7

MODELING VARIATION IN ENCOUNTER PROBABILITY

In previous chapters we showed how to fit basic spatial capture-recapture models using Bayesian analysis (in **WinBUGS** or **JAGS**; Chapt. 5) or by classical likelihood methods (Chapt. 6 or using `secr`). We mostly focused on a specific observation model, the Bernoulli or binomial model for devices such as "proximity detectors" (although we extend this model to Poisson and multinomial type observation models in Chapt. 9). We have not, however, described a general framework for modeling covariates that might influence encounter probability of individuals, traps or over time. In practice, investigators are invariably concerned with explicit factors or covariates that might influence variation in parameters. Such covariates include time (e.g., day of year, or season), behavior (e.g., is there an effect of trapping on subsequent capture probabilities), sex of the individual, and trap type (e.g., various camera types, or different constructions for hair snares). Traditionally, in the non-spatial capture recapture literature, such models were called "model M_t", "model M_h", or "model M_b", identifying models that account for variation in detection probability as a function of time, "individual heterogeneity" or "behavior", where behavior describes whether or not an individual had been previously captured. In SCR models, more complex covariate models are possible because we might also have trap-specific covariates, or covariates that vary spatially over the landscape, and because we generally have more than one parameter describing the detection function: Most encounter probability functions include a baseline encounter rate (λ_0) or probability (p_0) parameter, and a scale parameter (σ), which takes on different interpretations depending on the specific encounter probability function under consideration.

In this chapter, we generalize the basic SCR model to accommodate both alternative detection functions as well as many different kinds of covariates. We focus on the binomial observation model used throughout Chapts. 5 and 6 and the Gaussian encounter model (also called the "half-normal" model in the distance sampling literature), but the extension to other observation models is straightforward (and other encounter probability models with different functions of distance are considered in Sec. 7.1). Specifically, we consider three distinct types of covariates – those which are fixed, partially observed or completely unobserved (latent). Fixed covariates are those that are fully observed; for example, the date of all sampling occasions. Partially observed covariates are those which are not known for all observations; for example, the sex of an individual cannot always be determined from photos taken during camera trapping. Even if we are able to observe the sex of all individuals sampled, we cannot know it for those individuals never observed during the study. And finally, unobserved covariates are those which we cannot observe at all, for example, the home range size of individuals, or unstructured random "individual effects".

We will see that models containing these different types of covariates are relatively easy to describe in **WinBUGS** or **JAGS**, and therefore to analyze using Bayesian analysis of the joint likelihood based on data augmentation thus providing a coherent and flexible framework for inference for all classes of SCR models. Throughout the chapter, we will continue to develop the analysis of the black bear study introduced in Chapt. 4, using the software **JAGS**. We also consider the likelihood analysis of many of these models; to do so, we continue to use the **R** package `secr` , and we introduce some ideas of model comparison using AIC (Sec. 7.4 at the end of the chapter). There are other types of covariates that we do *not* cover in this chapter; for example, covariates that vary across the landscape might affect density, and we consider these covariates in Chapt. 11. Alternatively, these landscape covariates might affect the way individuals use space. There are probably very few circumstances under which animals use all space uniformly and we develop more realistic models of encounter probability in which covariates affect space usage in Chapt. 12.

7.1 ENCOUNTER PROBABILITY MODELS

In Chapt. 5, we developed a basic spatial capture recapture model using a standard encounter probability function based on the kernel of a normal (Gaussian) probability distribution:

$$p_{ij} = p_0 \exp(-\alpha_1 * ||\mathbf{x}_j - \mathbf{s}_i||^2)$$

where $||\mathbf{x}_j - \mathbf{s}_i||$ is the distance between $\mathbf{x}_j$ and $\mathbf{s}_i$ and $\alpha_1 = 1/(2 * \sigma^2)$. We argued (see Sec. 5.4) that one can view this model as corresponding to an explicit model of space usage – namely, that individual locations are draws from a bivariate normal distribution. We also mentioned that other detection models are possible, including a logit model of the form:

$$\text{logit}(p_{ij}) = \alpha_0 + \alpha_1 ||\mathbf{x}_j - \mathbf{s}_i||. \tag{7.1.1}$$

However, there's nothing preventing us from constructing a myriad of other models for encounter probability as a function of distance. The most commonly used detection probability models are also those used in the distance sampling literature: the half-normal (Gaussian), the hazard, and the negative exponential. The negative exponential model is:

$$p_{ij} = p_0 * \exp(-\alpha_1 * ||\mathbf{x}_j - \mathbf{s}_i||)$$

where we define $\alpha_1 = 1/\sigma$. We could use the general power model (Russell et al., 2012):

$$p_{ij} = p_0 * \exp(-\alpha_1 * ||\mathbf{x}_j - \mathbf{s}_i||^{\theta})$$

of which the Gaussian and exponential models are special cases. Another model that could be considered is the Gaussian hazard rate model (Hayes and Buckland, 1983):

$$p_{ij} = 1 - \exp(-\lambda_0 * \exp(-\alpha_1 * ||\mathbf{x}_j - \mathbf{s}_i||^2))$$

which was previously discussed in Sec. .

In each of the cases, the relationship of α_1 to σ varies and must be properly specified. The **R** package `secr` allows the user to access 12 different encounter probability models (termed "distance functions" in `secr`), of which some are only used for simulating data (see Table 7.1). These encounter probability models can also be implemented in **R**, **WinBUGS**, **JAGS** etc..

Table 7.1. Basic encounter probability models ("distance functions") available in `secr`. (Table taken from the `secr` help files). Notation deviates from that used in the text. In this table g_0 is the baseline encounter rate or probability parameter used in `secr` which is equivalent to our p_0 or λ_0 depending on context. d is distance defined as we have done throughout, as the distance between the activity center and the trap. One can read more on this specific table by loading the `secr` package and using the `help` command in **R** (`?detectfn`).

	Name	Params	Function
0	half-normal	g_0, σ	$g(d) = g_0 e^{-d^2/(2\sigma^2)}$
1	hazard rate	g_0, σ, z	$g(d) = g_0(1 - e^{-(d/\sigma)^{-z}})$
2	exponential	g_0, σ	$g(d) = g_0 e^{-d/\sigma}$
3	compound half-normal	g_0, σ, z	$g(d) = g_0[1 - \{1 - e^{-d^2/(2\sigma^2)}\}^z]$
4	uniform	g_0, σ	$g(d) = g_0, d \leq \sigma$; $g(d) = 0$, otherwise
5	w exponential	g_0, σ, w	$g(d) = g_0, d < w$; $g(d) = g_0 e^{(-(d-w)/\sigma)}$, otherwise
6	annular normal	g_0, σ, w	$g(d) = g_0 e^{(-(d-w)^2/(2\sigma^2))}$
7	cumulative lognormal	g_0, σ, z	$g(d) = g_0[1 - F(d-\mu)/s)]$
8	cumulative gamma	g_0, σ, z	$g(d) = g_0\{1 - G(d; k, \theta)\}$
9	binary signal strength	b_0, b_1	$g(d) = 1 - F\{-(b_0 + b_1 d)\}$
10	signal strength	β_0, β_1,S	$g(d) = 1 - F[\{c - (\beta_0 + \beta_1 d)\}/S]$
11	signal strength spherical	β_0, β_1,S	$g(d) = 1 - F[\{c - (\beta_0 + \beta_1(d-1) - 10 * log_{10}(d^2))\}/S]$

Insofar as all these encounter probability models are symmetric and stationary, they are pretty crude descriptions of space usage by real animals. This is not to say they are inadequate descriptions of the data and, as we discuss in Chapts. 13 and 12, we can use them as the basis for producing more realistic models of space usage.

By changing the encounter probability model and the specification of α_1, we can basically create any function of distance for the data. It is important to note that σ is not comparable under these different encounter probability models and should not be regarded as "home range radius" in general. While there is generally a relationship between σ and home range size, that relationship varies depending on the model under consideration. We demonstrate how to fit different encounter probability models in the Bayesian framework here, and then provide information on the likelihood analysis (in `secr`) in a separate section below.

7.1.1 Bayesian analysis with `bear.JAGS`

To demonstrate how to incorporate various types of covariates into models for encounter probability using **JAGS**, we return to the data collected during the Fort Drum bear study. This data set was first introduced in Chapt. 4, but, to refresh your memory, there were 38 baited hair snares that were operated between June and July 2006. The snares were checked each week for a total for $K = 8$ sample occasions and $n = 47$ individual bears were encountered at least once. The data are provided in the **R** package `scrbook` and an **R** function called `bear.JAGS` allows the user to easily pick which model to analyze. The function `bear.JAGS` will set up the data, write the model, define the MCMC specifications (e.g., initial values, etc.) and, finally, run the selected model in **JAGS**. In addition to choosing which model to run, the user can also specify the number of chains, iterations and length of the burn-in phase. Calling the function will provide all the code to implement the models independently as well. In the following sections we will present the model code and output for the most commonly employed models; for all analyses we ran 3 chains with a burn-in of 500 iterations and 20000 saved iterations.

7.1.2 Bayesian analysis of encounter probability models

In Panel 7.1, we present the basic SCR model and show how to specify the negative exponential encounter probability model. To call each of these from the function `bear.JAGS` set `model='SCR0'` or `model='SCRexp'` in the function call, respectively. To reduce repetition of the R coding, we include the basic code here and then only show modifications when necessary throughout the chapter. All of the R coding can be found within the `bear.JAGS` function as well. The function begins by loading the required **R** libraries as well as the Ft. Drum bear data set. This data set includes a 3-d data array (called `bearArray` in our code), with dimensions `nind` $\times$ `ntraps` $\times$ `nreps` representing the capture histories of `nind` captured individuals at `ntraps` trap locations. In the Bayesian analysis, data augmentation is used to estimate N and therefore the `bearArray` data must be augmented with $M -$ `nind` all zero encounter histories. In models without time dependence, the augmented `bearArray` (called `Yaug` in the code) will be reduced to a 2 dimensional array (denoted `y` in the code) that has dimensions `M` $\times$ `ntraps`.

```
> library(rjags)  # Load the necessary libraries
> library(scrbook)

> data(beardata)   # Attach the bear data for Ft. Drum
> ymat <- beardata$bearArray
> trapmat <- beardata$trapmat
> nind <- dim(beardata$bearArray)[1]
> K <- dim(beardata$bearArray)[3]
> ntraps <- dim(beardata$bearArray)[2]
> M <- 650
> nz <- M-nind

# Create augmented array
> Yaug <- array(0, dim=c(M,ntraps,K))
```

```
> Yaug[1:nind,,] <- ymat
> y <- apply(Yaug,1:2, sum)
```

The function `bear.JAGS` also establishes the upper and lower limits on the state space by centering the trap array coordinates (which are imported with the `beardata` and saved in the code above as `trapmat`) and then buffering by 20km.

```
model{
alpha0 ~ dnorm(0,.1)                          # Prior distributions
logit(p0) <- alpha0
alpha1 <- 1/(2*sigma*sigma)
sigma ~ dunif(0, 15)
psi ~ dunif(0,1)

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:J){
  d[i,j] <- pow(pow(s[i,1]-X[j,1],2) + pow(s[i,2]-X[j,2],2),0.5)
  y[i,j] ~ dbin(p[i,j],K)
  p[i,j] <- z[i]*p0*exp(- alpha1*d[i,j]*d[i,j])  # Gaussian model
 #p[i,j] <- z[i]*p0*exp(- alpha1*d[i,j])        # exponential model
 }
}
N <- sum(z[])
D <- N/area
}
```

Panel 7.1: **JAGS** model specification for a basic SCR model with Gaussian encounter probability function and the alternative exponential encounter probability function.

Applying the SCR model with Gaussian encounter probability model provides an estimate (posterior mean) of $D = 0.167$ bears per km^2 and with the negative exponential encounter probability model the posterior mean is virtually the same $D = 0.167$. In distance sampling, the use of different encounter probability models often results in very different estimates of density (especially when using the negative exponential model). There are two main reasons why the different models may have less of an impact on the density estimates under the SCR models. First, we can estimate the baseline encounter probability parameter (p_0). In most distance sampling models, detection at distance 0 is set to 1. In Table 7.2, the posterior mean of p_0 is 0.11 under the Gaussian model and 0.34 under the negative exponential model. The larger baseline encounter probability under the negative exponential model reduces the impact of the quick decline in detection as a function of distance. Secondly, the detection probability function here is governing 'movement' of individuals (which we have more information on than in distance sampling), not the whole detection process, so the shape of the detection probability function does not impact the density estimation as much.

In all analyses it is important to check that the size of the augmented data set (M) is sufficiently large and does not impact the estimate of N. Here, the 97.5% percentile for N is 628 (Table 7.2), thus not reaching our $M = 650$ value. We could also increase M and compare the posterior of N under the different scenarios as another check that the data augmentation is sufficient.

Table 7.2. Posterior summaries of SCR model parameters having different encounter probability models, for the Fort Drum black bear data.

Parameter	Mean	SD	2.5%	97.5%
Gaussian				
N	500.63	66.652	371.000	628.000
D	0.17	0.022	0.122	0.207
p_0	0.11	0.014	0.081	0.135
σ	1.99	0.131	1.762	2.275
ψ	0.77	0.104	0.566	0.966
Exponential				
N	512.06	65.771	382.000	634.000
D	0.17	0.022	0.130	0.210
p_0	0.34	0.056	0.246	0.465
σ	1.12	0.095	0.951	1.323
ψ	0.79	0.102	0.584	0.974

A very important consideration when using different detection probability functions is the interpretation of σ. The estimate (posterior mean) of σ under the negative exponential model is 1.12, which is distinct from our estimate of σ under the Gaussian model, $\sigma = 1.996$. The interpretation of σ in the two models is really quite distinct. In the normal model it can be interpreted as the standard deviation of a bivariate normal movement model whereas the manner in which σ relates to "area used" for the negative exponential model has nothing to do with a bivariate normal model of movement. This highlights that it is important for the user to know what detection probability function is used and what the interpretation of σ might be in relation to the home range size. This relationship was discussed in Sec. 5.4.

We now move onto incorporating covariates into the model using the **JAGS** language. For this part, we will stick with the Gaussian encounter probability model shown in Panel 7.1 above.

7.2 MODELING COVARIATE EFFECTS

The basic strategy for modeling covariate effects is to include them on the baseline encounter rate or probability parameter, p_0 (or λ_0), or the scale parameter of the encounter model, σ, or in some cases, both parameters.

Broadly speaking, we recognize (here) 3 types of covariates. Fixed covariates are fully observable and might vary by trap alone (e.g., type of trap, baited or not, disturbance regime, even habitat), sample occasion (e.g., day of season or weather conditions), or both (e.g., behavior, weather - if over a large region). Another class of covariates are those which vary at the level of the individual (and possibly also over time). As a technical matter, and as noted before, these are different from fixed covariates because we cannot see all of the individuals and the covariates are almost always incompletely observed (if at all). The lone exception is the effect of previous capture, used to model a behavioral response to capture, which is known for all individuals, captured or not (an animal never captured/observed has never been captured before). We noted may times before that space itself (i.e., the activity centers) is a type of individual covariate and this notion actually helped us derive the fully spatial capture-recapture model from the traditional, non-spatial model (Chapt. 4). We do not get to observe the activity center for any individuals, but for individuals that are encountered we get to observe some information about it in the form of which traps the individual was encountered in. And finally, we have completely unobserved covariates such as heterogeneity in home range size. We consider heterogeneity in a separate section below since there are a suite of models for describing latent heterogeneity.

Table 7.3. Examples of different types of covariates in SCR models.

Covariate type	Examples
individual	sex, age, home range
trap	baited/not, habitat (see also Chapter 13)
time	season, shedding, weather
individual x time	global behavioral response
trap x time	trap failures
individual x trap x time	local behavioral response

To develop covariate models, we assume a standard sampling design in which an array of J traps is operated for K sample occasions, which produces encounter histories for n individuals. For the null model, there are no time-varying covariates that influence encounter, there are no explicit individual-specific covariates, and there are no covariates that influence density. For fixed effects, those which we observe fully, we can easily incorporate these into the encounter probability model, just as we would do in any standard GLM or GLMM, on some suitable scale for the encounter probability, p_{ijk}. For example,

$$\begin{aligned} \text{logit}(p_{0,ijk}) &= \alpha_0 + \alpha_2 * C_{ijk} \\ p_{ijk} &= p_{0,ijk} \exp(-\alpha_1 * ||\mathbf{x}_j - \mathbf{s}_i||^2) \end{aligned}$$

where C_{ijk} is some covariate that varies (potentially) by individual (i), trap (j) and occasions (k), and α_2 is the coefficient to be estimated. How we define specific covariates (e.g., trap specific versus individual specific) will influence exactly how we include them in the model. Table 7.3 shows examples of covariates by type – trap, individual, and time – and also gives examples of some combined types. These are the types of covariates we will specifically address in this chapter, demonstrating how to analyze the different types in the following sections.

7.2.1 Date and time

Often, researchers are interested in modeling the effect of date or chronological time on encounter probability. For example, in a long term hair snare study, we may expect that seasonal shedding (Wegan et al., 2012) will influence encounter probabilities directly. Or, we may expect behaviors such as denning, mating, etc., to influence the encounter of certain species at certain times of year (Kéry et al., 2011). There are two common ways to incorporate date or time information into a model for encounter probability. For cases with a small number of sampling occasions we can fit a time-specific intercept (analogous to "model M_t" in classical capture-recapture (Otis et al., 1978)). In this model, there are K sampling occasion-specific parameters to reflect potential variation in sampling effort or other factors that might vary across samples. Alternatively, we can model parametric functions of date or time such as polynomial or sinusoidal functions.

In the first case, we allow each sampling occasion, k, to have its own baseline encounter probability, e.g.,

$$\text{logit}(p_{0,k}) = \alpha_{0,k}$$

so that

$$p_{ijk} = p_{0,k} \exp(-\alpha_1 * ||\mathbf{x}_j - \mathbf{s}_i||^2).$$

This description of the model includes k occasion-specific baseline encounter probabilities. Thus, if there are 4 sampling occasions, then there are 4 different baseline encounter probabilities. We imagine that complete time-specificity of p_0 (i.e., one distinct value for each sample occasion) would be most useful in situations where there are just a few sampling occasions (if there are many, this formulation will dramatically increase the number of parameters to be estimated) or we do not expect systematic patterns over time (e.g., explainable by a polynomial function or time-varying covariates).

To implement this in **JAGS**, α_0 has to be estimated for each time period k either using an index vector or dummy variables (as described in Chapt. 2 and Sec. 4.3)and this can be done by only changing only a few lines in Panel 7.1:

```
alpha0[k] ~ dnorm(0,.1)
logit(p0[k]) <- alpha0[k]
.......
.......
y[i,j,k] ~ dbin(p[i,j,k],K)
p[i,j,k] <- z[i]*p0[k]*exp(- alpha1*d[i,j]*d[i,j])
```

Since the model contains a parameter for each time period, the encounter histories must be time-dependent. Thus, a 3-d data array (called `bearArray` in our code), with dimensions `nind` $\times$ `ntraps` $\times$ `nreps` is required (recall that we use the 3-d augmented array called `Yaug` with dimensions `M` $\times$ `ntraps` $\times$ `nreps` for the Bayesian analysis). In addition to using the 3-d data array, the initial values must be updated so that there are K values generated for α_0. And finally, this means that another nested *for loop* is needed in the code to account for the K sample occasions. A side note: the computation time will increase quite a bit (this model for the bear data may take up to 15 hours or more on your machine to obtain a sufficient posterior sample).

Running this model with the function `bear.JAGS` by setting `model=SCRt`, returns estimates of density similar to those from the model without covariates (see Table 7.4), but now we have a characterization of variation in encounter probability over time. Encounter probability seems to increase for the first few time periods before stabilizing around 0.14, dropping off again at the end of the study. The differences in encounter probability from the first time periods to the others might actually be due to something like a behavioral response (see below) or possibly seasonal differences in the efficiency of the sampling technique. Researchers have found that hair snares are more effective at different times of the year (even within season) due to shedding (Wegan et al., 2012). In this particular example, our density estimates (posterior means) are similar to the base model, likely because the differences in encounter probability between occasion were not that large. In a longer term study or in one with greater variation in the encounter probability, the implication of such differences might have a bigger impact on the estimates of density and σ.

Table 7.4. Posterior summaries of parameter estimates from a SCR model with time-dependent baseline encounter probability for the Ft. Drum black bear data set.

Parameter	Mean	SD	2.5%	97.5%
N	509.24	66.13	381	632
D	0.17	0.02	0.13	0.21
$p_0(t=1)$	0.06	0.02	0.03	0.10
$p_0(t=2)$	0.05	0.02	0.02	0.09
$p_0(t=3)$	0.15	0.03	0.09	0.22
$p_0(t=4)$	0.14	0.03	0.09	0.21
$p_0(t=5)$	0.15	0.03	0.09	0.22
$p_0(t=6)$	0.12	0.03	0.07	0.19
$p_0(t=7)$	0.15	0.03	0.09	0.22
$p_0(t=8)$	0.08	0.02	0.04	0.13
σ	1.96	0.12	1.73	2.22
ψ	0.78	0.10	0.58	0.97

The occasion specific intercepts (baseline encounter probability) model might not be the most appropriate for all scenarios and could require the estimation of many parameters if we had many sampling occasions, take the wolverine example from Chapt. 5.9 where there were 165 daily sampling occasions. Particularly in such a case as the wolverine study, variation in the encounter process over time is to be expected. For example, if a camera trap study is conducted for an entire year, it is expected that there would be behavioral patterns in individuals due to mating or denning. Instead of fitting a model with K baseline encounter probabilities, we can include date as a linear (or quadratic, ...) effect. An example can be found in Kéry et al. (2011) who incorporated a day-of-year covariate, both as a linear and a quadratic effect, into their SCR model of European wildcats; the data had been collected over a year-long period and cat behavior was expected to vary seasonally thus influencing the probability of encounter. In these cases, we would specifically incorporate day of year (variable "`Date`") as a numeric covariate as:

$$\begin{aligned} \text{logit}(p_{0,ijk}) &= \alpha_0 + \alpha_2 * \texttt{Date}_k \\ p_{ijk} &= p_{0,ijk} \exp(-\alpha_1 * ||\mathbf{x}_j - \mathbf{s}_i||^2) \end{aligned}$$

or a quadratic effect of day-of-year:

$$\text{logit}(p_{0,ijk}) = \alpha_0 + \alpha_2 * \texttt{Date}_k + \alpha_3 * \texttt{Date}_k^2$$
$$p_{ijk} = p_{0,ijk} \exp(-\alpha_1 * ||\mathbf{x}_j - \mathbf{s}_i||^2)$$

where the variable `Date` is an integer coding of day-of-year, indexed to some arbitrary start point in time.

7.2.2 Trap-specific covariates

In some studies it makes sense to model encounter probability as a function of local or trap-specific covariates. These can be one of two types: genuine trap covariates that describe the trap or encounter site, such as whether a trap is baited or not, or how many traps were set at a sampling location, or what kind of bait was used, etc., or local covariates that describe the likelihood that an animal would use the habitat in the vicinity of the trap (see Chapt. 13 for more on this situation). We imagine that these covariates, of either type, should affect baseline encounter probability. For example, Sollmann et al. (2011) found a large difference in the encounter probability of jaguars due to traps being located on roads, which the animals were using to travel along, as opposed to traps placed off of roads. In this case, the trap type is a binary variable – on/off road, (another binary variable could be baited/non-baited). We can write this as:

$$\text{logit}(p_{0,j}) = \alpha_{0,type_j}$$
$$p_{ijk} = p_{0,j} \exp(-\alpha_1 * ||\mathbf{x}_j - \mathbf{s}_i||^2).$$

Here, we use an index variable, "type", an integer value for the trap-specific covariate. Thus for our example of on/off road, we would have $type_j = 1$ if trap j is on a road and $type_j = 2$ otherwise, and we would estimate two separate α_0 parameters – one for on-road and one for off-road cameras. An alternative way to express the 2-category model, using dummy variables, requires that we specify our "type" vector as $\texttt{Type}_j = 0$ if trap j is on a road and $\texttt{Type}_j = 1$ otherwise, and write the model as

$$\text{logit}(p_{0,ijk}) = \alpha_0 + \alpha_2 * \texttt{Type}_j.$$

Now, α_0 is the baseline encounter probability (on the logit scale) for traps on a road ($\texttt{Type}_j = 0$) and α_2 is the effect on baseline encounter probability of a trap being of $\texttt{Type} = 1$. This general set up also allows for more than 2 categories, say if 4 different camera models were used in a study, we would use a set of 3 binary dummy variables to allow for estimation of the different encounter rates (i.e., the intercept). While these models are equivalent, and should yield identical results, sometimes one parameterization might work better than the other in **WinBUGS** or **JAGS** (Kéry, 2010).

7.2.3 Behavior or trap response by individual

One of the most basic of encounter models is that which accommodates a change in encounter probability as a result of initial encounter. This is colloquially referred to as "trap happiness" or "trap shyness", or in other words, a behavioral response of individuals to being captured (Otis et al., 1978). If a trap is baited with a food source, an individual might come back for more. On the other hand, if being captured is traumatic then an individual might learn to avoid traps. Both of these types of responses can occur in most species depending on the type of encounter mechanisms being employed. Moreover, behavioral response can be either global (Gardner et al., 2010b) or local (Royle et al., 2011b). The local response is a trap-specific response while a global response suggests that initial capture provides a net increase or decrease in subsequent probabilities of capture (across all traps). A behavioral response does not need to be enduring (i.e., persist for the entire study after the individual has been captured/observed for the first time) but can also be ephemeral, if, for example, an animal only avoids a trap on the occasion immediately after it was captured (Yang and Chao, 2005; Royle, 2008). While we will focus the examples in this chapter on enduring behavioral effects, extending such a model to the case of an ephemeral response should not pose any difficulties.

To describe these behavioral models we need to create a binary matrix that indicates if an individual has been captured previously. For the global behavioral response, define the $n \times K$ matrix, $\mathbf{C}$, where $C_{ik} = 1$ if individual i was captured at least once prior to session k, otherwise $C_{ik} = 0$.

$$\begin{aligned}\text{logit}(p_{0,ik}) &= \alpha_0 + \alpha_2 * C_{ik}\\ p_{ijk} &= p_{0,ik}\exp(-\alpha_1 * ||\mathbf{x}_j - \mathbf{s}_i||^2).\end{aligned}$$

For the local behavioral response, which is trap specific, we create an array, C_{ijk}, that indicates if an individual i has been previously captured in trap j at time k. (For the augmented individuals, the entries are all 0 since the animals were never captured.) We then include this in the model in the exact same form as above (with the sole difference that both C and p are now also indexed by k):

$$\begin{aligned}\text{logit}(p_{0,ijk}) &= \alpha_0 + \alpha_2 * C_{i,j,k}\\ p_{ijk} &= p_{0,ijk}\exp(-\alpha_1 * ||\mathbf{x}_j - \mathbf{s}_i||^2).\end{aligned}$$

Since the behavioral response is occasion specific, to implement either the local or global response model in **JAGS**, we will have to use the 3-d array of the augmented capture histories (`M`$\times$`ntraps`$\times$`nreps`) as we did for the time-varying encounter probability model above. The code must loop over each sampling occasion, but otherwise, the model varies only a little from the basic SCR model shown in Panel 7.1. Here is the specification of the the occasion specific (k) loop:

```
for(k in 1:K){
  logit(p0[i,j,k]) <- alpha0 + alpha2*C[i,j,k]
  y[i,j,k] ~ dbin(p[i,j,k],1)
  p[i,j,k] <- z[i]*p0[i,j,k]*exp(- alpha1*d[i,j]*d[i,j]).
}
```

Despite only minor changes to the **BUGS** code, this model can require quite a bit of time and computational effort. Implementing the behavioral models with the function `bear.JAGS` by setting `model=SCRb or model=SCRB` for the local or global model respectively, returns the results shown in Table 7.5. There is a strong global behavioral response suggested by the posterior mean of $\alpha_2 = 0.90$. The estimate of N and subsequently D are larger than under the model without a behavioral response; here we estimate the posterior mean of $N = 577.56$, whereas in the SCR0 model, we estimated the posterior mean as $N = 500$. This makes sense given the large estimate of α_2, which suggests that bears are trap happy. In situations where animals are trap happy, the null model tends to over estimate encounter probability (i.e., the bears that are never observed have a lower encounter probability than those that have been captured in the study) and thereby reduce the estimate of N. We do not include the results here, but the estimates were similar under the local behavioral response model.

Table 7.5. Posterior summaries of parameter estimates from the SCR model with a global behavioral response in encounter for the Fort Drum black bear data set.

Parameter	Mean	SD	2.5%	97.5%
N	577.56	54.30	452	648
D	0.19	0.02	0.15	0.21
α_0	-2.81	0.24	-2.91	-2.36
α_2	0.90	0.23	0.45	1.35
σ	2.00	0.13	1.77	2.28
ψ	0.88	0.08	0.69	0.99

7.2.4 Individual covariates

Individual covariates are those which are measured (or measurable) on individuals, so we get to observe them only for the captured individuals. Sex is a simple example of an individual covariate, but one of the most commonly used in capture-recapture studies. The sex of an individual can influence many aspects of its ecology and behavior, including for example, the frequency of movement, seasonal behavior, and its home range size. This is common in studies of carnivores where females often have smaller home ranges than males (Gardner et al., 2010b; Sollmann et al., 2011). Additionally, we may find differences in the baseline encounter probability between males and females because females may move around less frequently, or possibly because they are less likely to use landscape structures that researchers may target with sampling devices in order to increase sample size, such as roads (e.g. Salom-Pérez et al., 2007). Therefore, we can imagine that sex may impact both the baseline encounter probability α_0 and the typical home range size, so that α_1 might also be sex-specific also. The fully sex-specific model is:

$$\text{logit}(p_{0,i}) = \alpha_{0,sex_i}$$
$$p_{ijk} = p_{0,i}\exp(-\alpha_{1,sex_i} * ||\mathbf{x}_j - \mathbf{s}_i||^2)$$

where sex_i is a vector indicating the sex of each individual (1 = male, 2 = female). While we might know the sex of all individuals observed in the study, we will never know the sex of individuals that are not observed (Gardner et al., 2010b). It is also possible that we may not be able to determine the sex of individuals that are observed during the study. For example photographic captures do not necessary result in pictures that allow the sex to be absolutely determined, thus sometimes resulting in missing values of this covariate for animals captured in the study. We deal with this slightly differently depending on the inference framework that we adopt (Bayesian or likelihood). Here we demonstrate the Bayesian implementation and we discuss the likelihood approach using `secr` in detail below in Sec. 7.4.2. Before proceeding with that, we note that it would be possible also to model covariates directly on the parameter σ (or its logarithm), e.g., $\log(\sigma_i) = \theta_1 + \theta_2 \texttt{sex}_i$ (see Sec. 8.1). One or the other (or perhaps *some* other) parameterization may yield a better performing MCMC algorithm or provide a more natural or preferred interpretation. In the context of Bayesian analysis, given that priors are not invariant to transformation of the parameters, this may be a consideration in choosing the particular parameterization.

Specifying a fully sex-specific model for **JAGS** is similar to the time-specific model shown above. We need to use an index or dummy variable to let α_0 and/or α_1 be defined separately for males and females. The main difference in this specification is that we do not observe sex for the augmented individuals. Therefore, we have missing observations of the covariate for those individuals. As a result, sex is regarded as a random variable and so the missing values can be estimated along with the other structural parameters of the model.

Because we are regarding sex as a random variable, we have to specify a distribution for it. With only two possible outcomes, it is natural to suppose that $\texttt{Sex}_i \sim \text{Bernoulli}(\psi_{sex})$ where the parameter ψ_{sex} is the sex ratio of the population. We assume our default non-informative prior for this parameter: $\psi_{sex} \sim \text{Uniform}(0, 1)$. The model specification in Panel 7.2 demonstrates how to incorporate a partially observed covariate (i.e., "sex"). It is important to note that in the previous equation, sex_i is a vector with two categories indicating the sex of each individual (e.g., 1 = male, 2 = female). This corresponds directly to having a binary indicator of sex (e.g., $\texttt{Sex}_i = 1$ if individual i is female, and 0 otherwise). In the Bayesian formulation of the model, we use both the binary indicator (`Sex`) and a categorical indicator ($\texttt{Sex2} = \texttt{Sex} + 1$). The former (termed `Sex` in Panel 7.2) allows us to specify the Bernoulli distribution for the random variable, and the latter (termed `Sex2`) allows us to use the dummy or indicator variable specification in the model.

In both **JAGS** or **BUGS** missing data are indicated by `NA` in the data objects passed to the program through the `bugs` or `jags` functions in **R**. To set up the data, we need to create a vector of length M with the first n elements being 0 if individual i is a female, or 1 if i is a male (for the Fort Drum black bear data the function `bear.JAGS` extracts this information automatically from the `beardata` object), and the subsequent $M - n$ elements being `NA`. It is generally a good idea to provide starting values for the missing data, but we cannot provide starting values for observed data; in this case where one vector (or other object) contains both observed and missing data, initial values for the observed data have to be specified as `NA`. The code snippet below shows you how to set up the data including the `Sex` vector and the initial values function(the remainder of the code is identical to what we've shown before).

```
> sex <- beardata$sex  #the sex data for captured individual
> Sex <- c(sex-1, rep(NA, nz)) #sex enters as 1/2, this recodes it to 0/1
                               #so we can use Bernoulli distribution

> data <- list(y=y,Sex=Sex, M=M,K=K, J=ntraps, xlim=xlim, ylim=ylim,area=areaX)
> params <- c('psi','p0','N', 'D', 'sigma', 'psi.sex')
> inits <- function() { list(z=c(rep(1,nind), rbinom(nz,1,0.5)),psi=runif(1),
            s=cbind(runif(M, xlim[1],xlim[2]), runif(M,ylim[1],ylim[2])),
```

```
          psi.sex=runif(1),Sex=c(rep(NA, nind), rbinom(nz,1,0.5)),
          sigma=runif(2,2,3),alpha0=runif(2)) }
```

The **BUGS** model specification is shown in Panel 7.2.

```
model{

psi ~ dunif(0,1)                            # Prior distributions
psi.sex ~ dunif(0,1)
for(t in 1:2){
  alpha0[t] ~ dnorm(0,.1)
  logit(p0[t]) <- alpha0[t]
  alpha1[t] <- 1/(2*sigma[t]*sigma[t])
  sigma[t] ~ dunif(0, 15)
}

for(i in 1:M){
  z[i] ~ dbern(psi)
  Sex[i] ~ dbern(psi.sex)                    # Sex is binary
  Sex2[i] <- Sex[i] + 1                      # Convert to categorical
  s[i,1] ~ dunif(xlim[1],xlim[2])
  s[i,2] ~ dunif(ylim[1],ylim[2])

  for(j in 1:J){
    d[i,j] <- pow(pow(s[i,1]-X[j,1],2) + pow(s[i,2]-X[j,2],2),0.5)
    y[i,j] ~ dbin(p[i,j],K)
    p[i,j] <- z[i]*p0[Sex2[i]]*exp(-alpha1[Sex2[i]]*d[i,j]*d[i,j])
   }
 }
N <- sum(z[])
D <- N/area
}
```

Panel 7.2: **JAGS** model specification for an SCR model with sex-specific encounter probability parameters.

Our estimate of density under the fully sex-specific model is still very similar to the previous models (Table 7.6), and while the baseline detection was not very different between males and females, we can see that they had very different σ estimates (note that the BCIs do not overlap). As usual, you can reproduce this analysis by calling the function `bear.JAGS` and set `model='SCRsex'`.

Table 7.6. Posterior summaries of parameter estimates from sex-specific SCR models for the Fort Drum black bear data set.

Parameter	Mean	SD	2.5%	97.5%
N	509.982	66.355	376	631
D	0.168	0.022	0.12	0.21
$p_{0,female}$	0.136	0.025	0.09	0.19
$p_{0,male}$	0.092	0.017	0.06	0.13
σ_{female}	1.542	0.132	1.31	1.83
σ_{male}	2.682	0.389	2.09	3.62
ψ_{sex}	0.310	0.068	0.19	0.45
ψ	0.784	0.103	0.58	0.97

7.3 INDIVIDUAL HETEROGENEITY

Here we consider SCR models with individual heterogeneity. Capture-recapture models with individual heterogeneity in detection probability, so-called model M_h, have a long history in classical capture recapture models and they have special relevance to SCR (Sec. 4.4). While the advent of SCR models may appear to have rendered the use of classical model M_h obsolete (because one major source of heterogeneity, namely exposure to the trap array is being accounted for explicitly) we may still wish to consider heterogeneity models for other biological reasons. It is reasonable to expect in real populations that there exists heterogeneity in home range size and so we think that α_1 could exhibit heterogeneity among individuals. As we noted previously, it may be advantageous or desirable in some cases to model heterogeneity directly in terms of the scale parameter of the encounter probability function, σ, or some other transformation of the "distance coefficient", perhaps even 95% home range area.

In this section, we describe a class of spatial capture-recapture models to allow for individual heterogeneity in encounter probability. In particular, one class of models we propose explicitly admits individual heterogeneity in home range *size*. In addition, we consider a standard representation for heterogeneity in which an additive individual-specific random effect is included in the linear predictor for baseline encounter probability.

7.3.1 Models of heterogeneity

An obvious extension to the SCR model is to include an additive individual effect, analogous to classical "model M_h". We'll call this model "SCR+Mh":

$$\begin{aligned} \text{logit}(p_{0,i}) &= \alpha_0 + \eta_i \\ p_{ijk} &= p_{0,i} \exp(-\alpha_1 * ||\mathbf{x}_j - \mathbf{s}_i||^2) \end{aligned}$$

where η_i is an individual random effect having distribution $[\eta|\sigma_p]$. A popular class of models arises by assuming $\eta_i \sim \text{Normal}(0, \sigma_p^2)$ (Coull and Agresti, 1999; Dorazio and Royle, 2003). We show how to implement this specific SCR + Mh model in Panel 7.3, and this model can be used to analyze the Ft. Drum bear data by calling the function `bear.JAGS` and setting `model='SCRh'`. While we show one possible implementation here, many other random effects distributions are possible. A popular one is the finite-mixture of point masses (Norris and Pollock, 1996; Pledger, 2004) which we demonstrate how to fit using `secr` in Sec. 7.4.3.

```
model{

alpha0 ~ dnorm(0,.1)                          # Prior distributions
alpha1 <- 1/(2*sigma*sigma)
sigma ~ dunif(0, 15)
psi ~ dunif(0,1)
tau_p ~ dgamma(.001,.001)

for(i in 1:M){
  eta[i] ~ dnorm(0, tau_p)                    # Individual level variables
    z[i] ~ dbern(psi)
  s[i,1] ~ dunif(xlim[1],xlim[2])
  s[i,2] ~ dunif(ylim[1],ylim[2])

   for(j in 1:J){                             # The "likelihood" etc..
   d[i,j] <- pow(pow(s[i,1]-X[j,1],2) + pow(s[i,2]-X[j,2],2),0.5)
   y[i,j] ~ dbin(p[i,j],K)
   logit(p0[i,j]) <- alpha0 + eta[i]
   p[i,j] <- z[i]*p0[i,j]*exp(- alpha1*d[i,j]*d[i,j])
  }
 }
N <- sum(z[])                                  # N, D are derived
D <- N/area
}
```

Panel 7.3: **JAGS** model specification for the SCR + Mh model with Gaussian encounter probability model and additive normal random effect.

7.3.2 Heterogeneity induced by variation in home range size

An alternative heterogeneity model, one that has more of a direct biological motivation and interpretation, describes heterogeneity in home range size among individuals. To model heterogeneity in home range area, we can assume a distribution for a transformation of the scale parameter of the encounter probability model such as σ^2, or $\log(\sigma^2)$, etc.. We call this "model SCR + Ah" (Ah here for area-induced heterogeneity).

Consider the following log-normal model for the individual scale parameter of the Gaussian encounter probability model, σ_i^2:

$$\log(\sigma_i^2) \sim \text{Normal}(\mu_{hra}, \tau_{hra}^2)$$

then the 95% home range area has a scaled log-normal distribution with mean

$$6\pi \exp(\mu_{hra} + \tau_{hra}^2/2).$$

The variance is slightly more complicated, but you can look up the variance of a log-normal distribution and combine it with the 95% home range area calculation in Sec. 5.4 to work out the implied variance of home range area under this model. We show two examples of the implied *population* distribution of home range area under this log-normal model that indicates a mean home range area of about 6.9 area units (Figure 7.1). The left panel shows a standard deviation in home range area of 2.88 units and the right panel shows a standard deviation in home range area of 0.70 units. The two cases were generated by tweeking the μ_{hra} and τ_{hra}^2 parameters of the log-normal distribution to achieve a constant expected value of home range area, but modify the standard deviation.

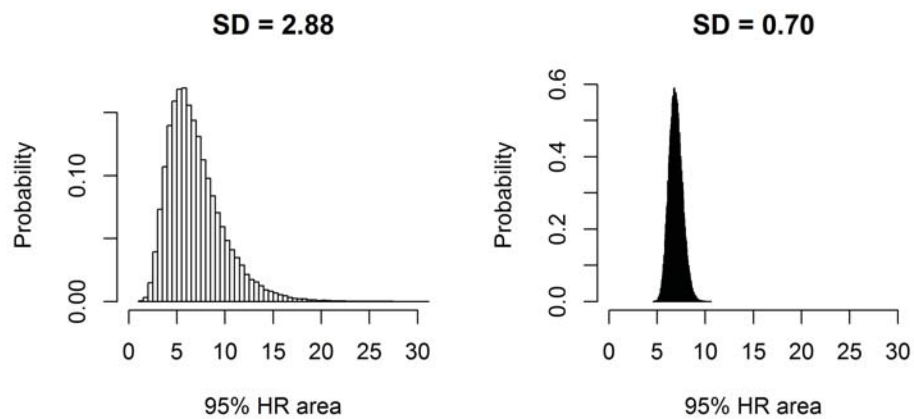

Figure 7.1. Population distribution of home range area for a model in which $\log(\sigma^2)$ has a normal distribution with mean μ_{hra} and variance τ_{hra}^2. The parameters were chosen to yield a constant expected value of about 6.9 units of area, but to produce two different levels of heterogeneity: A population standard deviation of 2.88 units (left panel) and 0.70 units (right panel).

7.4 LIKELIHOOD ANALYSIS IN SECR

Previously, in Chapt. 6, we introduced the **R** package `secr` and described the likelihood based inference approach taken by that package (see Sec. 6.5.3). Here we discuss how to implement some standard covariate models in `secr` and provide an example of model selection using AIC. As we saw in Chapt. 6, `secr` uses the standard **R** model specification syntax, defining the dependent and independent variable relationship using tildes (e.g., `y ~ x`). Thus, in `secr` we might have `g0 ~ behavior` or `sigma ~ time`; when left unspecified or set to 1 (e.g., `g0 ~ 1`), this will default to a model with no covariates (i.e., constant parameter values). A number of default model formulas for the baseline and scale parameter of the encounter probability model are available in `secr`. Additionally, `secr` allows us to specify covariates on density (we cover this in Chapt. 11), which are set for example as `D ~ habitat`.

To demonstrate models with various types of covariates using `secr`, we continue using the Fort Drum black bear data. We include in the `scrbook` package a function called `secr.bear` that will format the data (see Chapt. 6 for the `secr` data format) and then fit and compare 8 models (details shown in Panel 7.4). We have described all of these models in the previous sections, so we only briefly comment here on how to fit certain models in `secr` and compare them using AIC, and give a few helpful notes.

7.4.1 Notes for fitting standard models

In the `secr` package, the encounter probability model is called the "detection function" and it is specified by changing the "`detectfn`" option (an integer code) within the `secr.fit` command. Table 7.1 shows the possible encounter probability models that `secr` allows; the default is that based on the kernel of a bivariate normal probability distribution function (hence we call this the Gaussian model, but it is referred to as "half-normal" in `secr`) and the (negative) exponential is `detectfn = 2`. See model 2 in Panel 7.4 for how to fit the exponential model to the Fort Drum bear data set.

The `secr` package easily fits a range of SCR equivalents of standard capture-recapture models. The package has pre-defined versions of the classic model M_t where each occasion has its own encounter probability, as well as a linear trend in baseline encounter probability over occasions (in a spatial modeling framework σ could also be an occasion specific parameter, but having encounter probability change with time seems like the more common case). For the classical time-effects type of model with K distinct parameters `secr` uses 't' to denote this in the model specification formula (see model 3 in panel 7.4); whereas, for a linear trend over occasions `secr` uses 'T'.

The global trap response model (what we called model M_B), or a local trap-specific behavioral response (model M_b) can be fitted in `secr` using formulae with "b" for the global response model and "bk" for the local trap response model (see models 4 and 5 in Panel 7.4; note that to fit the trap specific behavioral response model you need version 2.3.1 or newer of `secr`).

7.4.2 Sex effects

Incorporating sex effects into models with `secr` can be done a few different ways, but there are not pre-defined models for this. A limitation of fitting models with sex effects in `secr` is that it does not accommodate missing values of the sex variable. Thus, in all cases, individuals that are of unknown sex must be removed from the data set (recall that in a Bayesian framework we can keep these individuals in the data set by specifying a distribution for the individual covariate "sex"). In `secr`, the easiest way to include sex effects is to code sex as a "session" variable using the multi-session models (see Sec. 6.5.4 for a description of the multi-session models), providing two sessions, one representing

```
1. null model with a bivariate normal encounter probability  model
bear_0=secr.fit(bear.cap, model=list(D ~ 1, g0 ~ 1, sigma ~ 1))

2. null model with an exponential encounter probability model
bear_0exp=secr.fit(bear.cap, model=list(D ~ 1, g0 ~ 1, sigma ~ 1),
                   detectfn=2)

3. model with fixed time effects
bear_t=secr.fit(bear.cap, model=list(D ~ 1, g0 ~ t, sigma ~ 1))

4. global behavioral model
bear_B=secr.fit(bear.cap, model=list(D ~ 1, g0 ~ b, sigma ~ 1))

5. trap specific behavioral response
bear_b=secr.fit(bear.cap, model=list(D ~ 1, g0 ~ bk, sigma ~ 1))

6. global behavior model with fixed time effects
bear_bt=secr.fit(bear.cap, model=list(D ~ 1, g0 ~ b+t, sigma ~ 1))

7. sex-specific model
bear_sex=secr.fit(bear.cap, model=list(D ~ session, g0 ~ session,
                  sigma ~ session))

8. heterogeniety model
bear_h2=secr.fit(bear.cap, model=list(D ~ 1, g0 ~ h2, sigma ~ h2))
```

Panel 7.4: Models called from `secr.bear` function. All models use `buffer = 20000` males and one for females (see model 7 in Panel 7.4). This method provides two separate density estimates, which can then be combined into a total density.

7.4.3 Individual heterogeneity

To incorporate heterogeneity, `secr` fits a set of finite mixture models (Norris and Pollock, 1996; Pledger, 2004). These are expensive in terms of parameters but they have been widely adopted because they are easy to analyze using likelihood methods, as the marginal distribution of the data is just a sum of a small number of components. Using `secr`, individual heterogeneity can be incorporated into the encounter probability model using default models for either a 2- or 3-component finite mixture model using the "`h2`" or "`h3`" model terms. The 2-part mixture is shown in model 8 of panel 7.4 and the 3-part mixture can easily be fit by substituting `h3` for `h2`. We only showed the SCR + Mh logit-normal mixture in the version above (see Sec. 7.3.1), but finite-mixture models can also be fit in **JAGS** or **BUGS**.

7.4.4 Model selection in `secr` using AIC

One practical advantage to using the `secr` package, or likelihood inference in general, is the convenience of automatic model selection using AIC (Burnham and Anderson, 2002). The `secr` package has a number of convenient functions for computing AIC and producing model selection tables, or doing model-averaging (as described in Chapt. 8). Running the function `secr.bear`, which calls all of the models we have described, will return, in addition to all model results, an AIC table with all of the summarized results including the AIC values, delta AIC, and model weights (see Table 7.7 or reproduce results in `R` using `out<-secr.bear(); out$AIC.tab`).

It is important to note that AIC is not comparable between a multi-session model and a model that is not a multi-session model. Therefore, to compare the sex-specific model (which uses "sessions") with all the other models including the null, time, and behavioral models, we coded the data set as a multi-session design when first loading it to `secr`. This results in all the model outputs listing separate parameter estimates for each session, even the null model with no covariates; however, the estimates are the same for both "sessions" in all but the sex-specific model (in other words, we don't specify any effect of session on parameters, except in the sex specific model).

The results from this AIC analysis are straightforward to interpret; the model with a local trap response of encounter probability, "bk", has a model weight of 1 and thus, according to AIC, 100% support compared with the other models in this model set. The 2-part finite mixture model for g_0 and σ has the second lowest AIC, but considering the large dAICc compared to the local trap response model we would probably not consider it any further.

7.5 SUMMARY AND OUTLOOK

There are endless covariates and encounter probability models that can be defined and our goal in this chapter was to introduce basic types of covariate models and demonstrate how to implement them in **BUGS** and `secr`. Essentially, SCR's are GLMMs and therefore

Table 7.7. Log-likelihood, AIC, deltaAIC and AIC weight for several models run in secr for the Fort Drum black bear data set.

model	logLik	AIC	AICc	dAICc	AICwt
bear.b	-641.7215	1291.443	1292.395	0.000	1
bear.h2	-653.8382	1319.676	1321.776	29.381	0
bear.0exp	-663.9152	1333.830	1334.389	41.994	0
bear.B	-677.6175	1363.235	1364.187	71.792	0
bear.bt	-668.3044	1358.609	1366.152	73.757	0
bear.sex	-677.7151	1367.430	1369.530	77.135	0
bear.t	-674.4134	1368.827	1374.938	82.543	0
bear.0	-686.2455	1378.491	1379.049	86.654	0

we develop covariate models in much the same way, using a suitable transformation (link function) of the parameter(s). In SCR models, we typically have 2 parameters of the encounter probability model for which we might specify covariate models – the baseline encounter probability (or rate) parameter, and a scale parameter that is related in many cases to the home range size of the species. A few examples of different covariate models are given in Table 7.3. We can also consider covariates by their classification as fixed, partially observed, or unobserved (see Table 7.8). This classification of covariate types can be important because the MLE and Bayesian approaches to dealing with partially and unobserved covariates is often different. This was seen above in how the covariate `Sex` was handled in the two frameworks.

Table 7.8. Examples of different covariate classifications.

Covariate class	Examples
Fixed	baited, weather, habitat
Partially observed	sex, age,
Unobserved	home range size, ind. effects

While the move to spatially explicit models in capture-recapture studies has largely rendered the basic CR models (Otis et al., 1978) obsolete, we continue to find this classification useful for categorizing the *spatial* extensions of these standard CR models. The extended models include the standard M_0, M_t, M_b, and M_h, but also new models that allow for trap-specific information such as "baited/not-baited" or "on/off road". In addition, in Chapts. 12, 13 and 11, we explore models for explaining variation in encounter probability and density based on spatial covariates that describe variation in landscape or habitat conditions.