

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 typically 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), using a link function to connect the intensity parameter to the linear predictor.

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 the the state-space, which we will refer to as state-space, or density, covariates. These may include continuous

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

covariates such as elevation, or discrete covariates such as habitat type.

Borchers and Efford [2008] 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.

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 will expand upon in this chapter. 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 $k = 1, \dots, K$ disjoint 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 more important 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 $\mu(x) = 1/4$.

73 Although the Poisson model is typically described in terms of μ , the binomial
 74 model is not; rather, it is more common to consider a discrete state space, for
 75 example a grid with K pixels. Under the binomial model, the number of points
 76 in each region is $n(B) \sim \text{Bin}(N, p)$ where $p(B) = A(B)/A(S)$, ie $p(B)$ is simply
 77 the fraction of the state-space area in B .

78 One additional property of the binomial model is that the K realizations of
 79 n are not independent since they must sum to N . Instead, the model for the
 80 entire vector is $\mathbf{n}(\mathbf{B}) \sim \text{Multinomial}(N, \pi = (p_1, p_2, \dots, p_K))$.

81 [below is text from Chapter 4.3 and it is great to have this material reit-
 82 erated here. Im thinking you could copy the last 2 mini-paragraphs here to
 83 expand on the last point you made above especially be sure to cite Illian et al.
 84 because thats a good book. Also I ordered a copy for you]

85 The collection of individual activity centers $s[1], \dots, s[N]$ represent a realiza-
 86 tion of a *binomial point process* (e.g., Illiana et al. 2008, p. XYZ). The binomial
 87 point process (BPP) is analogous to a Poisson point process in the sense that it
 88 represents a “random scatter” of points in space except that the total number
 89 of points is *fixed*, whereas, in a Poisson point process it is random (having a
 90 Poisson distribution). It is natural to consider a binomial point process in the
 91 context of capture-recapture models because it preserves N in the model and
 92 thus preserves the linkage directly with closed population models. In fact, under
 93 the binomial point process model then Model M0 and other closed models are
 94 simple limiting cases of SCR models. In addition, use of the BPP model allows
 95 us to use data augmentation for Bayesian analysis of the models as in chapter
 96 3, thus yielding a methodologically coherent approach to analyzing the different
 97 classes of models. One consequence of having fixed N , in the BPP model, is
 98 that the BPP is not strictly a model of “complete spatial randomness”. This is
 99 because if you form counts in any set of regions say A_1, \dots, A_k , even disjoint
 100 regions, let $n(A_1), \dots, n(A_k)$ be the counts then these counts are not indepen-
 101 dent. In fact, they have a multinomial distribution (see Illian et al. (2008. P
 102 XYZ)). Thus, the BPP model introduces a slight bit of dependence among the
 103 point locations (and areal totals). However, in most situations this will have no
 104 practical effect on any inference or analysis and, as a practical matter, we will
 105 usually regard the BPP model as one of spatial independence among individual
 106 activity centers .

107 1.2 Inhomogeneous binomial point process

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

115 to model $\mu(x)$ using the log-link.

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

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

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

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

131 Substituting this distribution for the uniform prior allows us to fit inhomoge-
 132 neous binomial point process models to spatial capture-recapture data. We can
 133 also use this distribution to obtain the expected number of individuals in any
 134 given region. Specifically, the proportion of N expected to occur in any region
 135 B when heterogeneity in density is present is $p(B) = \int_B f(x) dx$. These are also
 136 the multinomial cell probabilities if the regions are disjoint and compose the
 137 entire state-space.

138 As a practical matter, note that the integral in the denominator of $f(x)$
 139 is evaluated over space, and since we almost always regard space as two-
 140 dimensional, this is a two-dimensional integral that can be approximated using
 141 the methods discussed in refChXXX. These methods include Monte Carlo inte-
 142 gration, Gaussian quadrature, etc... One issue that often arises is that continu-
 143 ous spatial covariates are *not* represented as continuous, and instead are defined
 144 on discrete grids, called “rasters” in GIS-speak. In such cases, the integral in
 145 the denominator can be replaced with a sum over all pixels citep(diggle:2003),
 146 which is much more efficient computationally.

147 The inhomogeneous point process model for the activity centers results in
 148 another point process model for the observation process, which we have previ-
 149 ously called $\lambda(x)$. As a reminder, $\lambda(x)$ is the expected number of captures for a
 150 trap at point x . As was true for the homogeneous model, this intensity function
 151 is a convolution of the point process intensity ($\mu(x)$) and the encounter rate
 152 function ($g(x, s)$), $\lambda(x) = \mu(x)g(x, s)$.

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. In the last example, we model the intensity of activity centers for a real dataset collected on tigers.

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 the data in hand are the point locations themselves. 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 $f(x)$, if we assume 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, *ie* the observed number of activity centers.

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

Having defined the likelihood we may now obtain the posterior for α using Bayesian methods, or we can find the maximum likelihood estimates (MLEs) using standard numerical methods as is demonstrated below.

Simulating data under an inhomogeneous point process model is often accomplished using indirect methods such as rejection sampling. Rejection sampling proceeds by simulating data from a standard distribution and then accepting or rejecting each sample using probabilities defined by the distribution of interest. For more information, readers should consult an accessible text like [citetrobertcasella:2010](#). In our example, we simulate from a uniform distribution and then accept or reject using the (scaled) probability density function $f(x)$. Note that we first define a spatial covariate (elevation) that is a simple function of the spatial coordinates increasing from the southwest to the northeast of our state-space. It should be obvious that such functional forms of covariates are rarely available, which is why continuous spatial covariates are more often measured on a discrete grid. Nonetheless, we will proceed with our truly continuous covariate for illustrative purposes. However, to evaluate the integral we end up discretizing the state-space anyway.

The following R commands demonstrate the use of rejection sampling to simulate an inhomogeneous point process for the covariate depicted in Figure XYZ.

```

193 # spatial covariate
194 # Elevation as a function of the coordinates at point x
195 elev.fn <- function(x) x[,1]+x[,2]
196
197 # 2-dimensional integration over [-1, 1] square
198 int2d <- function(alpha, delta=0.02) {
199   z <- seq(-1+delta/2, 1-delta/2, delta)
200   len <- length(z)
201   cell.area <- delta*delta
202   S <- cbind(rep(z, each=len), rep(z, times=len))
203   sum(exp(alpha*elev.fn(S)) * cell.area)
204 }
205
206 # Simulate PP using rejection sampling
207 set.seed(395)
208 N <- 100
209 count <- 1
210 s <- matrix(NA, N, 2) # matrix to hold simulated activity centers
211 alpha <- 2 # parameter of interest
212 Q <- max(c(exp(alpha*elev.min) / int2d(alpha),
213           exp(alpha*elev.max) / int2d(alpha))) # Rejection sampling bound
214 while(count <= 100) {
215   x.c <- runif(1, -1, 1); y.c <- runif(1, -1, 1) # proposed activity center
216   s.cand <- cbind(x.c,y.c)
217   elev.min <- elev.fn(cbind(-1,-1)); elev.max <- elev.fn(cbind(1,1))
218   pr <- exp(alpha*elev.fn(s.cand)) / int2d(alpha)
219   if(runif(1) < pr/Q) {
220     s[count,] <- s.cand # accepted proposals
221     count <- count+1
222   }
223 }

```

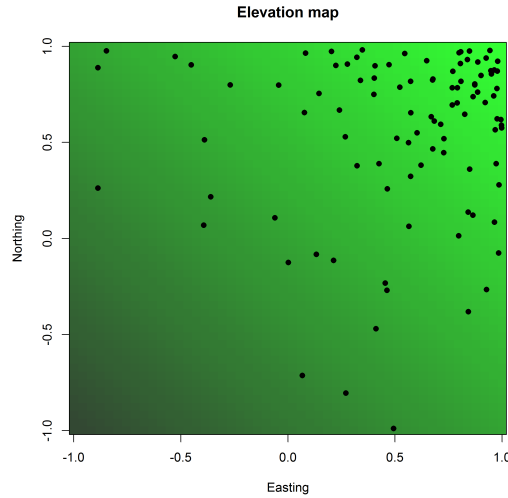
The simulated data are shown in Fig 1.3.1. High elevations are represented by light green and low elevations by dark green. The activity centers of one hundred animals are shown as points, and it is clear that these simulated animals prefer the high elevations. The underlying model describing this preference is $\log(\mu(x)) = \exp(\alpha \times \text{Elevation}(x))$ where $\alpha = 2$ 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 α by minimizing the negative-log-likelihood using R's `optim` function. Since, we only have one parameter to estimate, we use `method = "Brent"`.

```

233 # Negative log-likelihood
234 nll <- function(beta) {
235   -sum(beta*cov(S[,1], S[,2]) - log(int2d(beta)))

```



```

236   }
237   starting.value <- 0
238   fm <- optim(starting.value, nll, method="Brent",
239             lower=-5, upper=5, hessian=TRUE)
240   c(Est=fm$par, SE=sqrt(1/fm$hessian)) # estimates and SEs

```

241 Maximizing the likelihood took a small fraction of a second, and we obtained
 242 an estimate of $\hat{\alpha} = 2.01$. Not bad! We could plug in this estimate to our linear
 243 model at each point in the state-space to obtain the MLE for the intensity
 244 surface.

245 This example demonstrates that if we had the data we wish we had, *i.e.*
 246 if we knew the coordinates of the activity centers, we could easily estimate
 247 the parameters governing the underlying point process. Unfortunately, in SCR
 248 models, the activity centers cannot be directly observed. Rather, they are latent
 249 variables that we must either estimate or at least integrate out of a likelihood.
 250 In SCR studies, spatial re-captures, that is captures of individuals at multiple
 251 locations in space, provide us with the information needed to estimate individual
 252 activity centers.

253 1.3.2 Fitting inhomogeneous point process SCR model

254 One of the nice things about hierarchical models is that they allow us to break
 255 a problem up into a series of simple conditional relationships. Thus, we can
 256 simply add the methods described above into our existing MCMC algorithm
 257 to simulate the posteriors of α conditional on the simulated values of \mathbf{s}_i . To
 258 demonstrate, we will continue with the previous example. Specifically, we will
 259 overlay a grid of traps upon the map shown in Fig. 1.3.1. We will then simulate
 260 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.

[note the use of Poisson model below]

```

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

```

Now that we have a simulated capture-recapture dataset y , and we have augmented it to create the new data object yz , we are ready to begin sampling from the posteriors. A commented Gibbs sampler written in R is available online. You will see that only two small parts of the R code were changed. First, we need to update the parameter α conditional on all other parameters in the model. The code to do so is:

```

D1 <- int2d(beta1, delta=.05)
beta1.cand <- rnorm(1, beta1, tune[3])
D1.cand <- int2d(beta1.cand, delta=0.05)
ll.beta1 <- sum( beta1*cov(S[,1],S[,2]) - log(D1) )
ll.beta1.cand <- sum( beta1.cand*(S[,1]+S[,2]) - log(D1.cand) )
if(runif(1) < exp(ll.beta1.cand - ll.beta1) ) {
  beta1<-beta1.cand
}

```

Next, we need to use α in the prior for the activity centers:

Parameter	Mean	SD	q0.025	q0.5	q0.975
α					
λ_0					
σ					
N					
Density					

```

306 #ln(prior), denominator is constant
307 prior.S <- beta1*cov(S[i,1], S[i,2]) # - log(D1)
308 prior.S.cand <- beta1*(Scand[1] + Scand[2]) # - log(D1)
309 if(runif(1)< exp((11.S.cand+prior.S.cand) - (11.S+prior.S))) {
310     S[i,] <- Scand
311     lam <- lam.cand
312     D[i,] <- dtmp
313 }
```

314 Applying this modified sampler to our data we obtain posterior distributions
315 summarized in Table 1.3.2. Mixing is good, and as usual, life is very nice when
316 we are working with simulated data.

317 It is worth noting that, although this method of fitting inhomogeneous point
318 process models does not require much modification of our custom MCMC code,
319 it is not so trivial to implement these models in BUGS. The reason being that the
320 prior we use is not a standard distribution available by default. It is, however,
321 possible to use arbitrary distribution in BUGS using the ??-trick.. Anyone
322 remember how to do this? Here is an example.

323 Actually what you do is this: Discretize the state-space (see Chapter 4.XYZ
324 to be written by Andy) preferable at the same resolution as your raster and then
325 define $s[i] = \text{integer from } 1:N_{\text{gridpoints}}$ and $s[i] \sim \text{dcat}(\text{probs}[])$ where $\text{probs}[k]$
326 $= \exp(\alpha * x) / [\text{sum of all that stuff}]$ This works. In fact Marc's capricaille
327 paper has an example. In that case there were only 30 or so spatial units (forest
328 tracts) and the covariate was "size of unit" so the model was putting activity
329 centers in each pixel in proportion to area).

330 I think it is worth: (1) showing this example here possible or (2) give a sample
331 WinBUGS analysis (simulated data) that shows this and discuss relevant issue:
332 large rasters is really really expensive computationally. Might use JAGS/parallel
333 to do big problems with thousands of raster points. I wonder if that's possible?

334 In chapter 5 I'm adding information about the discrete state-space formula-
335 tion of the model.

336 1.3.3 The tiger data

337 Hopefully Arjun can send me something. Something will turn up I'm sure. I
338 also don't object to using simulated data here and there if we have to. Maybe
339 SECR has a canned example we could rip off?

340 1.4 MLE

341 Maybe its easy to adapt the MLE code from chapter 5 for doing a spatial
342 covariate? For completeness it might be worth having that.

343 1.5 Other ideas

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

348 1.6 Summary

349 When spatially-referenced covariates are available, we can model density by
350 replacing the uniform prior on the activity centers with a prior based on a
351 log-linear function of covariates.

352 1.6.1 The tiger data

353 Hopefully Arjun can send me something.

354 1.7 Summary

355 When spatially-referenced covariates are available, we can model density by
356 replacing the uniform prior on the activity centers with a prior based on a
357 log-linear function of covariates.

358 Bibliography

- 359 D.L. Borchers and MG Efford. Spatially explicit maximum likelihood methods
360 for capture–recapture studies. *Biometrics*, 64(2):377–385, 2008.