

Chapter 1

State-space Covariates

Underlying all spatial capture recapture models is a point process model describing the distribution of individual activity centers (\mathbf{s}_i) within the state space (\mathcal{S}). So far we have focused our discussion on the homogeneous binomial point process, $\mathbf{s}_i \sim \text{Uniform}(\mathcal{S})$, $i = 1, 2, \dots, N$, where N is the size of the population. This is a model of “spatial-randomness”¹ because the intensity of the activity centers is constant across the study area and the activity centers are distributed independently of each other.

The spatial-randomness assumption is often viewed as restrictive because ecological processes such as territoriality and habitat selection can result in non-random distributions of organisms. We have argued, however, that this assumption is less restrictive than may be recognized because the homogeneous point process actually allows for infinite possible configurations of activity centers. Furthermore, given enough data, the uniform prior will have very little influence on the estimated locations of activity centers. Nonetheless, the homogeneous point process model does not allow one to model population density using covariates—a central objective of much ecological research. For example, a homogeneous point process model may result in a density surface map indicating that individuals were more abundant in one habitat than another, but it does not do so explicitly. A more direct approach would be to model density using covariates as is done in generalized linear models (GLMs).

In this chapter we will present a method for fitting inhomogeneous binomial point process models using covariates in much the same way as is done with GLMs. The covariates we consider differ from those covered in previous chapters, which were typically attributes of the animal (*e.g.* sex, age) and were used to model movement or encounter rate. In contrast, here we wish to model covariates that are defined for all points in \mathcal{S} , which we will refer to as state-space, or density, covariates. These may include continuous covariates such as elevation, or discrete covariates such as habitat type.

¹The phrase “complete spatial-randomness” is reserved for the homogeneous Poisson point process

? were the first to propose an inhomogeneous point process model for SCR models, and our approach is similar to theirs with the exception that we will use a binomial rather than a Poisson model because the binomial model is easily integrated into our data augmentation scheme and is consistent with the objective of determining how a *fixed* number of activity centers are distributed with respect to covariates.

The method we use to accommodate inhomogeneous binomial point process models within our MCMC algorithm is simple—we replace the uniform prior with a prior describing the distribution of the N activity centers conditional on the covariates. Development of this prior, which does not have a standard form, is a central component of this chapter. First we will begin with a review of homogeneous point process models.

1.1 Homogeneous point process revisited

The homogeneous Poisson point process is *the* model of “complete spatial randomness” and it is often used in ecology as a null model to test for departures from randomness. Given its central role in the analysis of point processes, it is helpful to compare it with the binomial model that we use in our SCR models. The primary descriptor of the homogeneous point process model is the “intensity” parameter, μ which describes the expected number of points in an infinitesimally small area. Thus the intensity parameter can also be used to determine the expected number of points in any region of the state-space \mathcal{S} . To denote this, we say that the expected number of points in region $B \in \mathcal{S}$ is $n(B) = A(B)\mu$ where $A(B)$ is the area of region B . One property of the Poisson model is that if we divide the entire state-space into $k = 1, \dots, K$ disjunct regions, the counts $\{n(B_k)\}$ are independent and identically distributed, (*i.i.d.*). This is one of the distinctions between the Poisson model and the binomial model, for which the counts $n(B_k)$ are not *i.i.d.* as we will explain shortly. This difference is also related to another distinction between the two models, namely that the binomial model conditions on the number of points to be simulated N ; whereas under the Poisson model N is random. Here is some simple **R** code to illustrate this point.

```
mu <- 4                                # intensity
Np <- rpois(1, mu)                     # Np is random
PPP <- cbind(runif(Np), runif(Np)) # Poisson point process

Nb <- 4
BPP <- cbind(runif(Nb), runif(Nb)) # Binomial point process
```

Note that in both models, the N points are independent of one another and distributed uniformly throughout \mathcal{S} . Thus, the intensity at any point $x \in \mathcal{S}$ is $\mu = 1/A(\mathcal{S})$ where $A(\mathcal{S})$ denotes the area of the state-space. For example, if the area of our state-space is 4 km², under a homogeneous model, the intensity is $\mu = 1/4$.

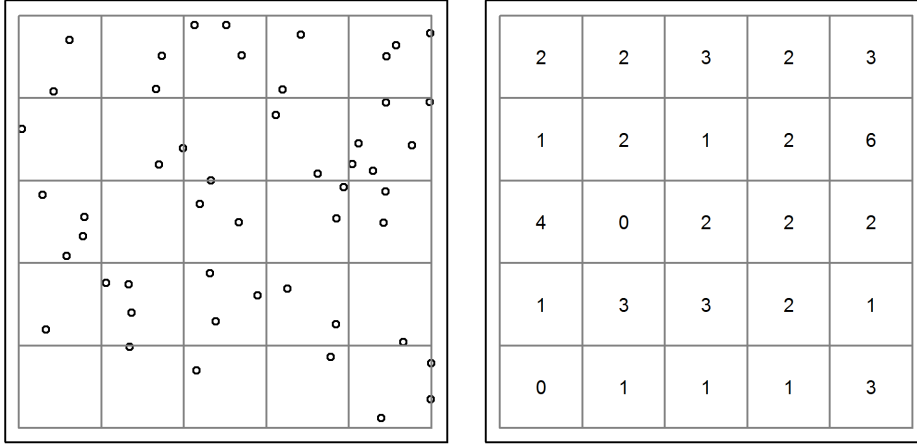


Figure 1.1: Homogeneous binomial point process with $N=50$ points represented in continuous and discrete space.

Although the Poisson model is typically described in terms of μ , the binomial model is not; rather, it is more common to consider a discrete state space, such as a grid with K pixels. Under the binomial model, the number of points in each region is $n(B_k) \sim \text{Bin}(N, p_k)$ where $p_k = A(B)/A(S)$, ie p_k is simply the fraction of the state-space area in B_k . This discrete space representation of the binomial point process is shown in Fig. 1.1. The state-space in this case is the unit square, and thus the probability of a point falling in each of the 25 disjunct regions is $p_k = 1/25$ and thus the expected counts are simply $\mathbb{E}(n(B_k)) = Np_k$. In the figure $N = 50$ and thus we would expect 2 points per pixel, which happens to be the empirical mean of the data in Fig. 1.1. Note also that these counts are not independent realizations from a binomial distribution since $\sum_k n(B_k) = N$. Instead, the model for the entire vector is $\mathbf{n}(\mathbf{B}) \sim \text{Multinomial}(N, \pi = (p_1, p_2, \dots, p_K))$ (?). The dependence among counts has virtually no practical consequence when the number of pixels is large. For example, if we have 100 pixels, the number of counts in one pixels tells you very little about the expected count in another pixel. However, if there are only 2 pixels, then clearly the number of points in one pixel tells you exactly how many will occur in the remaining pixel. To gain familiarity with the multinomial distribution and the discrete representation of space, use the `rmultinom` function in **R** to simulate counts similar to those shown in Fig. 1.1, for example using a command such as:

```

n.B_k <- rmultinom(1, size=50, probs=rep(1/25, 25))
matrix(n.B_k, 5, 5)

```

96 The discrete space representation of the binomial point process is of practical
 97 importance when fitting SCR models because spatial covariates are almost
 98 always represented in a discrete format, often called “rasters” in GIS-speak. In
 99 such cases, we often need to change our definition of the prior for an activity
 100 center from $s_i \sim \text{Uniform}(\mathcal{S})$ to $s_i \sim \text{Multinomial}(1, \pi)$. In the latter case, the
 101 activity center is simply defined as an integer representing pixel “id”. Note also
 102 that the multinomial distribution with an index of 1 (*i.e.* `size=1` in `rmultinom`)
 103 is referred to as the categorical distribution, which we will often make use of in
 104 the BUGS language.

105 1.2 Inhomogeneous binomial point process

106 As with the homogeneous model, the inhomogeneous binomial point process
 107 model is developed conditional on N . The primary distinction is that the uni-
 108 form distribution is replaced with another distribution allowing for the intensity
 109 parameter to vary spatially. To arrive at this new distribution, define $\mu(x, \beta)$ to
 110 be a function of spatially-referenced covariates (β) available at all points of the
 111 state space. To be concise we will subsequently drop the vector of coefficients
 112 from our notation, and simply use $\mu(x)$. Since an intensity must be strictly
 113 positive, it is natural to model $\mu(x)$ using the log-link.

$$\log(\mu(x)) = \sum_{j=1}^J \beta_j v_j(x), \quad x \in \mathcal{S}$$

114 where β_j is the regression coefficient for covariate $v_j(x)$. To be clear, $v(x)$ is
 115 the value of any covariate, such as habitat type or elevation, at location x . This
 116 equation should look familiar because it is the standard linear model used in
 117 log-linear GLMs. Note, however, that we have no need for an intercept because
 118 it would be confounded with N . This should be intuitive since an intercept
 119 would represent the expected value of N when $\beta = 0$, but we already have a
 120 parameter in the model for expected abundance, namely $\mathbb{E}[N] = \psi M$. Thus an
 121 intercept would be redundant, and without it we are still able to achieve our
 122 goal of describing the distribution of N activity centers as a function of spatial
 123 covariates.

124 Now that we have a model of the intensity parameter $\mu(x)$, we need to
 125 develop the associated probability density function to use in the place of the
 126 uniform prior used in the homogeneous model. Remembering that the integral
 127 of a pdf must be unity, we can create a pdf by dividing $\mu(x)$ by a normalizing
 128 constant, which in this case is the integral of $\mu(x)$ evaluated over the entire
 129 state-space. The probability density function is therefore

$$f(x) = \frac{\mu(x)}{\int_{x \in \mathcal{S}} \mu(x) \, dx} \quad (1.1)$$

130 Substituting this distribution for the uniform prior allows us to fit inhomoge-
 131 neous binomial point process models to spatial capture-recapture data. We can

also use this distribution to obtain the expected number of individuals in any given region. Specifically, the proportion of N expected to occur in any region B when heterogeneity in density is present is $p(B) = \int_B f(x) dx$. These are also the multinomial cell probabilities if the regions are disjoint and compose the entire state-space.

As a practical matter, note that the integral in the denominator of $f(x)$ is evaluated over space, and since we almost always regard space as two-dimensional, this is a two-dimensional integral that can be approximated using the methods discussed in refChXXX. These methods include Monte Carlo integration, Gaussian quadrature, etc... Alternatively, if our state-space covariates are in raster format, *i.e* they are in discrete space, the integral can be replaced with a sum over all pixels, which is much more efficient computationally.

We now have all the tools needed to fit inhomogeneous point process (IPP) models. Before doing so, we note that the IPP for the activity centers results in another IPP for the observation process, $\lambda(x)$. As a reminder, $\lambda(x)$ is the expected number of captures for a trap at point x . As was true for the homogeneous model, this intensity function is a product of the point process intensity and the encounter rate function, $\lambda(x) = \mu(x)g(x)$.

In the next section we walk through a few examples, building up from the simplest case where we actually observe the activity centers as though they were data. In the second example, we fit our new model to simulated data in which density is a function of a single continuous covariate. Example three shows an analysis in discrete space using both **secr** (?) and **JAGS** (?). In the last example, we model the intensity of activity centers for a real dataset collected on jaguars (*Panthera onca*) in Argentina.

1.3 Examples

1.3.1 Simulation and analysis of inhomogeneous point processes

In SCR models, the point process is not directly observed, but in other contexts it is. Examples include the locations of disease outbreaks or the locations of trees in a forest. Fitting inhomogeneous point process models to such data is straight-forward and illustrates the fundamental process that we will later embed in our MCMC algorithm used to fit SCR models.

Suppose we knew the locations of 100 animals' activity centers. To estimate the intensity surface $\mu(x)$ underlying these points, we need to derive the likelihood for our data under this model. Given the pdf $f(x)$, and assuming that the points are mutually independent of one another, we may write the likelihood as the product of R such terms, where $R = 100$ is the sample size in this case, *i.e* the observed number of activity centers.

$$\mathcal{L}(\beta|\mathbf{x}_i) = \prod_{i=1}^R f(x_i)$$

171 Having defined the likelihood we could choose a prior and obtain the posterior
 172 for β using Bayesian methods, or we can find the maximum likelihood estimates
 173 (MLEs) using standard numerical methods as is demonstrated below.

174 First, let's simulate some data. Simulating data under an inhomogeneous
 175 point process model is often accomplished using indirect methods such as rejection
 176 sampling. Rejection sampling proceeds by simulating data from a standard
 177 distribution and then accepting or rejecting each sample using probabilities
 178 defined by the distribution of interest. For more information, readers should
 179 consult an accessible text such as ?. In our example, we simulate from a uni-
 180 form distribution and then accept or reject using the (scaled) probability density
 181 function $f(x)$. Note that we first define a spatial covariate (elevation) that is a
 182 simple function of the spatial coordinates increasing from the southwest to the
 183 northeast of our state-space.²

184 The following **R** commands demonstrate the use of rejection sampling to
 185 simulate an inhomogeneous point process for the covariate depicted in Fig. 1.3.1.

186 **use R2Cuba instead of int2d**

```

187 # spatial covariate (with mean 0)
188 elev.fn <- function(x) x[,1]+x[,2]-1
189
190 # 2-dimensional integration over unit square
191 int2d <- function(beta, delta=0.02) {
192   z <- seq(delta/2, 1-delta/2, delta)
193   len <- length(z)
194   cell.area <- delta*delta
195   S <- cbind(rep(z, each=len), rep(z, times=len))
196   sum(exp(beta*elev.fn(S)) * cell.area)
197 }
198
199 # Simulate PP using rejection sampling
200 set.seed(300225)
201 N <- 100
202 count <- 1
203 s <- matrix(NA, N, 2)
204 beta <- 2 # parameter of interest
205 while(count <= 100) {
206   x.c <- runif(1, 0, 1); y.c <- runif(1, 0, 1)
207   s.cand <- cbind(x.c,y.c)
208   elev.min <- elev.fn(cbind(0,0))
209   elev.max <- elev.fn(cbind(1,1))
210   pr <- exp(beta*elev.fn(s.cand)) / int2d(beta)
211   Q <- max(c(exp(beta*elev.min) / int2d(beta),
212             exp(beta*elev.max) / int2d(beta)))
213   if(runif(1) < pr/Q) {
214     s[count,] <- s.cand
215     count <- count+1

```

²Such functional forms of covariates are rarely available, which is why continuous spatial covariates are more often measured on a discrete grid.

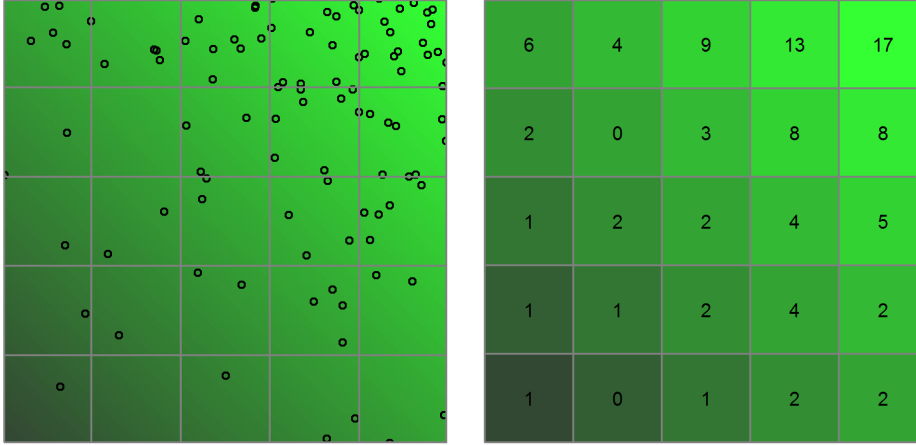


Figure 1.2: An example of a spatial covariate, say elevation, and a realization of an inhomogeneous binomial point process with $N=100$ and $\mu(x) = \exp(\beta \text{Elev})$ where $\beta = 2$.

```

216     }
217 }

```

The simulated data are shown in Fig 1.3.1. High elevations are represented by light green and low elevations by dark green. The activity centers of one hundred animals are shown as points, and it is clear that these simulated animals prefer the high elevations. The underlying model describing this preference is $\log(\mu(x)) = \exp(\beta \times \text{Elevation}(x))$ where $\beta = 2$ is the parameter to be estimated and $\text{Elevation}(x)$ is a function of the coordinates at x , as displayed on the map.

Given these points, we will now estimate β by minimizing the negative-log-likelihood using R's `optim` function.

```

226 # Negative log-likelihood
227 nll <- function(beta) {
228   -sum(beta*elev.fn(s) - log(int2d(beta)))
229 }
230 starting.value <- 0
231 fm <- optim(starting.value, nll, method="Brent",
232            lower=-5, upper=5, hessian=TRUE)
233 c(Est=fm$par, SE=sqrt(1/fm$hessian)) # estimates and SEs

```

Maximizing the likelihood took a small fraction of a second, and we obtained an estimate of $\hat{\beta} = 2.47$. We could plug in this estimate to our linear model at each point in the state-space to obtain the MLE for the intensity surface.

This example demonstrates that if we had the data we wish we had, *i.e.* if we knew the coordinates of the activity centers, we could easily estimate

the parameters governing the underlying point process. Unfortunately, in SCR models, the activity centers cannot be directly observed, but spatial re-captures, that is captures of individuals at multiple locations in space, provide us with the information needed to estimate these latent parameters.

1.3.2 Fitting inhomogeneous point process SCR models

Continuous space

One of the nice things about hierarchical models is that they allow us to break a problem up into a series of simple conditional relationships. Thus, we can simply add the methods described above into our existing MCMC algorithm to simulate the posteriors of β conditional on the simulated values of \mathbf{s}_i . To demonstrate, we will continue with the previous example. Specifically, we will overlay a grid of traps upon the map shown in Fig. 1.3.1. We will then simulate capture histories conditional upon the activity centers shown on the map. Then, we will attempt to estimate the activity center locations as though we did not know where they were, as is the case in real applications.

Here is some **R** code to simulate the encounter histories under a Poisson observation model, which would be appropriate if animals could be detected multiple times at a trap during a single occasion.

```

add this code to the R package help file for scrIPP

# Create trap locations
xsp <- seq(-0.8, 0.8, by=0.2)
len <- length(xsp)
X <- cbind(rep(xsp, each=len), rep(xsp, times=len))

# Simulate capture histories, and augment the data
ntraps <- nrow(X)
T <- 5
y <- array(NA, c(N, ntraps, T))

nz <- 50 # augmentation
M <- nz+nrow(y)
yz <- array(0, c(M, ntraps, T))

sigma <- 0.1 # half-normal scale parameter
lam0 <- 0.5 # basal encounter rate
lam <- matrix(NA, N, ntraps)

set.seed(5588)
for(i in 1:N) {
  for(j in 1:ntraps) {
    distSq <- (s[i,1]-X[j,1])^2 + (s[i,2] - X[j,2])^2
    lam[i,j] <- exp(-distSq/(2*sigma^2)) * lam0
    y[i,j,] <- rpois(T, lam[i,j])
  }
}

```



```
284 yz[1:nrow(y),] <- y # Fill
```

285 Now that we have a simulated capture-recapture dataset y , and we have
 286 augmented it to create the new data object yz , we are ready to begin sampling
 287 from the posteriors. A commented Gibbs sampler written in **R** is available
 288 in the accompanying **R** package **scrbook** (see `?scrIPP`). There are two small
 289 parts of the **R** code that distinguish it from previous code we have shown to
 290 fit homogeneous point processes. First, we need to update the parameter β
 291 conditional on all other parameters in the model. The code to do so is:

```
292 D1 <- int2d(beta1, delta=.05)
293 beta1.cand <- rnorm(1, beta1, tune[3])
294 D1.cand <- int2d(beta1.cand, delta=0.05)
295 ll.beta1 <- sum( beta1*elev.fn(S) - log(D1) )
296 ll.beta1.cand <- sum( beta1.cand*elev.fn(S) - log(D1.cand) )
297 if(runif(1) < exp(ll.beta1.cand - ll.beta1) ) {
298   beta1<-beta1.cand
299 }
```

300 Next, we need to put the new prior on the activity centers:

```
301 #ln(prior), denominator is constant
302 prior.S <- beta1*cov(S[i,1], S[i,2]) # - log(D1)
303 prior.S.cand <- beta1*(Scand[1] + Scand[2]) # - log(D1)
304 if(runif(1) < exp((ll.S.cand+prior.S.cand) - (ll.S+prior.S))) {
305   S[i,] <- Scand
306   lam <- lam.cand
307   D[i,] <- dtmp
308 }
```

309 We can apply this modified sampler to our data using the code shown in
 310 the following panel. We obtain posterior distributions summarized in Table 1.1.
 311 Mixing is good, and as usual, life is very nice when we are working with simulated
 312 data.

```
313 library(scrbook)
314 fm1 <- scrIPP(yz, X, M, 3000, xlims=c(-1,1), ylims=c(-1,1),
315               tune=c(0.002, 0.1, 0.25, 0.07) )
316 plot(mcmc(fm1$out))
```

317 Fitting continuous space IPP models is somewhat difficult in **BUGS** because
 318 our prior $f(x)$ is not one of the available distributions³ **secr** allows users to fit
 319 continuous space using polynomials of the x- and y- coordinates, but not for
 320 truly continuous covariates. However, these are not really important limitations
 321 because discrete space versions are straight-forward, and virtually all spatial
 322 covariates are defined as such.

³It is possible, if somewhat cumbersome, to add new distributions in **BUGS**.

Table 1.1: Posterior summaries from inhomogeneous point proces model

	Mean	SD	2.5%	50%	97.5%
$\sigma = 0.10$	0.1026	0.0048	0.0935	0.1025	0.1123
$\lambda_0 = 0.50$	0.4419	0.0493	0.3496	0.4400	0.5390
$\psi = 0.66$	0.6826	0.0554	0.5762	0.6820	0.7923
$\beta = 2.00$	2.1601	0.3390	1.5193	2.1583	2.8043
$N = 100$	102.7696	6.2689	92.0000	102.0000	117.0000

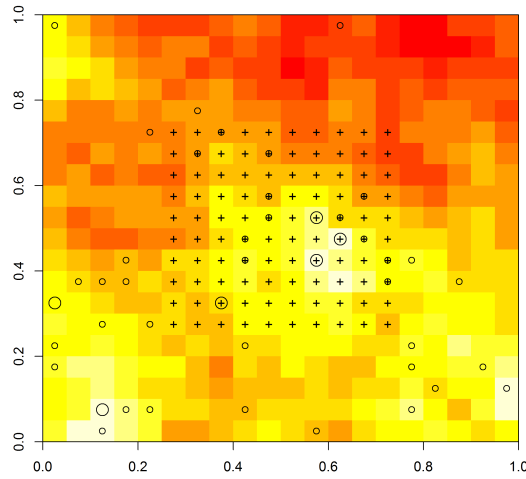


Figure 1.3: Simulated activity centers in discrete space. The spatial covariate, elevation, is highest in the higher areas. Density of activity centers (circles) increases with elevation. Trap locations are shown as crosses.

323 Discrete space

324 To fit the discrete space models, we follow the same steps as outlined in Chapter
 325 5—we define s_i as pixel ID, and we use the categorical distribution as a prior. A
 326 good example of this is in `+citeKery capricaille`. Here we present an analysis of
 327 the simulated data shown in the right panel of Fig. 1.3.1. The spatial covariate,
 328 let's call it elevation again, was simulated from a kriging type of model as
 329 shown on the help page `ch9simData` in `scrbook`. The points are the number of
 330 activity centers in each pixel, generated from a single realization of the IPP
 331 $\mu(x) = 2elev$.

332 The **BUGS** code to fit an IPP model to these data is shown in the following
 333 panel.

334 `model{`

```

335 sigma ~ dunif(0, 1)
336 lam0 ~ dunif(0, 5)
337 beta ~ dnorm(0,0.1)
338 psi ~ dbeta(1,1)
339
340 for(j in 1:nPix) {
341   theta[j] <- exp(beta*elevation[j])
342   probs[j] <- theta[j]/sum(theta[])
343 }
344
345 for(i in 1:M) {
346   w[i] ~ dbern(psi)
347   s[i] ~ dcat(probs[])
348   x0g[i] <- Sgrid[s[i],1]
349   y0g[i] <- Sgrid[s[i],2]
350   for(j in 1:ntraps) {
351     dist[i,j] <- sqrt(pow(x0g[i]-grid[j,1],2) + pow(y0g[i]-grid[j,2],2))
352     lambda[i,j] <- lam0*exp(-dist[i,j]*dist[i,j]/(2*sigma*sigma)) * w[i]
353     y[i,j] ~ dpois(lambda[i,j])
354   }
355 }
356
357 N <- sum(w[])
358 Density <- N/1 # unit square
359 }

```

360 This model can also be fit in **secr**, which refers to the pixel locations as
361 a “mask”. **R** code to fit the models using **secr** and **JAGS** is available in
362 **scrbook**, see **help(ch9secrYjags)**. Results of the comparison are shown in
363 Table ?? and are very similar as expected.

364 Density surface maps can be created for fun, and of course to inform man-
365 agement decisions. [describe how to do this]

Table 1.2: Comparison of **JAGS** and **secr** results

Software	Par	Est.	SD	lower	upper
secr	N	49.2803	5.7535	41.0087	64.3879
	β	2.1772	0.5628	1.0741	3.2804
	λ_0	0.9203	0.0764	0.7824	1.0825
	σ	0.0990	0.0038	0.0918	0.1068
JAGS	N	48.2072	5.4053	39.0000	60.0000
	β	2.1026	0.5323	1.0889	3.1506
	λ_0	0.9328	0.0766	0.7898	1.0921
	σ	0.1004	0.0041	0.0929	0.1089

1.3.3 The jaguar data

Estimating density of large felines has been a priority for many conservation organizations, but no robust methodologies existed before the advent of SCR. Distance sampling is not feasible for such rare and cryptic species, and traditional capture-recapture methods yield estimates that are highly sensitive to the subjective choice of the effective survey area. In this example, we demonstrate how readily density can be estimated for a globally imperilled species using SCR. Furthermore, we show how inhomogeneous point process models can be used to test important hypotheses regarding the factors affecting density.

[describe study]

A few aspects of this design are noteworthy. First, the dimensions and configuration of the trap array differed among the regions of the trap array. This fact alone could explain variation in the number of animals exposed to sampling, which would have no biological meaning. Furthermore, the area of inference is an irregular polygon that was not sampled uniformly. Only by estimating density can we hope to extrapolate our estimates from the sampled region to get what we are after. In this case, this is readily accomplished since the entire state-space can be classified as one of the 3 levels of protection from poaching. Of course, in general it is always preferable to sample more uniformly throughout the area of interest in case some unmeasured covariate biases the extrapolation.

To assess the influence of poaching on jaguar density, we considered 2 metrics of poaching pressure, one political and one continuous measure of accessibility (Fig xxx).

1.4 Summary

When state-space covariates are available, we can model density by replacing the uniform prior on the activity centers with a prior based on a normalized log-linear function of covariates. This yields a model of the inhomogeneous point process describing the location of activity centers, which can be used to test hypotheses about covariates affecting density. In rare cases, these covariates are truly continuous in the sense that they are defined as a function of space. More often, covariates are represented on rasters, which simplifies the analysis. Fitting these models can be accomplished using **BUGS**, **secr**, or the custom **R** code presented in this chapter and found in the package **scrbook**.

All the examples in this section included a single state-space covariate, but this was for simplicity only. Including multiple covariates poses no additional challenges. Likewise, additional model structure such sex-specific encounter rate parameters or behavioral responses can be accommodated.

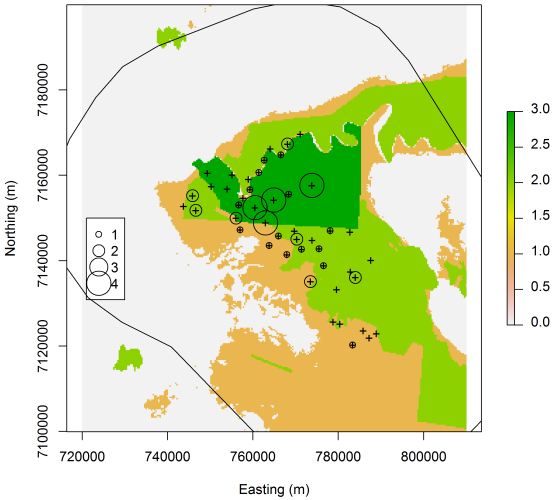


Figure 1.4: Jaguar detections

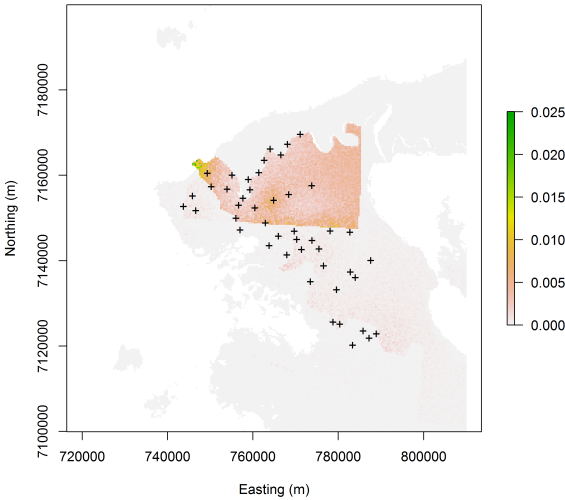


Figure 1.5: Estimated density surface for the jaguar dataset

404 1.5 Other ideas

405 Should have some discussion on some ideas for building flexible models. Might
406 be cool to use the Ickstadt/Wolpert as a model for the inhomogeneous point
407 process. Dont have to do it, just mention it. Also some kind of a spline model
408 or similar.

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