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, $\mathbf{s}_i \sim Uniform(\mathcal{S}), i = 1, 2, \ldots, N$, 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 using 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 covariates, or spatially-referenced covariates. These may

[1] However, the phrase "complete spatial-randomness is reserved for the homogeneous Poisson point process"

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

citetborchersefford:2010 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 accomodate 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 may be the most commonly-used model of spatial randomness in ecology, thus it is helpful to compare it with the binomial model that we will expand upon in this chapter. The primary difference between the two models is that the binomial model conditions on N, the number of points to be simulated; whereas under the Poisson model N is random. Here is some simple R code to illustrate this difference.

```
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 "point process intensity" at any point $x \in \mathcal{S}$ is $\mu(x) = 1/A(\mathcal{S})$ where $A(\mathcal{S})$ denotes the area of the state-space. For example, if the area of our state-space is 4 km^2, under a homogeneous model, the intensity is $\mu(x) = 1/4$.

Although the Poisson model is typically described in terms of $\mu(x)$, the binomial model is not; rather, it is more common to consider a discrete state space, which we mention here for clarity. Suppose that $\mathcal{S}$ is divided into K non-overlapping regions, the number of points in each region B is $n(B) \sim Bin(N, p)$ where $p(B) = A(B)/A(\mathcal{S})$, ie $p(B)$ is simply the fraction of the state-space area in B.

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

1.2 Inhomogeneous binomial point process

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

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

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

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

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

Substituting this distribution for the uniform prior allows us to fit inhomogeneous 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 proprotion of N expected to occur in any region B when heterogeneity in density is present is $p(B) = \int_B f(x)\,\mathrm{d}x$. Once again these are also the multinomial cell probabilities if the regions are non-overlapping and compose the entire state-space.

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

The inhomogeneous point process model for the activity centers results in another point process model for the observation process, which we have previously called $\lambda(x)$. 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 convolution of the point process intensity ($\mu(x)$) and the encounter rate 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 that we knew the locations of 100 animals' activity centers. To estimate the intensity surface $\mu(x)$ underlying these points, we need to express the likelihood of our data for various values of α. Given the pdf $f(x)$, if we assume that the points are conditionally 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.

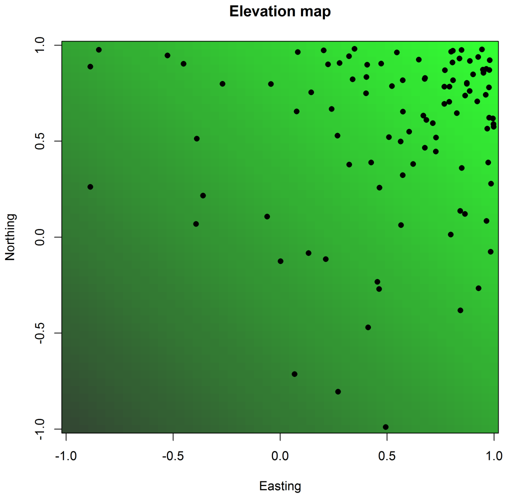
```r
# spatial covariate
# Elevation as a function of the coordinates at point x
elev.fn <- function(x) x[,1]+x[,2]

# 2-dimensional integration over [-1, 1] square
int2d <- function(alpha, delta=0.02) {
  z <- seq(-1+delta/2, 1-delta/2, delta)
  len <- length(z)
  cell.area <- delta*delta
  S <- cbind(rep(z, each=len), rep(z, times=len))
  sum(exp(alpha*elev.fn(S)) * cell.area)
  }

# Simulate PP using rejection sampling
set.seed(395)
N <- 100
count <- 1
s <- matrix(NA, N, 2) # matrix to hold simulated activity centers
alpha <- 2 # parameter of interest
Q <- max(c(exp(alpha*elev.min) / int2d(alpha),
           exp(alpha*elev.max) / int2d(alpha))) # Rejection sampling bound
while(count <= 100) {
  x.c <- runif(1, -1, 1); y.c <- runif(1, -1, 1) # proposed activity center
  s.cand <- cbind(x.c,y.c)
  elev.min <- elev.fn(cbind(-1,-1)); elev.max <- elev.fn(cbind(1,1))
  pr <- exp(alpha*elev.fn(s.cand)) / int2d(alpha)
  if(runif(1) < pr/Q) {
    s[count,] <- s.cand # accepted proposals
    count <- count+1
    }
  }
```

The simulated data are shown in Fig **??**. 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 $\log(\mu(x)) = exp(\alpha \times Elevation(x))$ where $\alpha = 2$ is the parameter to be estimated and $Elevation(x)$ 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".

```
# Negative log-likelihood
nll <- function(beta) {
  -sum(beta*cov(S[,1], S[,2]) - log(int2d(beta)))
  }
starting.value <- 0
fm <- optim(starting.value, nll, method="Brent",
            lower=-5, upper=5, hessian=TRUE)
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 $\hat{\alpha} = 2.01$. Not bad! 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, *ie* 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, and thus are latent variables that we must either estimate or at least integrate out of a likelihood. The good news is that capturing an individual at multiple locations in space provides us with the information needed to estimate the location of its activity.

1.3.2 Fitting inhomogeneous point process SCR model

As we have stated before, 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 α 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. **??**. 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.

```
# 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
}
```

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

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

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

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

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

1.3.3 The tiger data

Hopefully Arjun can send me something.

1.4 Summary

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