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## ALTERNATIVE OBSERVATION MODELS

In previous chapters we considered various models of *encounter probability*, both in terms of parametric functions of distance and also a myriad of covariate models (Chapt. 7 and elsewhere). However, we have so far only considered a specific probability model for the observations (we'll call this the "observation model") – the Bernoulli encounter process model which, in `secr`, is the *proximity detector* model. This assumes that individual and trap-specific encounters are independent Bernoulli trials.

In this chapter, we focus on developing additional observation models. The observation model could be thought of as being determined by the type of device – or the type of "detector" using the terminology of `secr` (Efford, 2011). We consider models that apply when observations are not binary and, in some cases, that do not require independence of the observations. We present models when the data are encounter *frequencies*, based on the Poisson distribution, and observation models based on the multinomial distribution. For example, if sampling devices can detect an individual some arbitrary number of times during an interval, then it is natural to consider observation models for encounter frequencies, such as the Poisson model. Another type of encounter device is the "multi-catch" device (Efford et al., 2009a) which is a physical device that can capture and hold an arbitrary number of individuals. A typical example is a mist-net for birds (Borchers and Efford, 2008). It is natural to regard observations from these kinds of studies as independent multinomial observations. A related type of device that produces *dependent* multinomial observations are the so-called *single-catch* traps (Efford, 2004; Efford et al., 2009a). The canonical example are small-mammal live traps which catch and hold a single individual. Competition among individuals for traps induces a complex dependence structure among individual encounters. To date, no formal inference framework has been devised for this method although it stands to reason that the independent multinomial model should be a good approximation in some situations (Efford et al., 2009a). We analyze a number of examples of these different observation models using `JAGS` and also the `R` package `secr` (Efford, 2011).

## 9.1 POISSON OBSERVATION MODEL

The models we analyze in Chapt. 5 assumed binary observations – i.e., standard encounter history data – so that individuals are captured at most one time in a trap on any given sample occasion. This makes sense for many types of DNA sampling (e.g., based on hair snares) because distinct visits to sampled locations or devices cannot be differentiated. However, for some encounter devices, or methods, the potential number of encounters is *not* fixed, and so it is possible to encounter an individual some arbitrary number of times during any particular sampling episode. That is, we might observe encounter frequencies  $y_{ijk} > 1$  for individual  $i$ , trap  $j$  and sampling interval  $k$ . As an example, if a camera device is functioning properly it may be programmed to take photos every few seconds if triggered. For a second example, suppose we are searching a quadrat or length of trail for scat, we may find multiple samples from the same individual. Therefore, we seek observation models that accommodate such encounter frequency data. In general, any discrete probability mass function could be used for this purpose, including the standard models for count data used throughout ecology, the Poisson and negative binomial. Here we focus on using the Poisson model only although other count frequency models are possible for SCR models (Efford et al., 2009b).

Let  $y_{ijk}$  be the frequency of encounter for individual  $i$ , in trap  $j$ , during occasion  $k$ , then assume:

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

where the expected encounter frequency  $\lambda_{ij}$  depends on both individual and trap. As we did in the binary model of Chapt. 5, we now seek to model the expected value of the observation (which was  $p_{ij}$  in Chapt 5) as a function of the individual activity center  $\mathbf{s}_i$ . We propose

$$\lambda_{ij} = \lambda_0 k(\mathbf{x}_j, \mathbf{s}_i)$$

Where  $k(\mathbf{x}, \mathbf{s})$  is any positive valued function, such as the negative exponential or the bivariate Gaussian kernel, and  $\lambda_0$  is the baseline encounter rate – the expected number of encounters if a trap is placed precisely at an individuals home range center (note: in **secr** the notation for this is  $g_0$ ). Then,  $\lambda_0 k(\mathbf{x}_j, \mathbf{s}_i)$  is the expected encounter rate in trap  $\mathbf{x}_j$  for an individual having activity center  $\mathbf{s}_i$ . Note that

$$\log(\lambda_{ij}) = \log(\lambda_0) + \log(k(\mathbf{x}_j, \mathbf{s}_i)).$$

Equating  $\alpha_0 \equiv \log(\lambda_0)$ , and, if  $k(\mathbf{x}, \mathbf{s}) \equiv \exp(-d(\mathbf{x}, \mathbf{s})^2/(2\sigma^2))$  (i.e., the Gaussian model), then:

$$\log(\lambda_{ij}) = \alpha_0 - \alpha_1 d(\mathbf{x}_j, \mathbf{s}_i)^2 \quad (9.1.1)$$

where  $\alpha_1 = 1/(2\sigma^2)$ , which is the same linear predictor as we have seen for the Bernoulli model in Chapt. 5. This Poisson SCR model is therefore a type of Poisson generalized linear mixed model (GLMM).

We can accommodate covariates at the level of individual-, trap- or sample occasion by including them on the baseline encounter rate parameter  $\lambda_0$ . For example, if  $C_j$  is some covariate that depends on trap only, then we express the relationship between  $\lambda_0$  and  $C_j$  as:

$$\log(\lambda_{0,ijk}) = \alpha_0 + \alpha_2 C_j$$

and therefore covariates on the logarithm of baseline encounter probability appear also as linear effects on  $\lambda_{ij}$ . In general, covariates might also affect the coefficient on the distance

term ( $\alpha_1$ ) (e.g., sex of individual). We don't get into too much discussion of general covariate models here, but we covered them in some detail in both Chaps. 7 and 8.

For models in which we do not have covariates that vary across the sample occasions  $k$ , we can aggregate the observed data by the property of compound additivity of the Poisson distribution (if  $x$  and  $y$  are *iid* Poisson with mean  $\lambda$  then  $x + y$  is Poisson with mean  $2\lambda$ ). Therefore,

$$y_{ij} = \left( \sum_{k=1}^K y_{ijk} \right) = \text{Poisson}(K\lambda_0 k(\mathbf{x}_j, \mathbf{s}_i))$$

We see that  $K$  and  $\lambda_0$  serve the same role as affecting the base encounter rate. Since the observation model is the same, probabilistically speaking, for all values of  $K$ , evidently we need only  $K = 1$  “survey” from which to estimate model parameters (Efford et al., 2009b). We know this intuitively, as sampling by multiple traps serves as replication in SCR models. This has great practical relevance to the conduct of capture-recapture studies and the use of SCR models. For example, if individuality is obtained by genetic information from scat sampling, one should only have to carry out a single spatial sampling of the study area. However, one must be certain that sufficient spatial recaptures will be obtained so that effective estimation is possible.

### 9.1.1 Poisson model of space usage

It is natural to interpret the Poisson encounter model as a model of space usage resulting from movement of individuals about their home range (Sec. 5.4). Imagine we have perfect samplers in every pixel of the landscape so that whenever an individual moves from one pixel to another, we can record it. Let  $m_{ij}$  be the number of times individual  $i$  was recorded in pixel  $j$  (i.e., it selected or used pixel  $j$ ). Then, we might think of the Poisson model for the observed *use* frequencies:

$$m_{ij} \sim \text{Poisson}(\lambda_0 k(\mathbf{x}_j, \mathbf{s}_i))$$

where  $\lambda_0$  is related to the baseline movement rate of the animal (how often it moves). This model of space usage gives rise to the standard resource selection function (RSF) models (see Chapt. 13). But now suppose our samplers are not perfect but, rather, record only a fraction of the resulting visits. A sensible model is

$$y_{ij} | m_{ij} \sim \text{Binomial}(m_{ij}, p).$$

The marginal distribution of  $y_{ij}$  is:

$$y_{ij} \sim \text{Poisson}(p_0 k(\mathbf{x}_j, \mathbf{s}_i)).$$

where  $p_0$  is a composite of the movement rate and conditional detection probability  $p$ . Therefore, we see that encounters accumulate in proportion to the frequency of outcomes of an individual using space (or “selecting resources”).

We introduced an interpretation of SCR models in terms of movement and space usage in Sec. 5.4, and it is one of the main underlying concepts of SCR models that is not present in ordinary capture-recapture models. As we noted there, the underlying model of space usage is only as complex as the encounter probability model which has been, so far in this book, only symmetric and stationary (does not vary in space). We generalize this model of space usage substantially in Chapt. 13.

### 9.1.2 Poisson relationship to the Bernoulli model

There is a sense in which the Poisson and Bernoulli models can be viewed as consistent with one another. Note that under the Poisson model, the relationship between the expected count and the probability of counting “at least 1”, is given by

$$\Pr(y > 0) = 1 - \exp(-\lambda) \quad (9.1.2)$$

where  $\mathbb{E}(y) = \lambda$ . Therefore, if we equate the event “encountered” with the event that the individual was captured at least 1 time under the Poisson model, i.e.,  $y > 0$ , then it would be natural to set  $p_{ij} = \Pr(y > 0)$  according to Eq. 9.1.2. That is, we can use Eq. 9.1.2 as the model for encounter probability for binary observations. This is the “hazard rate” model in distance sampling.

In fact, as  $\lambda$  gets small, the Poisson model is a close approximation to the Bernoulli model in the sense that outcomes concentrate on  $\{0, 1\}$ , i.e.,  $\Pr(y \in \{0, 1\}) \rightarrow 1$  as  $\lambda \rightarrow 0$ . Indeed, under the Poisson model,  $\Pr(y > 0) \rightarrow \lambda$  for small values of  $\lambda$ . This phenomenon is shown in Fig. 9.1 where the left panel shows a plot of  $\lambda_{ij} = \lambda_0 k(\mathbf{x}_j, \mathbf{s}_i)$  vs. distance and superimposed on that is a plot of  $p_{ij} = 1 - \exp(-\lambda_{ij})$  vs. distance, for values  $\lambda_0 = 0.1$  and  $\sigma = 1$ , and the right panel shows a plot of  $\Pr(y > 0)$  vs.  $\mathbb{E}(y)$ . We see that the two quantities are practically indistinguishable. This is convenient in some cases because the Poisson model might be more tractable to fit (or even vice versa). For an example, see the models described in Chapt. 18, and we also consider another case in Sec. 9.3 below. To evaluate the closeness of the approximation, you can use the following **R** commands which we used to produce Fig. 9.1:

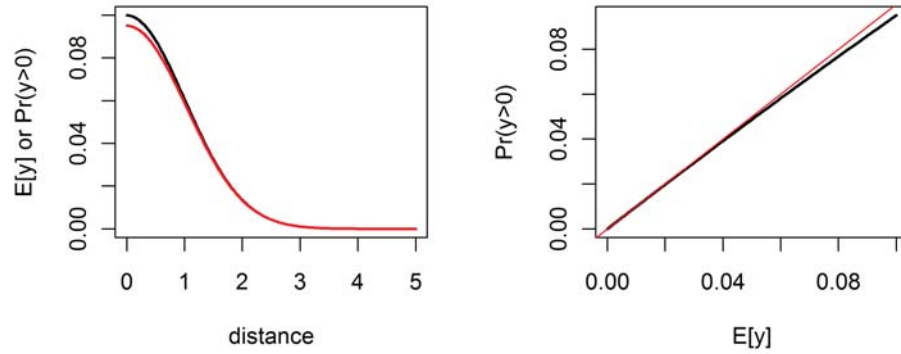
```
> x <- seq(0.001,5,,200)
> lam0 <- .1
> sigma <- 1
> lam <- lam0*exp(-x*x/(2*sigma*sigma))

> par(mfrow=c(1,2))
> p1 <- 1-exp(-lam)
> plot(x, lam, ylab="E[y] or Pr(y>0)",xlab="distance",type="l",lwd=2)
> lines(x,p1,lwd=2,col="red")
> plot(lam, p1, xlab="E[y]",ylab="Pr(y>0)",type="l",lwd=2)
> abline(0,1,col="red")
```

To summarize, if  $y$  is Poisson then, as  $\lambda$  gets small,

$$\begin{aligned} \Pr(y > 0) &\approx \mathbb{E}(y) \\ 1 - \exp(-\lambda_0 k(\mathbf{x}, \mathbf{s})) &\approx \lambda_0 k(\mathbf{x}, \mathbf{s}) \end{aligned} \quad (9.1.3)$$

What all of this suggests is that if we have very few observations  $> 1$  in our SCR data set, then we won’t lose much information by using the Bernoulli model. On the other hand, the Poisson model may have some advantages in terms of analytic or numerical tractability in some cases. Further, this approximation explains the close correspondence we have found between these two versions of the Gaussian encounter probability model (Sec. 5.4). Namely, the Gaussian hazard model and the Gaussian encounter probability model are close approximations because  $1 - \exp(-\lambda) \approx \lambda$  if  $\lambda$  is small.



**Figure 9.1.** Poisson approximation to the binomial. As the Poisson mean approaches 0, then  $\Pr(y > 0)$  under the Poisson model approaches  $\lambda$  and therefore  $y \sim \text{Poisson}(\lambda)$  is well-approximated by a Bernoulli model with parameter  $\lambda$ .

Even in such cases where the Poisson and Bernoulli models are not quite equivalent, we might choose to truncate individual encounter frequencies to binary observations anyhow (transforming counts to 0/1 is called “quantizing”). We might do this intentionally in some cases, such as when the distinct encounter events are highly dependent as often happens in camera trap studies when the same individual moves back-and-forth in front of a camera during a short period of time. But sometimes, truncation is a feature of the sampling. For example, in the case of bear hair snares, the number of encounters might be well approximated by a Poisson distribution but we cannot determine unique visits and so only get to observe the binary event “ $y > 0$ ”. In this case, we might choose to model the encounter probability for the binary encounter using Eq. 9.1.4. This is equivalent to the complementary log-log link model, or the “Gaussian hazard” as we called it in Chapt. 5:

$$\text{cloglog}(p_{ij}) = \log(\lambda_0) + \log(k(\mathbf{x}, \mathbf{s}))$$

where  $\text{cloglog}(u) = \log(-\log(1 - u))$ .

### 9.1.3 A cautionary note on modeling encounter frequencies

Other models for counts might be appropriate. For example, ecologists are especially fond of negative binomial models for count data (Ver Hoef and Boveng, 2007; White and Bennetts, 1996; Kéry et al., 2005) but other models for excess-Poisson variation are possible. For example, we might add a normally distributed random effect to the linear predictor (Coull and Agresti, 1999).

As a general rule we favor the Bernoulli observation model even if our sampling scheme

produces encounter frequencies. The main reason is that, with frequency data, we are forced to confront a model choice problem (i.e., Poisson, negative binomial, log-normal mixture) that is wholly unrelated to the fundamental space usage process that underlies the genesis of many types of SCR data. Repeated encounters over short time intervals are not likely to be the result of independent encounter events. E.g., an individual moving back and forth in front of a camera yields a cluster of observations that is not informative about the underlying spatial structure of the population. Similarly in scat surveys dogs are used to locate scats which are processed in the lab for individuality (Kohn et al., 1999; MacKay et al., 2008; Thompson et al., 2012). The process of local scat deposition is not strictly the outcome of movement or space usage but rather the outcome of complex behavioral considerations as well as dependence in detection of scat by dogs. For example, dogs find (or smell) one scat and then are more likely to find one or more nearby ones, if present, or they get into a den or latrine area and find many scats. The additional assumption required to model variation in observed frequencies (i.e., conditional on location) provides relatively no information about space usage and density, and we feel that the model selection issue should therefore be avoided.

To elaborate on this, we suppose that an individual with activity center  $\mathbf{s}$  visits a particular pixel  $\mathbf{x}$  with some probability  $p(\mathbf{x}, \mathbf{s})$ , and then, once there, deposits a number of scat, or visits a camera some number of times with frequency  $y(\mathbf{x}, \mathbf{s}) \geq 0$ . We describe the outcome of this movement/usage process with a two-level hierarchical model of the form:  $[y|w][w|p(\mathbf{x}, \mathbf{s})]$  where  $w(\mathbf{x}, \mathbf{s})$  is a binary variable that indicates whether the individual with activity center  $\mathbf{s}$  used pixel  $\mathbf{x}$  during some interval, and let  $w(\mathbf{x}, \mathbf{s}) \sim \text{Bernoulli}(p(\mathbf{x}, \mathbf{s}))$ . If we suppose encounter frequency  $y$  is independent of  $\mathbf{x}$  and  $\mathbf{s}$  conditional on the use variable  $w$ , then we see that the model for  $y$  (amount of use) does not depend on  $\mathbf{s}$ .

#### 9.1.4 Analysis of the Poisson SCR model in BUGS

We consider the simplest possible model here in which we have no covariates that vary over sample occasions  $k = 1, 2, \dots, K$  so that we work with the aggregated individual- and trap-specific encounters:

$$y_{ij} = \left( \sum_{k=1}^K y_{ijk} \right) = \text{Poisson}(K \lambda_0 k(\mathbf{x}_j, \mathbf{s}_i))$$

and we consider the bivariate normal form of  $k(\mathbf{x}, \mathbf{s})$ :

$$k(\mathbf{x}, \mathbf{s}) = \exp(-d(\mathbf{x}, \mathbf{s})^2 / (2\sigma^2))$$

so that

$$\log(\lambda_{ij}) = \alpha_0 - \alpha_1 d(\mathbf{x}_j, \mathbf{s}_i)^2$$

where  $\alpha_0 = \log(\lambda_0)$  and  $\alpha_1 = 1/(2\sigma^2)$ .

As usual, we approach Bayesian analysis of these models using data augmentation (Sec. 4.2). Under data augmentation, we introduce a collection of all-zero encounter histories to bring the total size of the data set up to  $M$ , and a corresponding set of data augmentation variables  $z_i \sim \text{Bern}(\psi)$ . Then the observation model is specified conditional on  $z$  according to:

$$y_{ij} \sim \text{Poisson}(z_i K \lambda_{ij})$$

which evaluates to a point mass at  $y = 0$  if  $z = 0$ . In other words, the observation model under data augmentation is a zero-inflated Poisson model which is easily analyzed by Bayesian methods, e.g., in one of the **BUGS** dialects or, alternatively, using likelihood methods, which we neglect here although the same principles as in Chapt. 6 apply.

### 9.1.5 Simulating data and fitting the model

Simulating a sample SCR data set under the Poisson model requires only a couple minor modifications to the procedure we used in Chapt. 5 (see the function `simSCR0`). In particular, we modify the block of code which defines the model to be that of  $\mathbb{E}(y)$  and not  $\Pr(y = 1)$ , and we change the random variable generator from `rbinom` to `rpois`:

```
##
## S=activity centers and traplocs defined as in simSCR0()
##
## Compute distance between activity centers and traps:
> D <- e2dist(S,traplocs)

## Define parameter values:
> alpha0 <- -2.5
> sigma <- 0.5
> alpha1 <- 1/(2*sigma*sigma)

## Encounter probability model:
> muy <- exp(alpha0)*exp(-alpha1*D*D)

## Now generate the encounters of every individual in every trap
> Y <-matrix(NA,nrow=N,ncol=ntraps)
> for(i in 1:nrow(Y)){
  Y[i,] <- rpois(ntraps,K*muy[i,])
}
```

We modified our simulation code from Chapt. 5 to simulate Poisson encounter frequencies for each trap and then we analyze an ideal data set using **BUGS**. This Poisson simulator function `simPoissonSCR` is available in the `scrbook` package (it can produce 3-d encounter history data too, although we don't do that here). Here is an example of simulating a data set and harvesting the required data objects, and doing the data augmentation:

```
## Simulate data and extract data elements
##
> data <- simPoissonSCR(discard0=TRUE,rnd=2013)
> y <- data$Y
> nind <- nrow(y)
> X <- data$traplocs
> K <- data$K
> J <- nrow(X)
```

```

8338 > xlim <- data$xlim
8339 > ylim <- data$ylim
8340
8341 ## Data augmentation
8342 > M <- 200
8343 > y <- rbind(y,matrix(0,nrow=M-nind,ncol=ncol(y)))
8344 > z <- c(rep(1,nind),rep(0,M-nind))

```

8345 The process for fitting the model in **WinBUGS** or **JAGS** is identical to what we've  
 8346 done previously in Chapt. 5. In particular, we set up some starting values, package  
 8347 the data and inits, identify the parameters to be monitored, and then send everything  
 8348 off to our MCMC engine. Here it all is for fitting the Poisson observation model (these  
 8349 commands are shown in the help file for `simPoissonSCR`):

```

8350 ## Starting values for activity centers
8351 ##
8352 > sst <- X[sample(1:J,M,replace=TRUE),]
8353 > for(i in 1:nind){
8354   if(sum(y[i,])==0) next
8355   sst[i,1] <- mean( X[y[i,]>0,1] )
8356   sst[i,2] <- mean( X[y[i,]>0,2] )
8357 }
8358 ## Dithered a little bit from trap locations
8359 > sst <- sst + runif(nrow(sst)*2,0,1)/8
8360 > data <- list (y=y,X=X,K=K,M=M,J=J,xlim=xlim,ylim=ylim)
8361 > inits <- function(){
8362   list (alpha0=rnorm(1,-2,.4),alpha1=runif(1,1,2),s=sst,z=z,psi=.5)
8363 }
8364 > parameters <- c("alpha0","alpha1","N","D")

```

8365 Next, we write the **BUGS** model to an external file:

```

8366 > cat("
8367 model{
8368   alpha0 ~ dnorm(0,.1)
8369   alpha1 ~ dnorm(0,.1)
8370   psi ~ dunif(0,1)
8371
8372   for(i in 1:M){
8373     z[i] ~ dbern(psi)
8374     s[i,1] ~ dunif(xlim[1],xlim[2])
8375     s[i,2] ~ dunif(ylim[1],ylim[2])
8376     for(j in 1:J){
8377       d[i,j] <- pow(pow(s[i,1]-X[j,1],2) + pow(s[i,2]-X[j,2],2),0.5)
8378       y[i,j] ~ dpois(lam[i,j])
8379       lam[i,j] <- z[i]*K*exp(alpha0)*exp(- alpha1*d[i,j]*d[i,j])
8380     }
8381   }

```



```

8382 N <- sum(z[])
8383 D <- N/64
8384 }
8385 ",file = "SCR-Poisson.txt")

```

8386 To fit the model we execute **bugs** in the usual way:

```

8387 > library(R2WinBUGS)
8388 > out1 <- bugs (data, inits, parameters, "SCR-Poisson.txt", n.thin=1,
8389               n.chains=3,n.burnin=1000,n.iter=2000,working.dir=getwd(),
8390               debug=TRUE)

```

8391 Or, using **JAGS** via **rjags** we would do something like this:

```

8392 > library(rjags)
8393 > jm <- jags.model("SCR-Poisson.txt", data=data, inits=inits,
8394                  n.chains=3, n.adapt=1000)
8395 > out2 <- coda.samples(jm, parameters, n.iter=1000, thin=1)

```

8396 Summarizing the output from the **WinBUGS** run produces the following:

```

8397 > print(out1,digits=2)
8398 Inference for Bugs model at "SCR-Poisson.txt", fit using WinBUGS,
8399 3 chains, each with 2000 iterations (first 1000 discarded)
8400 n.sims = 3000 iterations saved
8401      mean    sd  2.5%   25%   50%   75%  97.5% Rhat n.eff
8402 alpha0  -2.57  0.19  -2.95  -2.69  -2.57  -2.44  -2.19  1.00  2600
8403 alpha1   2.34  0.36   1.69   2.08   2.32   2.57   3.12  1.00  3000
8404 N       114.13 15.25  87.97 103.00 113.00 124.00 147.00 1.01   370
8405 D         1.78  0.24   1.37   1.61   1.77   1.94   2.30  1.01   370
8406 deviance 329.95 21.92 290.00 314.20 329.50 344.40 375.80 1.00  1700
8407 ...
8408 [..some output deleted..]
8409 ...

```

### 8410 9.1.6 Analysis of the wolverine study data

8411 We reanalyzed the data from the wolverine camera trapping study that were first intro-  
8412 duced in Sec. 5.9. We modified the **R** script from the function **wolvSCRO** to fit the Poisson  
8413 model (see the help file for **wolvSCROpois**). Executing this function produces the results  
8414 shown in Table 9.1. The results are almost indistinguishable from the Bernoulli model  
8415 fitted previously, where we had a posterior mean for  $N$  of 59.84 and  $\sigma$  was 0.64. You can  
8416 edit the script **wolvSCROpois** to obtain more posterior samples, or modify the model in  
8417 some way.

**Table 9.1.** Results of fitting the SCR model with Poisson encounter frequencies to the wolverine camera trapping data. Posterior summaries were obtained using **WinBUGS** with 3 chains, each with 6000 iterations, discarding the first 1000 as burn-in, to yield a total of 15000 posterior samples.

Parameter	Mean	SD	2.5%	50%	97.5%	Rhat	n.eff
$N$	60.12	11.91	40.00	59.00	87.00	1	630
$D$	5.80	1.15	3.86	5.69	8.39	1	630
$\log(p_0)$	-2.89	0.17	-3.22	-2.89	-2.57	1	5000
$\lambda_0$	0.06	0.01	0.04	0.06	0.08	1	5000
$\sigma$	0.64	0.06	0.54	0.64	0.76	1	730
$\psi$	0.30	0.07	0.19	0.30	0.45	1	650

### 9.1.7 Count detector models in the `secr` package

The **R** package `secr` will fit Poisson or negative binomial encounter frequency models. The formatting of data and structure of the analysis proceeds in a similar fashion to the Bernoulli model described in Sec. 6.5, except that we specify the `detector='count'` option when the traps object is created. The set-up proceeds as follows:

```
> library(secr)
> library(scrbook)
> data(wolverine)

> traps <- as.matrix(wolverine$wtraps)
> dimnames(traps) <- list(NULL,c("trapID","x","y",paste("day",1:165,sep="")))
> traps1 <- as.data.frame(traps[,1:3])
> trapfile1 <- read.traps(data=traps1,detector="count")
```

You can proceed with analysis of these data and compare/contrast with the Bayesian analysis given above, or the results of the Bernoulli model fitted in Chapt. 6.

## 9.2 INDEPENDENT MULTINOMIAL OBSERVATIONS

Several types of encounter devices yield multinomial observations in which an individual can be caught in a single trap during a particular encounter occasion, but traps might catch any number of individuals. Mist netting is the canonical example of such a “multi-catch” device (Efford et al., 2009a). Also some kinds of bird or mammal cage-traps hold multiple animals, as do pit-fall traps which are commonly used for many species of herptiles. Another type of sample method that might be viewed (in some cases) as a multi-catch device are area-searches of, for example, reptiles where we think of a small polygon as the “trap” – we could get multiple individuals (turtles, lizards) in the same plot but not, in the same sample occasion, at different plots. The key features of this independent multinomial or multi-catch model are: (1) capture of an individual in a trap is *not* independent of its capture in other traps, because initial capture precludes capture in any other trap and (2) individuals behave independently of one another, so whether a trap captures some individual doesn’t have an affect on whether it captures another. A

type of model in which the 2nd assumption is violated are the “single catch” trap systems which we address in Sec. 9.3 below.

In this case we assume the observation  $\mathbf{y}_{ik}$  for individual  $i$  during sample occasion  $k$  is a multinomial observation which consists of a sequence of 0’s and a single 1 indicating the trap of capture, or “not captured”. For the “not captured” event we define an additional outcome, by convention element  $J + 1$  of the vector. As an example, if we capture an individual in trap 2 during some occasion of a study involving  $J = 6$  traps. Then, the multinomial observation has length  $J + 1 = 7$ , and the observation is  $\mathbf{y}_i = (0, 1, 0, 0, 0, 0, 0)$ . An individual not captured at all would have the observation vector  $(0, 0, 0, 0, 0, 0, 1)$ . If we sample for 5 occasions in all and the individual is also caught in trap 4 during occasion 3, but otherwise uncaptured, then the 5 encounter observations for that individual are as follows:

8458	occassion	-----trap -----  "not captured"						
8459		1	2	3	4	5	6	7
8460		-----						
8461	1	0	1	0	0	0	0	0
8462	2	0	0	0	0	0	0	1
8463	3	0	0	0	1	0	0	0
8464	4	0	0	0	0	0	0	1
8465	5	0	0	0	0	0	0	1

Statistically we regard the *rows* of this data matrix as *independent* multinomial trials.

Analogous to our previous Bernoulli and Poisson models, we seek to construct the multinomial cell probabilities for each individual, as a function of *where* that individual lives, through its center of activity  $\mathbf{s}$ . Thus we suppose that

$$\mathbf{y}_{ik}|\mathbf{s}_i \sim \text{Multinomial}(1, \boldsymbol{\pi}(\mathbf{s}_i)) \quad (9.2.1)$$

where  $\boldsymbol{\pi}(\mathbf{s}_i)$  is a vector of length  $J + 1$ , where  $\pi_{i,J+1}$ , the last cell, corresponds to the probability of the event “not captured”. Now we have to construct these cell probabilities in some meaningful way that depends on each individual’s  $\mathbf{s}$ . We use the standard multinomial logit with distance as a covariate:

$$\pi_{ij} = \frac{\exp(\alpha_0 - \alpha_1 d_{ij})}{1 + \sum_j \exp(\alpha_0 - \alpha_1 d_{ij})}$$

for  $j = 1, 2, \dots, J$  and, for  $J + 1$ , i.e., “not captured”,

$$\pi_{i,(J+1)} = \frac{\exp(0)}{1 + \sum_j \exp(\alpha_0 - \alpha_1 d_{ij})}$$

or, more commonly, we use  $d_{ij}^2$  to correspond to our Gaussian kernel model for encounter probability. Whatever function of distance we use in the construction of multinomial probabilities will have a direct correspondence to the standard encounter probability models we used in the Bernoulli or Poisson models as well (see Sec. 5.4).

It is convenient to express these multinomial models short-hand as follows, e.g., for the Gaussian encounter probability model:

$$\text{mlogit}(\pi_{ij}) = \alpha_0 - \alpha_1 d_{ij}^2$$

In this way we can refer to models with covariates in a more concise way. For example, a model with a trap-specific covariate, say  $C_j$ , is:

$$\text{mlogit}(\pi_{ij}) = \alpha_0 - \alpha_1 d_{ij}^2 + \alpha_2 C_j$$

or we could include occasion-specific covariates too, such as behavioral response.

A statistically equivalent distribution to the multinomial is the *categorical* distribution. If  $\mathbf{y}$  is a multinomial trial with probabilities  $\boldsymbol{\pi}$  then the *position* of the non-zero element of  $\mathbf{y}$  is a categorical random variable with probabilities  $\boldsymbol{\pi}$ . We express this for SCR models as

$$\mathbf{y}|\mathbf{s} \sim \text{Categorical}(\boldsymbol{\pi}(\mathbf{s}))$$

In the SCR context, the categorical version of the multinomial trial corresponds to the *trap of capture*. Using our example above with 6 traps then we could as well say  $y_{ik}$  is a categorical random variable with possible outcomes  $(1, 2, 3, 4, 5, 6, 7)$  where outcome  $y = 7$  corresponds to “not captured.” Obviously, how this is organized or labeled is completely irrelevant, although it is convenient to use the integers 1 to  $(J + 1)$  where  $J + 1$  is the event not captured. Therefore, for our illustration in the previous table,  $y_{i1} = 2$ ,  $y_{i2} = 7$ ,  $y_{i3} = 4$  and so on.

For simulating and fitting data in the **BUGS** engines we will typically use the categorical representation of the model because it is somewhat more convenient. We have found that fitting multinomial models in **WinBUGS** is less efficient than **JAGS** (Royle and Converse, in review), which we use in the subsequent examples involving multinomial observation models.

### 9.2.1 Multinomial resource selection models

The multinomial probabilities in Eq. 9.2.2 look similar to the multinomial resource selection function (RSF) model for telemetry data (Manly et al., 2002; Lele and Keim, 2006). This suggests how we might model landscape or habitat covariates using such methods – i.e., by including them as explicit covariates in a larger multinomial model for “use” – which, if we take the product of use with encounter, produces a model for the observable encounter data. This leads naturally to the development of models that integrate RSF data from telemetry studies with SCR data (Royle et al., 2012b), which is the topic of Chapt. 13.

### 9.2.2 Simulating data and analysis using JAGS

We’re going to show the nugget of a simulation function which is used in the function **simMnSCR** found in the **R** package **scrbook**. The first lines of the following **R** code make use of some things that you need to define, but we omit them here (e.g., **xlim**, **yylim** are the boundaries of the state-space, **N** is the population size, etc.):

```
##
## Simulate random activity centers:
## (first define N, xlim, ylim, etc..)
##
> S <- cbind(runif(N,xlim[1],xlim[2]),runif(N,ylim[1],ylim[2]))
```

```

8519
8520 ## Distance from each individual to each trap
8521 > D <- e2dist(S,traplocs)
8522
8523 ## Set paramter values
8524 > sigma <- 0.5
8525 > alpha0 <- -1
8526 > alpha1 <- -1/(2*sigma*sigma)
8527
8528 ## make an empty data matrix and fill it up with data
8529 > Ycat <- matrix(NA,nrow=N,ncol=K)
8530 > for(i in 1:N){
8531   for(k in 1:K){
8532     lp <- alpha0 + alpha1*D[i,]*D[i,]
8533     cp <- exp(c(lp,0))
8534     cp <- cp/sum(cp)
8535     Ycat[i,k] <- sample(1:(ntraps+1),1,prob=cp)
8536   }
8537 }

```

8538 We save the data in the matrix `Ycat` to clarify that it is the categorical observation  
 8539 representing “trap of capture”. The matrix `Ycat` here has the maximal dimension  $N$   
 8540 and so, to do an analysis that mimics a real situation, we would have to discard the  
 8541 uncaptured individuals. The function `simMnSCR` in the package `scrbook` will also simulate  
 8542 data that includes a behavioral response which will be the typical situation in small-  
 8543 mammal trapping problems (see Converse and Royle, 2012, for details).

8544 Here we use our function `simMnSCR` to simulate a data set with  $K = 7$  occasions. We’ll  
 8545 run the model using `JAGS` which we have found is much more effective for this class of  
 8546 models. We get the data set-up for analysis by augmenting the size of the data set to  
 8547  $M = 200$ . In addition we choose starting values for  $\mathbf{s}$  and the data augmentation variables  
 8548  $\mathbf{z}$ . For starting values of  $\mathbf{s}$  we cheat a little bit here and use the true values for the observed  
 8549 individuals and then augment the  $M \times 2$  matrix  $\mathbf{S}$  with  $M - n$  randomly selected activity  
 8550 centers. Our function `spiderplot` returns the mean observed location of individuals for  
 8551 use as starting values for the `nind` encountered individuals. The parameters input to  
 8552 `simMnSCR` are the intercept  $\alpha_0$ ,  $\sigma = \sqrt{1/(2\alpha_1)}$  for the Gaussian encounter probability  
 8553 model, and  $\alpha_2$  is the behavioral response parameter. The data simulation and set-up  
 8554 proceeds as follows:

```

8555 > set.seed(2013)
8556 > parms <- list(N=100,alpha0= -.40, sigma=0.5, alpha2= 0)
8557 > data <- simMnSCR(parms, K=7, ssbuff=2)
8558 > nind <- nrow(data$Ycat)
8559
8560 > M <- 200
8561 > Ycat <- rbind(data$Ycat,matrix(nrow(data$X)+1,nrow=(M-nind),ncol=data$K))
8562 > Sst <- rbind(data$S,cbind(runif(M-nind,data$xlim[1],data$xlim[2]),
8563                               runif(M-nind,data$ylim[1],data$ylim[2])))

```

```
8564 > zst <- c(rep(1,160),rep(0,40))
```

8565 The model specification is not much more complicated than the binomial or Poisson  
8566 models given previously. The main consideration is that we define the cell probabilities for  
8567 each trap  $j = 1, 2, \dots, J$  and then define the last cell probability,  $J+1$ , for “not captured”,  
8568 to be the complement of the sum of the others. The code is shown in Panel 9.1. In the  
8569 last lines of code here we specify  $N$  and density,  $D$ , as derived parameters.

8570 To fit the model, we need to package everything up (inits, parameters, data) and send  
8571 it off to **JAGS** to build an MCMC simulator for us (these commands are executed in  
8572 the help file for **simMnSCR**). In addition to the usual data objects, we also pass the limits  
8573 of the assumed rectangular state-space (**ylim**, **xlim**, both  $1 \times 2$  vectors) and the scale of  
8574 the standardized units, called **trap.space** here because we typically will define the trap  
8575 coordinates to be an integer grid. If the trap spacing is 10 *m* and we want units of density  
8576 computed in terms of individuals per *meter*-squared, then we input **trap.space=10**. The  
8577 analysis is carried out as follows:

```
8578 > inits <- function(){ list (z=zst,sigma=runif(1,.5,1) ,S=Sst) }
8579
8580 # Parameters to monitor
8581 > parameters <- c("psi","alpha0","alpha1","sigma","N","D")
8582
8583 # Bundle the data. Note this reuses "data"
8584 > data <- list (X=data$X,K=data$K, trap.space=1,Ycat=Ycat,M=M,
8585               ntraps=nrow(data$X),ylim=data$ylim,xlim=data$xlim)
8586
8587 > library(R2jags)
8588 > out <- jags (data, inits, parameters, "model.txt", n.thin=1,
8589              n.chains=3, n.burnin=1000, n.iter=2000)
```

8590 The posterior summaries are provided in the following **R** output (recall that  $N = 100$ ,  
8591  $\alpha_0 = -.40$ , and  $\sigma = 0.5$ ):

```
8592 > out
8593 Inference for Bugs model at "model.txt", fit using jags,
8594 3 chains, each with 2000 iterations (first 1000 discarded)
8595 n.sims = 3000 iterations saved
8596
8597      mu.vect sd.vect   2.5%   25%   50%   75%  97.5%  Rhat n.eff
8598 D      1.873   0.189   1.531   1.750   1.859   2.000   2.250 1.006  1300
8599 N     119.867 12.107  98.000 112.000 119.000 128.000 144.000 1.006  1300
8599 alpha0  -0.435   0.151  -0.738  -0.535  -0.439  -0.331  -0.146 1.004   580
8600 alpha1   2.195   0.286   1.658   2.004   2.180   2.372   2.785 1.003  2400
8601 psi      0.599   0.069   0.465   0.552   0.599   0.645   0.739 1.006  1400
8602 sigma    0.480   0.032   0.424   0.459   0.479   0.500   0.549 1.003  2400
8603 deviance 892.164 21.988 850.922 877.417 891.561 906.246 937.728 1.003   950
8604
8605 [... output deleted ...]
```

---

```

model{
psi ~ dunif(0,1)
alpha0 ~ dnorm(0,10)
sigma ~dunif(0,10)
alpha1 <- 1/(2*sigma*sigma)

for(i in 1:M){
  z[i] ~ dbern(psi)
  S[i,1] ~ dunif(xlim[1],xlim[2])
  S[i,2] ~ dunif(ylim[1],ylim[2])
  for(j in 1:ntraps){
    #distance from capture to the center of the home range
    d[i,j] <- pow(pow(S[i,1]-X[j,1],2) + pow(S[i,2]-X[j,2],2),1)
  }
  for(k in 1:K){
    for(j in 1:ntraps){
      lp[i,k,j] <- exp(alpha0 - alpha1*d[i,j])*z[i]
      cp[i,k,j] <- lp[i,k,j]/(1+sum(lp[i,k,]))
    }
    cp[i,k,ntraps+1] <- 1-sum(cp[i,k,1:ntraps]) # last cell = not captured
    Ycat[i,k] ~ dcat(cp[i,k,])
  }
}

N <- sum(z[1:M])
A <- ((xlim[2]-xlim[1])*trap.space)*((ylim[2]-ylim[1])*trap.space)
D <- N/A
}

```

---

Panel 9.1: **BUGS** model specification for the independent multinomial observation model. For data simulation and model fitting see the help file `?simMnSCR` in the **R** package `scrbook`.

### 9.2.3 Multinomial relationship to the Poisson

The multinomial is related to the Poisson encounter rate model by a conditioning argument. Let  $y_{ij}$  be the number of encounters for individual  $i$  in trap  $j$ . If  $y_{ij} \sim \text{Poisson}(\lambda_{ij})$ , then, conditional on the *total* number of captures (i.e., across all traps),  $y_i = \sum_j y_{ij}$ , the trap encounter frequencies are multinomial with probabilities

$$\pi_{ij} = \frac{\lambda_{ij}}{\sum_j \lambda_{ij}}$$

for  $j = 1, 2, \dots, J$ . Or equivalently the *trap of capture* is categorical with probabilities  $\pi_{ij}$  as given above. Under the Gaussian kernel model, these probabilities are:

$$\pi_{ij} = \frac{\exp(-\alpha_1 d(\mathbf{x}_i, \mathbf{s}_i)^2)}{\sum_j \exp(-\alpha_1 d(\mathbf{x}_i, \mathbf{s}_i)^2)} \quad (9.2.2)$$

where, we note, the intercept  $\alpha_0$  has canceled from both the numerator and denominator. This makes sense because, here, these probabilities describe the trap-specific capture probabilities *conditional on capture*. Therefore, the model is not completely specified, absent a model for the “overall” probability of encounter or the expected frequency of captures, say  $\phi_i$ . Depending on how we specify a model for this quantity  $\phi_i$ , we can reconcile it directly with the Poisson model. Let  $y_i$  be the total number of encounters for individual  $i$  and suppose  $y_i$  has a Poisson distribution with mean  $\phi_i$ . Then, marginalizing Eq. 9.2.1 over the Poisson distribution for  $y_i$  produces the original set of *iid* Poisson frequencies with probabilities:

$$\lambda_{ij} = \phi_i \pi_{ij}$$

for  $j = 1, 2, \dots, J$ . In particular, if we suppose that  $\phi_i = \sum_j \exp(\alpha_0 - \alpha_1 d(\mathbf{x}, \mathbf{s})^2)$  then the marginal distribution of  $y_{ij}$  is Poisson with mean  $\exp(\alpha_0 - \alpha_1 d(\mathbf{x}, \mathbf{s})^2)$ , equivalent to Eq. 9.1.1.

In summary, the Poisson and multinomial models are equivalent in how they model the distribution of captures among traps. It stands to reason that, if the encounter rate of individuals is low, we could use the Poisson and multinomial models interchangeably. In fact, based on our discussion in Sec. 9.1.2 above we could use any of the binomial/Poisson/multinomial models with little ill-effect when encounter rate is low.

### 9.2.4 Avian mist-netting example

We analyze data from a mist-netting study of ovenbirds, conducted at the Patuxent Wildlife Research Center, Laurel MD, by D.K. Dawson and M.G. Efford. The data from this study are available in the `secr` package, and have been analyzed previously by Efford et al. (2004), see also Borchers and Efford (2008). Forty-four mist nets spaced 30 m apart on the perimeter of a 600-m x 100-m rectangle were operated on 9 or 10 non-consecutive days in late May and June for 5 years from 2005-2009. The ovenbird data can be loaded as follows:

```
> library(secr)
> data(ovenbird)
```



The data set consists of adult ovenbirds caught during sampling in each of 5 years, 2005–2009. (one ovenbird was killed in 2009, indicated by a negative net number in the encounter data file). As with most mist-netting studies, nets are checked multiple times during a day (e.g., every hour during a morning session). However, for this data set, the within-day recaptures are not included so each bird has at most a single capture per day. Therefore the multinomial model (detector type ‘multi’ in **secr**) is appropriate. Although several individuals were captured in more than one year, this information is not used in the models presently offered in **secr**, but we do make use of it in the development of open models in Chapt. 16.

### Multiple sample sessions

Up to this point we have only dealt with a basic closed population sampling situation consisting of repeated sample occasions on a single population of individuals using a single array of traps. In practice, many studies produce repeated samples over longer periods of time over which demographic closure isn’t valid, or at different locations where the populations are completely distinct. We adopt the **secr** terminology of *session* for such replication by groups of time or space, and the models are *multi-session* models, although we think of such models as being relevant to any stratified population (see Chapt. 14). We introduced **secr**’s multi-session models in Sec. 6.5.4. In the case of the ovenbird data, sampling was carried out in multiple years, with a number of sample occasions within each year (9 or 10), a type of data structure commonly referred to as “the robust design” (Pollock, 1982). In this context, it stands to reason that there is recruitment and mortality happening across years. In Chapt. 16 we model these processes explicitly but, here, we provide an analysis of the data that does not require explicit models for recruitment and survival, regarding the yearly populations as independent strata, and fitting a multi-session model.

When the sessions represent explicit time periods, the multi-session model of **secr** can be thought of as a type of open population model. In particular, a special case of open models arises when we assume  $N_t$  (time-specific population sizes) are independent from one time period or session to the next – this can be thought of as a “random temporary emigration” model of the Kendall et al. (1997) variety, and this is the multi-session model implemented in **secr**. In particular, by assuming that  $N_t$  is Poisson with mean  $\Lambda_t$ , one can model variation in abundance among sessions based on the Poisson-integrated likelihood in which parameters of  $\Lambda_t$  appear directly in the likelihood as we noted in Sec. 6.5.4. We provide an analysis (below) of the ovenbird data here using the multi-session models in **secr**. We formalize the multi-session model approach from a Bayesian perspective using data augmentation in Chapt. 14 (Converse and Royle, 2012; Royle and Converse, in review).

A 3rd way to develop models for stratified or grouped populations, not based on multi-session models, but that is convenient in **BUGS**, is to regard the data from each session as an independent data set with its own  $N_t$  parameter, and do  $T$  distinct data augmentations. Because each  $N_t$  is regarded as a free parameter, independent of the other parameters, we’ll call this the nonparametric multi-session model to distinguish it from the multi-session model which assumes the  $N_t$  are related to one another by having been generated from a common Poisson distribution. We can analyze this model in the normal context of data augmentation by augmenting each year separately in the same **BUGS** model specification. This approach avoids making explicit model assumptions

about the  $N_t$  parameters. This is distinct from the model implemented in **secr** in that **secr** is removing the  $N_t$  parameters by integrating the conditional-on- $N_t$  likelihood over the Poisson prior for  $N_t$ <sup>1</sup>

We demonstrate these 3 approaches to analyzing grouped/stratified data using the ovenbird data: (1) In the following section, we provide the nonparametric multi-session model with unconstrained  $N_t$ ; (2) we demonstrate the Poisson model-based multi-session models from **secr** both here (following section) and in Chapt. 14 from a Bayesian standpoint; (3) later, in Chapt. 16, we provide a fully dynamic “spatial Jolly-Seber” model and apply it to the ovenbird data.

### Analysis in JAGS

The ovenbird data are provided as a multi-session **capthist** object **ovenCH** which, by regarding years as independent strata, or sessions, allows for the fitting of the multi-session model. For doing a Bayesian analysis in one of the **BUGS** engines (we use **JAGS** here) there are a number of ways to structure the data and describe the model. We can analyze either a 2-d data set with all years (data augmented) “stacked” into a data set of dimension  $(5 * M) \times 10$  (5 years,  $M$  = size of the augmented data set,  $K = 10$  replicate sample occasions). Or, we could produce a 3-d array ( $M \times J \times K$ ). We adopted the former approach, analyzing the data as a 2-d array and creating an additional categorical variable for “year” to indicate which stratum (year) each record goes with.

Data on individual sex is included with **secr**, but we provide an analysis of a single model for all adults, constant  $\sigma$  across years, constant  $p_0$ , and year-specific values of  $N_t$  (and hence  $D_t$ ). There is a habitat mask provided with the data but the mask appears to just be a modified rectangle around the net locations, clipped to have rounded corners, and so we don’t use it here. Instead, we used a rectangular state-space buffer of 200 meters for our analysis. There was a single loss-on-capture which we accounted for by fixing  $p = 0$  for all subsequent encounters of that individual (indicated by the binary variable **dead**, as shown in Panel 9.2). We have an **R** script in **scrbook** package called **SCRovenbird**, so you can see how to set-up the data and run the model. Executing the script **SCRovenbird** produces the posterior summaries given in Table 9.2. Here, density is in units of birds per ha. The posterior mean of  $\sigma$  is about 76 meters, and there is considerable variability in density over the 5 year period with density peaking at 1.2 birds/ha in year 3, although there is considerable posterior uncertainty. The R-hat’s look a little bit peaked and so we might consider running the MCMC analysis longer.

### Analysis in secr

Included with the ovenbird data are a number of models fitted as examples. Those include:

```
ovenbird.model.1  fitted secr model -- null
ovenbird.model.1b fitted secr model -- g0 net shyness
ovenbird.model.1T fitted secr model -- g0 time trend within years
ovenbird.model.h2 fitted secr model -- g0 finite mixture
ovenbird.model.D  fitted secr model -- trend in density across years
```

<sup>1</sup>We do not know of **secr** documentation that states this (or contradicts it). We think this is what is being done, based partially on conversations or emails with M.G. Efford, D.L. Borchers, the various publications on **secr**, and our own thinking about it.

---

```

model{
  alpha0 ~ dnorm(0,.1)
  sigma ~ dunif(0,200)
  alpha1 <- 1/(2*sigma*sigma)

  A <- ((xlim[2]-xlim[1]))*((ylim[2]-ylim[1]))
  for(t in 1:5){
    N[t] <- inprod(z[1:bigM],yrdummy[,t])
    D[t] <- (N[t]/A)*10000 # Put in units of per ha
    psi[t] ~ dunif(0,1)
  }

  for(i in 1:bigM){ # bigM = total size of jointly augmented data set
    z[i] ~ dbern(psi[year[i]])
    S[i,1] ~ dunif(xlim[1],xlim[2])
    S[i,2] ~ dunif(ylim[1],ylim[2])

    for(j in 1:ntraps){ # X = trap locations, S = activity centers
      d2[i,j] <- pow(pow(S[i,1]-X[j,1],2) + pow(S[i,2]-X[j,2],2),.5)
    }
    for(k in 1:K){
      Ycat[i,k] ~ dcat(cp[i,k,])
      for(j in 1:ntraps){
        lp[i,k,j] <- exp(alpha0 - alpha1*d2[i,j])*z[i]*(1-dead[i,k])
        cp[i,k,j] <- lp[i,k,j]/(1+sum(lp[i,k,1:ntraps]))
      }
      cp[i,k,ntraps+1] <- 1-sum(cp[i,k,1:ntraps]) # Last cell = not captured
    }
  }
}

```

---

Panel 9.2: **BUGS** model specification for the non-parametric multi-session model in which each  $N_t$  is independent of the other. The implied prior (by data augmentation) is that  $N_t \sim \text{Uniform}(0, 100)$ . To fit this model to the ovenbird data, see ?SCRovenbird in the **R** package **scrbook**.

**Table 9.2.** Posterior summary statistics for the ovenbird mist-netting data based on the independent multinomial ("multi-catch") encounter process model. Parameters  $\psi$ ,  $N$  and  $D$  are indexed by year. MCMC was done using jags with 3 chains, each with 11000 iterations, discarding the first 1000, for a total of 30000 posterior samples.

Parameter	Mean	SD	2.5%	50%	97.5%	Rhat	n.eff
D[1]	0.983	0.211	0.636	0.966	1.455	1.002	1900
D[2]	1.023	0.209	0.673	1.003	1.492	1.001	7100
D[3]	1.208	0.238	0.807	1.186	1.749	1.004	740
D[4]	0.896	0.195	0.575	0.880	1.333	1.002	3000
D[5]	0.753	0.177	0.465	0.734	1.149	1.001	4000
$\alpha_0$	-3.479	0.160	-3.797	-3.477	-3.171	1.005	490
$\alpha_1$	0.000	0.000	0.000	0.000	0.000	1.003	1100
$\sigma$	76.214	6.125	65.569	75.758	89.360	1.003	1100
N[1]	80.423	17.283	52.000	79.000	119.000	1.002	1900
N[2]	83.685	17.077	55.000	82.000	122.000	1.001	7100
N[3]	98.822	19.483	66.000	97.000	143.000	1.004	740
N[4]	73.288	15.962	47.000	72.000	109.000	1.002	3000
N[5]	61.589	14.468	38.000	60.000	94.000	1.001	4000
$\psi$ [1]	0.403	0.092	0.246	0.395	0.606	1.002	1600
$\psi$ [2]	0.419	0.091	0.260	0.412	0.620	1.001	6400
$\psi$ [3]	0.494	0.102	0.315	0.486	0.723	1.004	760
$\psi$ [4]	0.368	0.086	0.221	0.361	0.555	1.002	3200
$\psi$ [5]	0.310	0.079	0.178	0.302	0.485	1.002	3500

The model fit objects provided in **secr** are based on the use of the habitat mask. To make the analyses consistent with our previous analysis in **JAGS**, we refit all of the models here without the habitat mask. The re-analysis proceeds as follows, changing the "trend in density across years" model to allow for year-specific density:

```
## Fit constant-density model
> ovenbird.model.1 <- secr.fit(ovenCH)
## Fit net avoidance model
> ovenbird.model.1b <- secr.fit(ovenCH, model = list(g0 ~ b))
## Fit model with time trend in detection
> ovenbird.model.1T <- secr.fit(ovenCH, model = list(g0 ~ T))
## Fit model with 2-class mixture for g0
> ovenbird.model.h2 <- secr.fit(ovenCH, model = list(g0 ~ h2))
## Fit a model with session (year)-specific Density
> ovenbird.model.DT <- secr.fit(ovenCH, model = list(D ~ session))
```

All of these can be fitted easily in **JAGS** but the model we fitted previously is roughly equivalent to the last model, **ovenbird.model.DT**, because we allowed for year-specific population sizes (and hence density). So, we'll compare our results from **JAGS** to that model. The **secr** output is extensive and so we do not reproduce it completely here. By

8744 default, it summarizes the trap information for each year, encounter information, and then  
8745 output for each year. Here is an abbreviated version for `ovenbird.model.DT`:

```
8746 > print(ovenbird.model.DT,digits=2)
8747
8748 secr.fit( capthist = ovenCH, model = list(D ~ session), buffer = 300 )
8749 secr 2.3.1, 14:46:52 23 Jan 2013
8750
8751 $'2005'
8752 Object class      traps
8753 Detector type     multi
8754 Detector number   44
8755 Average spacing   30.27273 m
8756 x-range           -50 49 m
8757 y-range           -285 285 m
8758
8759 [... deleted ...]
8760
8761           2005 2006 2007 2008 2009
8762 Occasions      9  10  10  10  10
8763 Detections     35  42  52  30  33
8764 Animals        20  22  26  19  16
8765 Detectors      44  44  44  44  44
8766
8767 Model           : D~session g0~1 sigma~1
8768 Fixed (real)    : none
8769 Detection fn    : halfnormal
8770 Distribution     : poisson
8771 N parameters    : 7
8772 Log likelihood  : -1119.845
8773 AIC              : 2253.689
8774 AICc            : 2254.868
8775
8776 [... deleted ...]
```

8777 To do model selection we use the handy helper-function `AIC` as follows (output edited  
8778 to fit on the page):

```
8779 AIC (ovenbird.model.1, ovenbird.model.1b, ovenbird.model.1T,
8780      ovenbird.model.h2, ovenbird.model.DT)
8781
8782      model detectfn npar logLik    AIC    AICc    dAICc
8783 ovenbird.model.1T [edited output]  4 -1111.850 2231.700 2232.109  0.000
8784 ovenbird.model.1b      ....      4 -1117.615 2243.229 2243.637 11.528
8785 ovenbird.model.h2      ....      3 -1121.164 2248.327 2248.570 16.461
8786 ovenbird.model.1       ....      5 -1119.762 2249.524 2250.143 18.034
8787 ovenbird.model.DT      ....      7 -1119.845 2253.689 2254.868 22.759
```

We see that our DT model is way down at the bottom of the list. Instead, the model with a time-trend (within-season) in detection probability is preferred, followed by a behavioral response. We encourage you to adapt the **JAGS** model specification for such models which is easily done (see Chapt. 7 for many examples). We provide the summary results for the model having  $D \sim \text{session}$  as follows:

```
> print(ovenbird.model.DT,digits=2)
seccr.fit( capthist = ovenCH, model = list(D ~ session), buffer = 300 )
seccr 2.3.1, 14:46:52 23 Jan 2013
[...deleted....]
Fitted (real) parameters evaluated at base levels of covariates
session = 2005
      link estimate SE.estimate    lc1    uc1
D      log      0.920      0.228 0.571 1.484
g0     logit     0.028      0.004 0.021 0.037
sigma  log     78.566      6.379 67.025 92.095
session = 2006
      link estimate SE.estimate    lc1    uc1
D      log      0.963      0.238 0.598 1.553
g0     logit     0.028      0.004 0.021 0.037
sigma  log     78.566      6.379 67.025 92.095
session = 2007
      link estimate SE.estimate    lc1    uc1
D      log      1.139      0.282 0.706 1.836
g0     logit     0.028      0.004 0.021 0.037
sigma  log     78.566      6.379 67.025 92.095
session = 2008
      link estimate SE.estimate    lc1    uc1
D      log      0.832      0.206 0.516 1.341
g0     logit     0.028      0.004 0.021 0.037
sigma  log     78.566      6.379 67.025 92.095
session = 2009
      link estimate SE.estimate    lc1    uc1
D      log      0.701      0.173 0.435 1.130
g0     logit     0.028      0.004 0.021 0.037
sigma  log     78.566      6.379 67.025 92.095
```

The point estimates (MLEs) of density are uniformly lower than the Bayesian estimates (posterior means) shown in Table 9.2. We expect some difference in this direction due

to small-sample skew of the posterior. In addition, there may be slight differences due to the fact that **secr** multi-session model assumes that the  $N_t$  have a Poisson prior, but the implementation in **JAGS** using data augmentation is based on a binomial prior. The estimated  $\sigma$  is very similar between the **JAGS** analysis and **secr**.

### 9.3 SINGLE-CATCH TRAPS

The classical animal trapping experiment is based on a physical trap which captures a single animal and holds that individual until subsequent molestation by a biologist. This type of observation model – the “single-catch” trap – was the original situation considered in the context of spatial capture-recapture by Efford (2004). Nowadays, capture-recapture data are more often obtained by other methods (DNA from hair snares, or scat sampling, camera traps etc...) but nevertheless the single-catch traps are still widely used in small mammal studies (Converse et al., 2006b; Converse and Royle, 2012) and other situations.

The single-catch model is basically a multinomial model but one in which the number of available traps is reduced as each individual is captured. As such, the constraints on the joint likelihood for the sample of  $n$  encounter histories are very complicated. As a result, at the time of this writing, there has not been a formal development of either likelihood or Bayesian analysis of this model and applications of SCR models to single-catch systems have used the independent multinomial model as an approximation (see below).

Nevertheless, we can make some progress to describing the basic observation model formally. In particular, if we imagine that all of the individuals captured queued up at the beginning of the capture session to draw a number indicating their order of capture, then there is a nice conditional structure resulting from a “removal process” operating on the traps. The first individual captured has the multinomial observation model:

$$\mathbf{y}_1 \sim \text{Multinomial}(\boldsymbol{\pi}_1)$$

whereas the 2nd individual captured also has a multinomial encounter probability model but with the trap which captured the first individual removed. We might express this as:

$$\mathbf{y}_2 \sim \text{Multinomial}(\boldsymbol{\pi}_2)$$

where

$$\pi_{2j} = \frac{(1 - y_{1j}) * \exp(\alpha_0 - \alpha_1 d_{ij}^2)}{\sum_j (1 - y_{1j}) * \exp(\alpha_0 - \alpha_1 d_{ij}^2)}$$

and so on for  $i = 3, 4, \dots, n$ . In a certain way, this model is a type of local behavioral response model but where the response is to other individuals being captured. Evidently, the **order of capture** is relevant to the construction of these multinomial cell probabilities. More generally, the *time* of capture of an individual in any trapping interval will affect the encounter probability of subsequently captured individuals, but we think that order of capture might lead to a practical approximation to the single-catch process (this is how we simulate the data in our function **simScSCR**). In the simulation of single catch data, we randomly ordered the population of individuals for each sample occasion, and then cycled through them, turning off each trap if an individual was captured in it.

### 9.3.1 Inference for single-catch systems

For the single-catch model, we argued that the observations have a multinomial type of observation model, but the multinomial observations have a unique conditional dependence structure among them owing to the “removal” of traps as they fill-up with individuals. Thus, competition for single-catch traps renders the independence assumptions for the independent multinomial model invalid. However, as Efford et al. (2009a) noted, we expect “bias to be small when trap saturation (the proportion of traps occupied) is low. Trap saturation will be higher when population density is high...” relative to trap density, or when net encounter probability is high. Efford et al. (2009a) did a limited simulation study and found essentially no effective bias and concluded that estimators of density from the misspecified independent multinomial model are robust to the mild dependence induced when trap saturation is low. Naturally then, we expect that the Poisson model could also be an effective approximation under the same set of circumstances.

In the **R** package **scrbook** we provide a function for simulating data from a single-catch system (function **simScSCR**) and fitting the misspecified model (**example(simScSCR)**) in **JAGS** so that you can evaluate the effectiveness of this misspecified model for situations that interest you.

### 9.3.2 Analysis of Efford’s possum trapping data

We provide an analysis here of data from a study of brushtail possums in New Zealand. The data are available with the **R** package **secr** (Efford et al., 2009a); see the help file **?possum** after loading the **secr** package. Originally the data were analyzed by Efford et al. (2005), and a detailed description of the data set is available in the help file, from which we summarize:

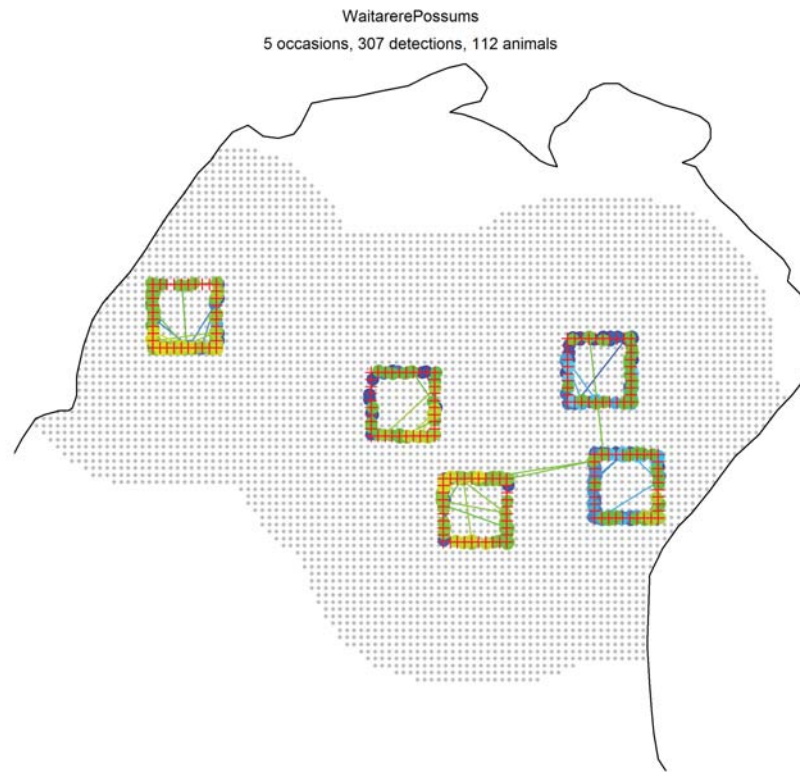
*Brushtail possums (Trichosurus vulpecula) are an unwanted invasive species in New Zealand. Although most abundant in forests, where they occasionally exceed densities of 15/ha, possums live wherever there are palatable food plants and shelter.*

To load the possum data, execute the following commands:

```
> library(secr)
> data(possum)
```

The study area encompasses approximately 300 ha, and 180 live traps were organized in 5 distinct grids, shown in Fig. 9.2. Each square arrangement of traps consisted of 36 traps with a spacing of 20 m. Thus the squares are 180 m on a side. Individuals were captured, tagged, and released over 5 days during April, 2002. A noteworthy aspect of this study is that it involves replicated grids selected in some fashion from within a prescribed region. From an analysis standpoint, we could adopt the use of the multi-session models which we used previously to analyze the ovenbird data. This would be useful if we had covariates at the trapping grid level that we wanted to model. Alternatively, we could pool the data from all of the grids and analyze them jointly as if they were based on a single trapping grid (with 180 traps) which is clearly a reasonable view in this case. In doing this sort of pooling, there is an implicit assumption that  $N_t$  ( $t$  indexing trapping grid in this case) is Poisson distributed, with constant mean (Royle, 2004a; Royle et al., 2012c) which we also address in Chapt. 14.





**Figure 9.2.** Trapping grids used in possum study from Efford et al. (2005), data are contained in the Rpackage `secr` (Efford, 2011), refer to the help file `?possum` for additional details of this study.

The data file `possumCH` contains 112 encounter histories, and we analyze those here although the last 8 of those are recaptures treated as new individuals<sup>2</sup>. The encounter process is not strictly a single-catch multinomial process because, as noted in the `possum` help file “One female possum was twice captured at two sites on one day, having entered a second trap after being released; one record in each pair was selected arbitrarily and discarded.” which is a similar situation to what might happen in bird mist net studies, as a bird might fly into a net upon release from another. By discarding the two extra-capture events, we can satisfactorily view these data as single-catch data, for which `secr` uses the independent multinomial likelihood (M. Efford, pers. comm.). If multiple, same-session captures were common, then it might be worth developing a model for  $n_{ik}$  = the number of captures of individual  $i$  during sample occasion  $k$ , in order to make use of all captures.

For our Bayesian analysis here, we used a rectangular state-space which doesn’t account for any geographic boundaries of the survey region, but we note that a habitat mask is included in `secr` and it could be used in a Bayesian analysis. Whether or not we use the mask is probably immaterial as long as we understand the predictions of  $N$  or  $D$  over the water don’t mean anything biological and we probably wouldn’t report such predictions. The `JAGS` model specification is based on that of the ovenbird analysis given previously, and so we don’t reproduce the model here. The `R/JAGS` script is called `SCRpossum`, which is in the `scrbook` package. The results are summarized in Table 9.3.

**Table 9.3.** Results of fitting the independent multinomial observation model to the possum trapping data. Strictly speaking, the trapping device is a “single-catch” trap, and the model represents an intentional misspecification. Density is reported in individuals per ha ( $Dha$ ). Posterior summaries were obtained using `JAGS` with 3 chains, each with 2000 iterations, discarding the first 1000 as burn-in, to yield a total of 3000 posterior samples.

Parameter	Mean	SD	2.5%	50%	97.5%	Rhat	n.eff
N	235.407	17.435	204.000	235.000	270.000	1.009	340
Dha	1.549	0.115	1.343	1.547	1.777	1.009	340
$\alpha_0$	-0.935	0.167	-1.270	-0.934	-0.605	1.007	870
$\alpha_1$	0.000	0.000	0.000	0.000	0.000	1.001	2800
$\sigma$	52.020	2.675	47.067	51.933	57.585	1.001	2800
$\psi$	0.783	0.062	0.666	0.782	0.903	1.008	340

The estimated density (posterior mean) is about 1.53 possums/ha. To obtain the `secr` results for the equivalent null model, we execute the following command

```
> secr.fit( capthist = possumCH, trace = F )
```

which produces (edited) summary output:

```
[... some output deleted ...]
```

Fitted (real) parameters evaluated at base levels of covariates

	link	estimate	SE.estimate	lcl	ucl
D	log	1.6988930	0.17352645	1.3913904	2.0743547

<sup>2</sup>M. Efford, personal communication

```

8937 g0    logit  0.1968542  0.02256272  0.1563319  0.2448321
8938 sigma  log 51.4689114  2.59981905 46.6204139 56.8216500
8939
8940 [... some output deleted ...]

```

8941 As we've discussed previously, there are many reasons for why there might be differences  
8942 between Bayesian and likelihood estimates. But even among likelihood estimates – any  
8943 time you run a model there is some numerical integration going on which requires some  
8944 specific choices of how to do the integration (see Chapt. 6). For now we just observe that  
8945 the estimated density is certainly in the ballpark (compared to those in Table. 9.3), and  
8946 so too is the estimated  $\sigma$ .

## 9.4 ACOUSTIC SAMPLING

8947 The last decade has seen an explosion of technology that benefits the study of animal  
8948 populations. This includes DNA sampling methods that allow for identification from  
8949 hair or scat, camera trapping and identification software that allow efficient sampling  
8950 of many mammals, and the resulting statistical technology that helps us to make sense  
8951 of such data (Borchers and Efford, 2008; Royle and Young, 2008; Efford et al., 2009b;  
8952 Gopalaswamy et al., 2012b; Sollmann et al., 2012b; Chandler and Royle, In press). One  
8953 other extremely promising technology area is that of acoustic sampling using microphones  
8954 or recording devices. That is, instead of having cameras record encounters, or humans pick  
8955 up scat, we can establish an array of (usually) electronic recording devices which, instead of  
8956 establishing a visual identity of individuals, record a vocal expression of each individual. In  
8957 this context, Efford et al. (2009b) referred to audio recorders as “signal strength proximity  
8958 detectors” to distinguish them from other types of proximity detections, including camera  
8959 traps, which are *visual* proximity detector. Using audio records, the spatial pattern of the  
8960 *signal strength* at the different audio recorders or microphones can be used for inference  
8961 about density (Dawson and Efford, 2009; Efford et al., 2009b) in the same way as the  
8962 spatial pattern of detections is used in the types of SCR models we have discussed so far.  
8963 The basic technical formulation of these models comes from Efford et al. (2009b), and it  
8964 was applied to field study of birds by Dawson and Efford (2009). In that study, recording  
8965 devices were organized in groups of 4 (in a square pattern), with an array of  $5 \times 15$  such  
8966 clusters of 4, separated by 100 m (300 total recorder locations). This data set, called  
8967 **signalCH**, is provided with the **secr** package along with some sample analyses and help  
8968 files. See Efford and Dawson (2010), a version of the document **secr-sound.pdf** (that  
8969 also comes with the **secr** package) which you can access directly from the main help file  
8970 (**?secr**).

8971 Our development here mostly follows Efford et al. (2009b), but we change some nota-  
8972 tion to be consistent with our previous material. Let  $S(\mathbf{x}, \mathbf{u})$  be the strength of a signal  
8973 emanating from signal location  $\mathbf{u}$ , as recorded by a device at location  $\mathbf{x}$ . Just as ordinary  
8974 SCR models represent a model of *encounter frequency* as a function of distance, in acoustic  
8975 models, the acoustic SCR model is a model of sound attenuation as a function of distance.  
8976 In particular, the acoustic models assumes that  $S$  (or a suitable transformation) declines  
8977 with distance  $d$  from the origin of the sound, to the recording device. In the context of  
8978 spatial sampling of animals, the origin is the actual location of some individual animal,

and the recording device is something we nailed to a tree, or mounted on a post. For example, a model of sound attenuation used by Dawson and Efford (2009) is the following:

$$S(\mathbf{x}, \mathbf{u}) = \alpha_0 + \alpha_1 d(\mathbf{x}, \mathbf{u}) + \epsilon \quad (9.4.1)$$

where  $\epsilon \sim \text{Normal}(0, \sigma_s^2)$ . In many standard situations,  $S$  will be measured in decibels, which can be any value on the real line. In the conduct of acoustic sampling and the development of custom models for your own situation, it would probably be helpful to know something about sound dynamics and signal processing. In this model, the parameters  $\alpha_0$ ,  $\alpha_1$  and  $\sigma_s^2$  are to be estimated. We abbreviate the set of parameters by  $\boldsymbol{\theta}$  for short.

The basic structure of an acoustic SCR study is not really much different from ordinary SCR studies. Just as ordinary SCR models require that individuals be encountered at  $> 1$  trap, these acoustic models require that individuals be heard at  $> 1$  recorder. Therefore, the acoustic signals (calls or vocalizations) must be reconcilable and, in fact, reconciled successfully by the investigator. In practice, this would require associating signals that occur at the same instant with the same individual (or making a decision one way or the other). Further, if individuals are actively moving during the sample period (that recorders are functioning) then individuals might be double-counted, thereby biasing estimates of density. In general, the models produce an estimate of density of *sources*, and how that is interpreted depends on whether individuals are stationary or mobile, and other things. In particular, if multiple survey occasions are used (e.g., on different days), then modeling movement of individuals would be essential in order to interpret estimates of density meaningfully. Models that allow some movement should be possible (see Sec. 9.4.3 below, and Chaps. 15 and 16).

#### 9.4.1 The signal strength model

We assert that an individual is detected if  $S$  exceeds a threshold,  $c$ . The reason for introducing this threshold  $c$  is that sound recorders will always record some background sound, and so effective use of the acoustic SCR models requires specification of the threshold of measured signal below which the record is censored (non-detection occurs) because the recorded sound is assumed to be background noise. So we assert that an individual is detected if  $S > c$  which occurs with probability  $\Pr(S > c)$ , the encounter probability. To expand on and formalize this, let  $S_{ij}$  be the observed value of  $S$  for animal  $i$  at detector  $j$ . The encounter probability is  $\Pr(S_{ij} > c)$  which is  $\Pr(S_{ij} > c) = 1 - \Pr(S_{ij} < c)$ , so that, if we standardize the variate we have

$$1 - \Pr\left(\frac{(S_{ij} - \mathbb{E}(S))}{\sigma_s} < \frac{(c - \mathbb{E}(S))}{\sigma_s}\right)$$

This probability calculation requires evaluation of the CDF of a standard normal variate say,  $\eta = (S_{ij} - \mathbb{E}(S))/\sigma_s$ , being less than  $\gamma(\boldsymbol{\theta}) = (c - \mathbb{E}(S))/\sigma_s$ , which is a function of all the parameters  $\alpha_0$ ,  $\alpha_1$ ,  $\sigma_s^2$  and also the individual location  $\mathbf{u}$  and trap location  $\mathbf{x}$ . We'll identify it by  $\gamma(\boldsymbol{\theta}, \mathbf{x}, \mathbf{u})$  when we need to be explicit about those things. We can compute  $\Pr(S_{ij} > c) = 1 - \Pr(\eta < \gamma(\boldsymbol{\theta}, \mathbf{x}, \mathbf{u}))$  easily using any software package including **R** which has a standard function, **pnorm**, for computing the normal cdf. To be more precise, we'll use the  $\Phi()$  to represent the normal cdf. Therefore, an individual is encountered whenever  $S_{ij} > c$  which happens with probability  $\Pr(S_{ij} > c) = 1 - \Phi(\gamma(\boldsymbol{\theta}, \mathbf{x}, \mathbf{u}))$ .

9019 Naturally this quantity should depend on *where* an individual is located at the time  
 9020 of recording – what we call it’s instantaneous location, say  $\mathbf{u}$ , to distinguish it from it’s  
 9021 home-range center  $\mathbf{s}$  (but we outline a model below that contains both  $\mathbf{u}$  and  $\mathbf{s}$ ), and  
 9022 also the trap  $\mathbf{x}$ , so we index the quantity  $\gamma$  by those two quantities, in addition to the  
 9023 parameters  $\alpha_0$ ,  $\alpha_1$  and  $\sigma_s$ . The probability of detection is therefore

$$p_{ij} = p(\alpha_0, \alpha_1, \sigma | \mathbf{x}_j, \mathbf{u}_i) = 1 - \Phi(\gamma(\cdot))$$

9024 where  $\mathbf{u}_i$  is the instantaneous location of individual  $i$  and  $\mathbf{x}_j$  is the location of trap  $j$ .  
 9025 We’ll suppose here that the random variables  $\mathbf{u}_i$  have state-space  $\mathcal{U}$ <sup>3</sup>.

9026 How do we interpret this probability? Well, two things have to happen for an individual  
 9027 to be encountered by a trap: (1) it has to vocalize; (2) the microphone has to record a  
 9028 signal  $> c$ . These two things together are a product of biological and environmental factors  
 9029 which could include time of day, wind direction and speed, or maybe rain, humidity and  
 9030 other things. The bottom line is a lot of factors are balled up in whether or not the  
 9031 microphone records a sound greater than the threshold.

9032 The observations from an acoustic survey are the signal strength measurements, and  
 9033 the likelihood of the observed signal strength from individual  $i$  at detection device  $j$  can  
 9034 be specified by noting that the likelihood is the normal pdf for the observed signal *if* the  
 9035 signal strength is  $> c$  and, otherwise, the contribution to the likelihood is  $\Phi(\gamma(\cdot))$  (see Eq.  
 9036 8 of Efford et al. (2009b)):

$$\Pr(S_{ij} | \mathbf{u}_i) = \Phi(\gamma(\cdot))^{1-I(S_{ij}>c)} \text{Normal}(S_{ij}; \alpha_0, \alpha_1, \sigma_s, \mathbf{x}_j, \mathbf{u}_i)^{I(S_{ij}>c)}$$

9037 We can use this as the basis for constructing the binomial-form of the likelihood as  
 9038 we did in Chapt. 6, which involves the number of individuals not encountered,  $n_0$ . The  
 9039 probability that an individual is *not* captured is equal to the probability that its signal  
 9040 strength doesn’t exceed  $c$  at any microphone. The probability of not being captured at a  
 9041 microphone  $\mathbf{x}_j$  is:

$$1 - p_{\mathbf{u},j} = \Phi(\gamma(\cdot))$$

9042 and therefore the probability of not being captured at any microphone is:

$$\Pr(\text{all } S_{\mathbf{u},j} < c | \mathbf{u}) = \prod_{j=1}^J (1 - p_{\mathbf{u},j}) = \prod_{j=1}^J \Phi(\gamma(\cdot, \mathbf{x}_j, \mathbf{u}))$$

9043 and therefore the marginal probability of not being captured is

$$\pi_0 = [\text{all } S_{\mathbf{u},j} < c | \boldsymbol{\alpha}] = \int_{\mathcal{U}} \left\{ \prod_{j=1}^J \Phi(\gamma(\boldsymbol{\theta}, \mathbf{x}_j, \mathbf{u})) \right\} d\mathbf{u}$$

9044 which can be used to construct the binomial form of the likelihood as we did in Chapt. 6  
 9045 (see Eq. 6.2.1).

---

<sup>3</sup>We use  $\mathcal{U}$  here to avoid confusion with definition of signal strength,  $S$ . However,  $\mathcal{U}$  is the same state-space as  $\mathcal{S}$  in the rest of the book

### 9.4.2 Implementation in `secr`

Fitting acoustic encounter models in `secr` is no more difficult than other SCR models. There is a handy manual (`secr-sound.pdf`) with examples (Efford and Dawson, 2010) which comes with the `secr` package. The basic process is that `make.caphist` will make a `caphist` object from a 3-dimensional encounter array – which is a binary array indicating whether each individual was detected or not at each recorder/microphone. In the case of signal strength data, `secr` handles the case where  $\# \text{ occasions} = 1$ , i.e., the recorders obtained data for a single sample occasion, but this is not a general requirement of the model for signal strength data (see next section). The “signal” attribute of the `caphist` object contains the signal strength in decibels. The best way to include the signal attribute is to use `make.caphist` in the usual way, providing it with the encounter data and trap data and, in addition, the variable “cutval” (which is  $c$  in our notation above) and then provide the signal strength data as an extra column of the `caphist` object. See `?make.caphist` for details.

### 9.4.3 Implementation in `BUGS`

We don’t know of any Bayesian applications of acoustic SCR models, although we imagine that implementation of such models in the `BUGS` engines should be achievable. It seems easy enough to write down a general hierarchical model that would accommodate sampling on repeated occasions. Let  $\mathbf{s}_i$  be the home range center, and let  $\mathbf{u}_{ik}$  the instantaneous location of individual  $i$  during sample occasion  $k$  (see Chapt. 15 for similar models). The model for  $\mathbf{u}_{ik}$  can be specified conditional on  $\mathbf{s}_i$ . For example, we could assume that  $\mathbf{u}_{ik}$  are bivariate normal draws with mean  $\mathbf{s}_i$  and some variance  $\sigma_u^2$ . Then, conditional on  $\mathbf{u}_{ik}$  an individual produces a signal according to the signal attenuation model (Eq. 9.4.1), or perhaps some other model. Then we generate the binary encounter data by truncating the observed signal at  $c$ . This general model then is an example of an SCR model in which parameters of a movement model are identifiable (see Sec. 2.6) because there is direct information about movement outcomes from the sampling method, unlike other types of encounter methods (e.g., camera traps) for which animal locations are restricted to a set of fixed, pre-determined points where traps are located. Other types of SCR methods allow for movement information too, including some of the search-encounter models (Chapt. 15).

Instead of developing a Bayesian version of this model here, we leave it to the reader to explore simulating data and devising a Bayesian implementation of the acoustic model in one of the `BUGS` engines. Note that for a single occasion, you can simulate the data using the two stage model (having both  $\mathbf{s}$  and  $\mathbf{u}$ ) or you can simulate  $\mathbf{u}$  uniformly without dealing with  $\mathbf{s}$  in the model. The kernel of the `BUGS` model specification should resemble the following snippet:

```
model {
  # Ignoring loops and data augmentation
  u[i,1] ~ dunif(xlim[1], xlim[2])
  u[i,2] ~ dunif(ylim[1], ylim[2])
  mu[i,j] <- alpha0 + alpha1*d[i,j]
  ###
```

```

9089   ### JAGS has this T() truncation feature
9090   S[i,j] ~ dnorm(mu[i,j], 1/sigma^2)T(c,Inf)
9091   ###
9092   gamma[i,j] <- (c - mu[i,j])/sigma
9093   p[i,j] <- 1 - pnorm(gamma[i,j], 0, 1) # JAGS has pnorm() function
9094   y[i,j] ~ dbern(p[i,j])
9095 }

```

#### 9.4.4 Other types of acoustic data

Efford and Dawson (2010) noted that various other types of acoustic data might arise for which SCR-like models would be useful<sup>4</sup>. For example, we could measure the *time of arrival* of a vocal queue of some sort at multiple recorders to estimate the number and origin of  $N$  queues. Another example is that where we measure *direction* to a queue from multiple devices and do, effectively, a type of statistical triangulation to the multiple but unknown number of sources. This has direct relevance to types of double or multiple-observer sampling that people do in field studies of birds. Normally 2 observers stand in close proximity and record birds, reconciling their detections after data collection. An SCR-based formulation of the double-observer method has two observers (or more) standing some distance apart, e.g., 50 or 100 meters, and marking individual birds on a map (or at least a direction) and a time of detection. The SCR/double-observer method could be applied to such data.

## 9.5 SUMMARY AND OUTLOOK

In this chapter we extended SCR models to accommodate alternative models for the observation process, including Poisson and multinomial models. Along with the binomial model described in Chapt. 5, this sequence of models will accommodate a substantial majority of contemporary spatial capture-recapture problems, including the 4 main types of encounter data: binary encounters, multinomial trials from “multi-catch” and “single-catch” (Efford, 2004, 2011; Royle and Gardner, 2011) trap systems, and Poisson encounter frequency data from devices that can record multiple encounters of the same individual at a device. We summarize the standard observation models and the corresponding **secr** terminology in Table 9.4. What we refer to as search-encounter (or area-search) models (see Chapt. 15) are distinct from most of the other classes in that the observation location can also be random (in contrast to traps, where the location is fixed by design). This auxiliary data is informative about an intermediate process related to movement (Royle and Young, 2008).

There is a need for other types of encounter models that arise in practice. We identify a few of them here, although we neglect a detailed development of them at the present time or, in some cases, put that off until later chapters: (1) Removal systems – Sometimes traps kill individuals and SCR models can handle that. This can be viewed as a kind of open model, with mortality only, and we handle such models (in part) in Chapt. 16; (2) There are models for which only specific summary statistics are observable (Chandler and

<sup>4</sup>Some of the following is also related to material presented by D.L. Borchers at the ISEC 2012 conference in Norway.

**Table 9.4.** Different observation models, where we discuss them in this book, and what the corresponding **secr** terminology is

observation model	Where in this book?	<b>secr</b> name
Bernoulli	Chapt. 5	<b>proximity</b>
Poisson	Sec. 9.1	<b>count</b>
Multinomial (ind)	Sec. 9.2	<b>multi-catch</b>
Multinomial (dep)	Sec. 9.3	<b>single-catch</b>
Acoustic	Sec. 9.4	<b>signal</b>
Search-encounter	Chapt. 15	<b>polygon</b> (in part)

9128 Royle, In press; Sollmann et al., 2012b) which we cover in Chapt. 18 - 19; (3) We can  
 9129 have multiple observation methods working together as in Gopalaswamy et al. (2012b).

9130 There remains much research to be done to formalize models for certain observation  
 9131 systems. For example, while we think one will usually be able to analyze single-catch  
 9132 systems using the multi-catch model, or even the Bernoulli model if encounter probability  
 9133 is sufficiently low, a formalization of the single-catch model would be a useful development  
 9134 and, we believe, it should be achievable using one or another of the **BUGS** engines. In  
 9135 addition, classical “trapping webs” (Anderson et al., 1983; Wilson and Anderson, 1985a;  
 9136 Jett and Nichols, 1987; Parmenter and MacMahon, 1989; Link and Barker, 1994) have  
 9137 been around for quite some time and it seems like they are amenable to formulation as  
 9138 a type of SCR model although we have not pursued that development simply because  
 9139 trapping webs are rarely used in practice.