruitment ((Pradel, 1996)), Burham JS, POPAN ((Schwarz and Arnason, 1996)) and the Pradel- models. In all of these models, we are interested in 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.

Pollock (1982) created the robust design in order to allow for heterogeneity in capture probability under the JS model. 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., nights) might be taken (*secondary* periods). Fig. 1.1 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.

Based on the robust design, we can easily create a non-spatial JS model. 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 at primary time t, as:

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

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.

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
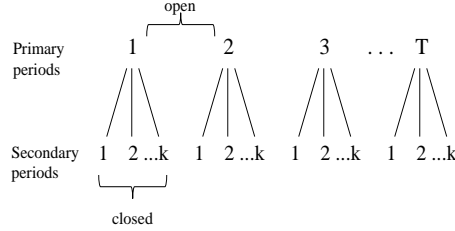
Figure 1.1: Schematic of the robust design with T primary sampling periods and K secondary periods. The populations are considered open between primary periods and closed within the secondary

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. Using this formulation simplifies the state model and also allows it to be implemented directly in the **JAGS** software Royle and Dorazio (2008). For example, considering the case $T = 2$, the state model is composed of the following two components: First the initial state is described by:

$$z(i, 1) \sim \text{Bernoulli}(\psi)$$

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

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

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:

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

This parameterization then 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.

1.2.2 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) 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 $N \sim \text{Bin}(M, \psi)$. This is the same as having a discrete uniform prior on N, when the prior for ψ is $\text{Unif}(0, 1)$. That is, the expected value of N under the model is equal to ψM. As a result of this repararameterization, 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. This can be dealt with by deriving N_t, and R_t, the population size and number of recruits in year t, as a function of the latent state variables $z(i, t)$. In particular, 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. We do this 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 latent indicator variables, $A(i, t)$, which describe the time interval $(t-1, t)$ at which individual is recruited into the population. Let $A(i, t) = 1$ if individual i is recruited in time interval $(t-1, t)$ otherwise $A(i, t) = 0$. To construct the recruitment process we make use of the standard conditional binomial construction of a removal process (Royle and Dorazio 2008). The initial state is given by:

$$A(i, 1) \sim \text{Bin}(1, \gamma_1)$$

²⁵⁵ for $i = 1, 2, \ldots, N$. Then, for $t > 1$

$$A(i,t)|A(i,t-1)\ldots A(i,1) \sim \text{Bin}((1 - \sum_{\tau=1}^{t-1} A(i,\tau)) \times \gamma_t, 1)$$

²⁵⁶ Each recruitment variable is conditional on whether the individual was ever
²⁵⁷ previously recruited and this construction forces the recruitment variable after
²⁵⁸ initial recruitment to be degenerate (have a sample size of 0). Then, we can
²⁵⁹ describe the state variables $z(i,t)$ by a 1st order Markov process. For $t = 1$, the
²⁶⁰ initial states are fixed:

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

²⁶¹ and, for subsequent states, we have

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

²⁶² Thus, if an individual is in the population at time t (i.e., $z(i,t) = 1$), then
²⁶³ that individual's status at time $t + 1$ is the outcome of a Bernoulli random
²⁶⁴ variable with parameter (survival probability) ϕ_t. If the individual, however,
²⁶⁵ is not in the population at time t (i.e., $z(i,t) = 0$), then the outcome is a
²⁶⁶ Bernoulli random variable with probability γ_t, a parameter that is related to
²⁶⁷ *per capita* recruitment. We carry out this process in **JAGS** by using the `sum()`
²⁶⁸ and `step()` functions together to ascertain if a particular individual i was ever
²⁶⁹ previously alive. The `step()` function is a logical test in **JAGS** for $x \geq 0$
²⁷⁰ such that `step`$(x \geq 0)$ returns a 1, otherwise 0. Individuals that were ever
²⁷¹ previously alive are no longer eligible to be "recruited" into the population.
²⁷² The implementation of this model in **JAGS** is shown in panel 1.1.

²⁷³   **Mist-netting example**

²⁷⁴   We now return to the ovenbird data collected during a mist-netting study,
²⁷⁵ and initially presented in Chapt. **??**. These data are available in the `secr` pack-
²⁷⁶ age (see, Efford et al. (2004); Borchers and Efford (2008)). To refresh your
²⁷⁷ memory: 44 mist nets spaced 30 m apart on the perimeter of a 600-m x 100-m
²⁷⁸ rectangle (see Fig. 1.2) were operated on 9 or 10 non-consecutive days in late
²⁷⁹ May and June for 5 years from 2005-2009.

²⁸⁰   In Chapt. **??**, we dealt with this dataset as a type of "multi-session" model
²⁸¹ where abundance in each year, N_t, was estimated separately. This is the simplest
²⁸² approach for modeling data collected over multiple years, but it does not allow
²⁸³ for inference about demographic processes, as does the JS model.

²⁸⁴   The first issue at hand is that each line in our 3-D encounter history array of
²⁸⁵ data must correspond to a single individual. Previously, we were not interested
²⁸⁶ in individual identity across years so this was not of concern; however, we need
²⁸⁷ to maintain the order of individuals across years in order to estimate the survival
²⁸⁸ and recruitment of the individual into the population. We organize the data set
²⁸⁹ so that each row in our array represents just one individual across all primary
²⁹⁰ periods. For the ovenbird dataset, we can organize the data by creating a master
²⁹¹ list of all individuals captured during the entire study. From this list, we can
²⁹² assign each individual a unique row in our dataset (in the **R** commands, we do

```
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)     #the 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 across 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])
        z[i,t] ~ dbern(mu[i,t])         #alive state at t is dependent on phi and gamma
       cp[i,t] <- z[i,t]*p.mean
        Y[i,t] ~ dbinom(cp[i,t], K)
         }
         }
}
```

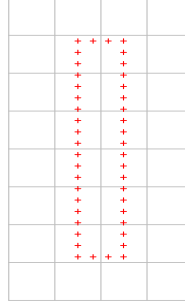Panel 1.1: **JAGS** model specification for the non-spatial JS model.

Figure 1.2: Arrangement of the mist nests in the ovenbird study. The nets are arranged in a 600-m by 100m rectangle, spaced 30 m apart.

this by using the `unique()` function on the row names for each year of our 3-D array and use `pmatch()` to associate the data to the correct column). The code to carry out this data organization are included in the **scrbook** package and are not shown here. Additionally, in Chapt. **??** we carried out data augmentation for each year separately; however, we must consider for example that individuals captured in year t could have been alive in year $t-1$. Our 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. 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 and we therefore make it time specific).

To implement the model in Panel 1.1, 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)

>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 is estimated to be between about 22 and 33 for each of the 5 years (see Table 1.1 for results). The posterior mean for detection (p.mean in the model) was 0.14, it is not included in the table because the spatial models do not have a parameter that directly corresponds to this one.

Shortcomings of the traditional JS models

As we have previously discussed, one of the biggest shortcomings of the non-spatial JS model is that we estimate N but have no explicit spatial reference area for that value. As you see in Table 1.1, the density estimate from the non-spatial JS model is listed as NA. This is because, again, the effective sampling area is unknown leaving us to determine that area in an *ad hoc* manner. Not making use of the spatial information in the data makes the estimation of density a non-formal process. As we saw in the closed models, the explicit incorporation of spatial information will allow us to provide a robust estimate of density. This improvement should also carry through in our estimation of other demographic parameters such as survival and recruitment. Also, while we can potentially model the relationship between density and the demographic parameters we are interested in by using standard JS models, we can make no inference regarding the spatial arrangement of individuals in the landscape nor the direct impact of movement.

1.2.3 Spatial Jolly-Seber models

To parameterize the spatial JS models, we essentially follow all of the same steps as the non-spatial model but we also include the trap location information into our detection function. Essentially, 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 we have done throughout the book:

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

with

$$p_{ijk} = p_0 * \exp(-\alpha_1 d_{ij}^2) \tag{1.1}$$

where $d_{ij} = ||\mathbf{s}_i - \mathbf{x}_j||$, the distance between $\mathbf{s}_i$ and $\mathbf{x}_j$.

If individual i is alive at time t ($z(i, t) = 1$), then the observations are Bernoulli as before. Conversely, if the individual is not alive ($z(i, t) = 0$), then the observations must be fixed zeros with probability 1. We can of course consider other encounter models such as the Poisson or multinomial models described in Chapt. **??**.

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

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

Previously, we described how this formulation of the model uses a set of latent indicator variables $A(i, t)$ which describes if individual is recruited into the population during time $(t - 1, t)$. Therefore, $A(i, t) = 1$ if individual i is recruited in time interval $(t - 1, t)$ otherwise $A(i, t) = 0$. Determining the number of recruits into the population, can be done using two steps. 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 1.2.

Mist-netting example

In the previous analysis of the ovenbird data, we did not make use of the spatial location for each net the ovenbird were captured in. However, there were 44 mist nets operational during each of the sampling occasions. We already organized the data above so that our 3-D encounter histories are set up. 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 encounter history array, `Yarr`), was created above in the code, so we do not reproduce the code here. To call the model, use the following **R** code which sets the initial values for $z[i,t]$, the parameters to monitor, and calls **JAGS**.

```
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, alpha0, and alpha1 are rather similar to those found in the multi-season analysis from Chapt. **??**. Since all of our parameters including alpha0 and alpha1 are shared between seasons, we would expect these results to be similar between the multi-season model and the JS model (see Table 1.1). There are some slight differences in the parameter estimates, for example, the density is smaller in year 4 in the multi-season model than in the JS model. This maybe be due to a smaller sample size in that year and the JS model is able to make use of the data a little more efficiently across the years. Because we have defined the same state space for the spatial JS model and multi-season, our estimates of N are directly comparable. However, the estimates of N 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 1.1

```
model {

psi ~ dunif(0,1)     #set the priors
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

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){
  S[i,1,t] ~ dunif(xlim[1],xlim[2]) # independent activity centers for each year
  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])  #last cell = 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 across 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 at time t
      mu[i,t]<- (phi*z[i,t-1]) + (gamma[t]*A[i,t-1])
       z[i,t]~dbern(mu[i,t])
         }
        }
}
```

Panel 1.2: **JAGS** model specification for the fully spatial JS model.

Table 1.1:   Posterior mean of model parameters for the non-spatial JS model (NS-JS), the spatial JS model (S-JS), and the spatial multi-season model (S-MS) fitted to the ovenbird data set. Density shown in individuals per hectare.

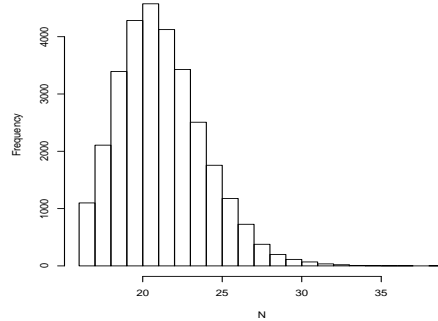|	NS-JS	S-JS	S-MS
D[1]	NA	0.96	0.93
D[2]	NA	1.00	1.00
D[3]	NA	1.10	1.20
D[4]	NA	1.10	0.89
D[5]	NA	0.79	0.76
N[1]	26.5	33	32.4
N[2]	30.2	36	35.8
N[3]	33.1	39	42.1
N[4]	29.5	37	30.8
N[5]	21.7	28	26.2
alpha0	NA	-2.9	-2.88
alpha1	NA	1.2e-04	1.22e-04
sigma	NA	6.4	6.44
gamma[1]	0.50	0.50	NA
gamma[2]	0.09	0.09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

Figure 1.3: Posterior distribution of N_5 from the spatial JS model for the oven-bird dataset. This graph suggests that there is no truncation of the posterior of N_5.

that N 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 know how much relative to the state-space to make useful comparisons between the Ns.

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 dataset. In this case, the 97.5% quantile of γ_5, the recruitment probability in the final 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 N to make sure they are not truncated. Fig. 1.3 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 it here, 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 literature. Some studies have found annual male ovenbird survival to be around 0.62 (Porneluzi and Faaborg, 1999; Bayne and Hobson, 2002); however, female ovenbird survival was much lower (0.21, Bayne and Hobson (2002)). With more individuals, we could run this model with survival estimated for each sex separately. However, we should be careful

431   not to over-parameterize our model based on the amount of data available.

1.3   Cormack-Jolly-Seber models

1.3.1   Traditional CJS models

434   The Cormack-Jolly-Seber models are used extensively in the literature to esti-
435   mate survival probabilities. There are essentially two ways to fit these models,
436   using either a multinomial approach (Lebreton et al., 1992) or a state-space
437   likelihood approach (Gimenez et al., 2007; Royle, 2008).

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

$$y_{it} | z_{it} \sim \text{Bernoulli}(p_t z_{it}).$$

444   Analogous to the JS model, if individual i is alive at time t ($z_{it} = 1$), then the
445   observations are Bernoulli with probability of detection p_t. If the individual is
446   not alive ($z_{it} = 0$), then the observations must be fixed zeros with probability
447   1. In the CJS formulation, as opposed to the JS, we condition on first capture
448   which means that z_{it} will be 1 when t is the first primary period of capture. We
449   can denote this z_{if_i} where f_i indicates the primary occasion in which individual
450   i is first captured, which can vary from $1 \ldots T$. This ensures that each individual
451   is alive upon entering the model.

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

$$z_{if_i} = 1$$

455   where f_i indicates the primary occasion in which individual i is captured and
456   the model for the transition of individual states from t to $t + 1$ for all $t > f_i$ is

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

457   Because we start with $z_{if_i} = 1$, the individual survives with probability ϕ to
458   time $f_i + 1$ and so forth. Once an individual leaves the population (i.e., $z_{it} = 0$),
459   there is no mechanism for the individual to return. This means that under this
460   specification individuals cannot temporarily emigrate. In the CJS model we are
461   not estimating N, so we do not incorporate any data augmentation here. This
462   version of the model is easy to construct in the **BUGS** (or **JAGS**) language
463   which is shown in Panel 1.3. Variations on this basic model and associated code
464   for fitting the model in **BUGS** are described in detail in Kéry and Schaub
465   (2012, Chapts. 7-9).

```
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 1.3: **JAGS** model specification for the non-spatial basic CJS model.

Figure 1.4: American shad caught in North Carolina, U.S.A. Credit: Joshua Raabe, North Carolina State University

Table 1.2: Results of the basic non-spatial CJS model for the American shad dataset.

	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

Migratory fish example The motivation for this example stems from an interest in better understanding survival and movement of migratory fishes. For this example, we will use data collected on American shad *Alosa sapidissima* in the New River in North Carolina, U.S.A. (see photo in Fig. 1.4). The data were collected and analyzed 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 7 upstream PIT antennas passively recaptured individuals during upstream and downstream migrations. Each time a fish passed over the antenna, it was recorded and summarized weekly for 12 weeks. The fish do not necessarily move past all antenna and may remain in the river between antenna for more than a week, thus they are not all detected at each time period. The antenna do always operate perfectly either and fish that pass may not be recorded at some times.

To apply the basic CJS model, we create the encounter history for each individual for the 12 weeks and we also create a vector to indicate the period of first capture.

Table 1.2 shows the estimated detection probability for each of the 12 primary periods in the study. The posterior mean for detection probability ranges from 0.126 to 0.880, which could potentially be due to variation in water flow, stream depth, storms, 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 temporally or permanently heading back to the ocean or possibly to other tributaries that are not monitored. We demonstrate in panel

493 1.3 how to allow p to vary by time, but we could also allow survival, ϕ to vary
494 by time by implementing it exactly as we do p. As we move into the multi-state
495 model, we can test for movement and survival by state, allow us to address more
496 specific biological questions.

1.3.2 Multi-state CJS models

498 The basic version of the CJS model only allows for estimation of survival and de-
499 tection. However, researchers are often interested in addressing other ecological
500 questions such as age-dependent survival rates, habitat based movements, etc.
501 Multi-state models allow researchers to directly address such questions by incor-
502 porating more than one state that an individual may potentially be in Arnason
503 (1972, 1973); Brownie et al. (1993). These possible states can be geographic
504 location, age class, or reproductive status among many others. Instead of just
505 having an encounter history for an individual, we will also have auxiliary infor-
506 mation on the state of that individual at capture (e.g., breeder or non-breeder).
507 Since our interest in movement of individuals, here we will consider states that
508 represent spatial units or geographic locations. Generally speaking, we might
509 think that the transition rates between locations could be due to habitat fea-
510 tures (or quality) and we can use multi-state models to help us address such
511 a question. In addressing movement through a multi-state modeling approach,
512 the movement is often parameterized as random or Markovian between patches
513 (Arnason (1972, 1973); Schwarz et al. (1993)).

514 In the simplest version of the multi-state model we have just two states.
515 Thus, individuals can be marked and recaptured in one of two states (we'll
516 call them A and B here). We will assume that the two "states" are different
517 geographic sites. In our single-state model above, an individual i was either
518 alive ($z_{it} = 1$) at time t or dead ($z_{it} = 1$). Now, we must consider that the
519 individual could be alive in a given state or dead and that individuals can
520 transition between states. An easy way to think about this is to look at the
521 state transition matrix in Table 1.3. Here, ϕ_A is the probability of surviving in
522 State A from time t to $t+1$ and ϕ_B is analogous for State B. The movement
523 parameters are $\psi_A B$ and $\psi_B A$, where $\psi_A B$ is the probability that an individual,
524 which survived from t to $t+1$ in Site A, moves to State B just before $t+1$ and
525 vice versa for $\psi_B A$

Table 1.3: Transition matrix for a multi-state model with just two states.

	State A	State B	Dead
State A	$\phi_A(1-\psi_{AB})$	$\phi_A\psi_{AB}$	1 - ϕ_A
State B	$\phi_B\psi_{BA}$	$\phi_B(1-\psi_{BA})$	1 - ϕ_B
Dead	0	0	1

526 We do not necessarily observe individuals in their given state though, so we
527 must estimate detection separately for each of the states. Hence we also have
528 p_A and p_B, the probability of detecting an individual in state A and state B

529 respectively.

530   To relate this back to the description of multi-state models in Chapt. **??**, we

531 can define **s** as the index of which state an individual is in and u_{it} as the state

532 in which individual i was observed during sample t. In this two state example,

533 u_{it} can only take on values for being observed in A or B (i.e., 1 or 2).

534   We can define a simplistic model such that

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

535 where ψ is a constant vector. We observe that individual with probability p_0,

536 that is:

$$\Pr(y_{it} = 1 | u_{it}) = p_0$$

537 The state-transition probabilities are constant.

538   To extend this model, we can define **s** as the index of which state an indi-

539 vidual is in and then condition the observed locations, u_{it} as a function of the

540 state an individual is in, **s**. This means that whether an individual moves or

541 not, or where it moves to, is a function of where it is located.

542   This commonly used model has successive movement outcomes that are *iid*

$$u_{it} \sim \text{dcat}(\psi(\mathbf{s}_i))$$

543   Conditional on the state in which individual i is located, we observe that

544 individual with probability p_0. That is:

$$\Pr(y_{it} = 1 | u_{it}) = p_0$$

545 The state-transition probabilities are still constant, conditional on **s**. Other

546 models for these transition probabilities are possible and we will discuss those

547 later.

548   A slight modification of this model would define **s** as a "home area" for each

549 individual. Then the region the animal goes to is a function, not of where he

550 was last time, but which region is his home area. This model is only subtlety

551 different from the Markovian model and as was shown in Chapt. **??** for closed

552 populations models is how we make the technical transition from multi-state

553 models to SCR models. Essentially increasing to a large number of strata, this

554 formulation of the multi-state model becomes an SCR model where the "area

555 of activity" **s** becomes the "activity center" for each individual.

556   To program this model in **JAGS**, we use a slightly different formulation

557 which essentially combines u_{it} and y_{it} as defined above into one observation

558 matrix such that $y_{it} = 1, 2,$ or 3 where 3 indicates "not observed". Additionally,

559 we use z_{it} to indicate the true state of individual i such that $z_{it} = 1, 2,$ or 3 where

560 1 indicates alive and in state 1, 2 indicates alive and in state 2, and 3 indicates

561 "not alive". Using this delineation, we just need to set up the transition matrix

562 based on Table 1.3 and define each item within the model specification, shown

563 in Panel 1.4. Note that this can become quite cumbersome when dealing with

564 models that have many states.

565   **Migratory fish example**

```
model{
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 1.4: **JAGS** model specification for a two state version of the multi-state CJS model. Code adjusted from (Kéry and Schaub, 2012, Chapt. 9).

Table 1.4:   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 down stream area. phi_A is the weekly survival probability in state A and $\psi_A B$ 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
$\psi_A B$	0.421	0.034	0.356	0.421	0.489
$\psi_B A$	0.927	0.014	0.897	0.937	0.952

Previously, we analyzed the American shad data using a basic CJS model. However, the researchers were interested in movement of fish during migration and so we classified the stream into 2 states (regions) – "downstream" and "upstream". Each antenna was assigned to a state based on the location, those below 20 river kilometers were considered in the downstream state. 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"). Again, 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.

Survival between the two areas is quite different (see Table 1.4). This might suggest that fish moving further upstream are expanding 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 1.2). Also, it should be noted that $\psi_B A$ is 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. We did have to reduce the dataset however to fit this model and information on spatial location was lost in creating just two states, downstream and upstream.

1.3.3   Spatial CJS models

In Chapt. **??**, we described how SCR models are essentially a type of multi-state model with spatially structured transition probabilities. As we noted, individuals can appear in > 1 states, simultaneously, which is not directly analogous to a standard multi-state model. However, building on the state-space and multi-state CJS models, we can explicitly incorporate individual movement as an individual covariate model (Royle, 2009). To move from the basic and

multi-state CJS models to the SCR version, we need only make a few changes
to the model. Essentially, 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 sub-sample) $k = 1, 2, \ldots, K$ and primary period t. We note that
in some cases we may have intervals ($K = 1$) 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:

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

Conversely, if the individual is not alive ($z(i,t) = 0$), then the observations must
be fixed zeros with probability 1. In the CJS formulation, we will condition on
first capture which means that $z(i,t)$ will be 1 when t is the first primary period
of capture. We can denote this $z(i, f_i)$ where f_i indicates the primary occasion
in which individual i is first captured. This ensures that each individual is alive
upon entering the model.

Modeling time-effects either within or across primary periods is straightfor-
ward. 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).

We follow the same model for survival as described in the non-spatial version
of the CJS. The model is initialized by setting the alive state at first capture to
one:

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

and for the transition of an individual's alive state from t to $t+1$, for all $t > f_i$,
we have

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

An individual survives with probability ϕ from one time step to the next. It is
easy to see that we can let survival be time specific by allowing ϕ to vary with
each time step:

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

In either case, once an individual leaves the population (i.e., $z_{it} = 0$), there
is no recruitment so individuals cannot return. Again, we are not estimating N
in this model, hence we do not need any data augmentation. This conveniently
makes the model run faster too!

Migratory fish example

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 7 PIT antennas and the number of times each fish passed over the antenna, we can apply the SCR CJS model to evaluate movement up and downstream of these fishes. 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 3-D array instead of a 4-D array. Given the structure of the encounters, we use a Poisson encounter model in this example.

```
library(reshape)

# Constants:
M <- 315        # Number of individuals
T <- 12         # Number of periods (weeks)
nantenna <- 7   # weir, 6 antennas
antenna.loc <- c(3,7,12,44,56,72,77)  # antenna locations

# Input and format data matrix:
AS10 <- read.table("AS10.txt" ,header=T)
melted.rkm <- melt(AS10, id=c("TagID","RKM"))
y <- cast(melted.rkm, TagID ~ RKM ~ value, fill=0, length)
first=read.csv("firstcap.csv")

sink("ModelCJS.txt")
cat("

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)

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]])
      }
```

```
682
683     for (t in first[i]+1:T) {
684           S[i,t] ~ dunif(xl, xu) # XXXX above you have dunif(0,50)?
685          for(j in 1:nantenna) {
686         D2[i,j,t] <- pow(S[i,t]-antenna.loc[j], 2)
687               lam[i,j,t] <- lam0 * exp(-D2[i,j,t]/(2*sigma2))
688            tmp[i,j,t] <- z[i,t]*lam[i,j,t]
689          y[i,j,t] ~ dpois(tmp[i,j,t])
690   }
691      phiUP[i,t] <-  z[i,t-1]*phi
692        z[i,t] ~ dbern(phiUP[i,t])
693   }
694   }
695   }
696
697   ",fill = TRUE)
698   sink()
699
700   data1<-list(y=y, first=first, M=M, T=T, xl=0, xu=80, nantenna=nantenna, antenna.loc=antenna.loc)
701
702   z=matrix(NA, M, T)
703   for(i in 1:M){
704   for(t in first[i]:12){
705   z[i,t] <-1
706   }
707   }
708
709   inits =  function() {list(z=z,phi=runif(1,0,1), lam0=runif(1,0,2),
710                       tauv=runif(1,10, 20), sigma=runif(1,0,10)) }
711
712   parameters <- c("sigma", "phi", "lam0")
713
714   library("rjags")
715   out1 <- jags.model("modelCJS.txt", data1, inits, n.chains=3, n.adapt=500)
716   out2CJS <- coda.samples(out1,parameters,n.iter=20000)
```

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 based under the Binomial encounter model. Because fish can swim over an antenna multiple times during a sampling occasion, the Poisson encounter model was used to allow the number of detections to be greater than 1. The posterior mean for ϕ was 0.784 (see Table 1.5), again showing that the survival probability is generally low, just as we saw in the two previous example analysis 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

Table 1.5: Results of the spatial CJS 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

mean of 13.954. Our system here is linear, so we do not think of fish as having a home range radius in this system. However, σ can still inform us about the linear distance fish are moving. One final note about this example, we have simplified the dataset for analysis here and some parameter estimates are different than found in Raabe (2012).

1.4   Activity Center Dynamics

We extend the model of individual encounter histories by specifying an additional model component that describes the spatial distribution of individual activity centers. A plausible "null model" for the distribution of individual activity centers is to assume they are static over time and do not change across primary periods, i.e., $\mathbf{s}_i \sim \text{Unif}(\mathcal{S})$. It might seem more likely that activity centers change over time but are independent from year to year for a given individual such $\mathbf{s}_i \sim \text{Unif}(\mathcal{S})$. This is how the spatial version of the JS and CJS models were formulated above. Another option would be to assume that $\mathbf{s}(i, t) \sim \text{Normal}(\mathbf{s}(i, t-1), \tau^2\mathbf{I})$ for $t > 1$ so that individual home range centers are perturbed randomly from their previous value. For example, many migratory passerines, like the ovenbird, return to the same location, or nearly so each year.

We could use this specification to model changes in home range centers with regards to habitat. For example, if our primary period is a season, we may expect that individuals move as the available food sources change. Using telemetry data and/or capture recapture models a number of developments have been made to understand animal movement patterns relative to habitat or dynamic systems(e.g., Jonsen et al. (2005); Hooten and Wikle (2010)). Similarly,

if we have an indicator of habitat that varies by season, then in SCR models we can model the location of activity centers as a function of the change in habitat. There are a number of options for modeling variation in activity centers or animal locations as a function of covariates such as habitat, season, or behavior. Other approaches to analyzing movement in a mark-recapture framework include but are not limited to diffusion and auto-regressive models(Ovaskainen (2004); Ovaskainen et al. (2008)), agent-based (Grimm et al. (2005); Hooten et al. (2010)) and dispersal kernels (Fujiwara et al. (2006)). For example, we define u_{ikt} as the individual's observed location at secondary period k in primary period t. Then $u_{ikt} \sim \text{Normal}(\mathbf{s}(i,t), \Sigma_t)$ where Σ_t is the variance-covariance matrix at time t. This is the model we have assumed quite frequently throughout the book, i.e., that individual observed locations are assumed to follow a bivariate normal distribution about the activity center, $\mathbf{s}$. This is similar to the Guassian and Laplace dispersal kernels. We could then allow the observed locations to follow an auto-regressive model such that $u_{ikt} \sim \text{Normal}(\rho \mathbf{s}(i, t-1), \Sigma_t)$ ==XXX figure out the variance XXX== This is just one simple example, as more information becomes available and data are collected over longer time periods, the ability to use different movement models will continue to be employed in open SCR models.

Rathbun and Cressie (1994) articulate 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, but are still analogous. 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.

Migratory fish example notes

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 upstream to spawn. 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.

$$\log(\sigma_t) = \mu_S + \alpha_2 \text{Flow}_t$$

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 correlation in activity centers to be a function of flow. In this case, for example, a low flow period might indicate that activity centers are more correlated to the previous time period because fish are not actively migrating during such a time. This means that we assume the activity centers are correlated so we have

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

where
$$\log(\tau) = \mu_T + \alpha_2 \text{Flow}_t.$$

These are just a few thoughts on simple ways to model movement as a function of habitat variables. As we discussed in the previous section, there are many other movement models that could be used.

1.5   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.

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 providing a huge advantage over traditional models. Also, models of individual dispersal can be used to examine dynamics of 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..

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