

₁ **Chapter 1**

₂ **Introduction**

³ Chapter 2

⁴ GLMS and WinBUGS

Chapter 3

Estimating the Size of a Closed Population

In this chapter we will consider ordinary capture-recapture (CR) models for estimating population size in closed populations. We will see that such models are closely related to binomial (or logistic) regression type models. In fact, when N is known, they are precisely such models. We consider some important extensions of ordinary closed population models that accommodate various types of “individual effects” — either in the form of explicit covariates (sex, age, body mass) or unstructured “heterogeneity” in the form of an individual random effect. In general, these models are variations of generalized linear or generalized linear mixed models (GLMMs). Because of the paramount importance of this concept, we focus mainly on fairly simple models in which the observations are individual encounter frequencies, y_i = the number of encounters of individual i out of K replicate samples of the population which, for the models we consider here, is the outcome of a binomial random variable. Along the way, we consider the spatial context of capture-recapture data and models and demonstrate that density cannot be formally estimated when spatial information is ignored. We also review some of the informal methods of estimating density using CR methods, and consider some of their limitations. We will be exposed to our first primitive spatial capture-recapture models which arise as relatively minor variations of so-called “individual covariate models” (of the ? and ? variety). In a sense, the point of this chapter is to establish that linkage in a direct and concise manner beginning with the basic “Model M0” and extensions of that model to include individual heterogeneity and also individual covariates. A special type of individual covariate models is distance sampling, which could be thought of as the most primitive spatial capture-recapture model. In later chapters we further develop and extend ideas introduced in this chapter.

We emphasize Bayesian analysis of capture-recapture models and we ac-

34 accomplish this using a method related to classical “data augmentation” from
 35 the statistics literature (?). This is a general concept in statistics but, in the
 36 context of capture-recapture models where N is unknown, it has a consistent
 37 implementation across classes of capture-recapture models and one that is really
 38 convenient from the standpoint of doing MCMC (?). We use data augmentation
 39 throughout this book and thus emphasize its conceptual and technical origins
 40 and demonstrate applications to closed population models. We refer the reader
 41 to ?, ch. 6 for an accessible and complimentary development of ordinary closed
 42 population models.

43 3.1 The Simplest Closed Population Model: Model 44 M0

45 We suppose that there exists a population of N individuals which we subject to
 46 repeated sampling, say over K nights, where individuals are captured, marked,
 47 and subsequently recaptured. We suppose that individual encounter histories
 48 are obtained, and these are of the form of a sequence of 0’s and 1’s indicating
 49 capture ($y = 1$) or not ($y = 0$) during any sampling occasion (“sample”). As
 50 an example, suppose $K = 5$ sampling occasions, then an individual captured
 51 during sample 2 and 3 but not otherwise would have an encounter history of
 52 the form $\mathbf{y} = (0, 1, 1, 0, 0)$. Thus, the observation \mathbf{y}_i for each individual (i)
 53 is a vector having elements denoted by y_{ik} for $k = 1, 2, \dots, K$. Usually this
 54 is organized as a row of a matrix with elements y_{ik} , see Table 3.1. Except
 55 where noted explicitly, we suppose that observations are independent within
 56 individuals and among individuals. Formally, this allows us to say that y_{ik} are
 57 Bernoulli random variables and we may write $y_{ik} \sim \text{Bern}(p)$. Consequently,
 58 for this very simple model in which p is in fact constant, then we can declare
 59 that the individual encounter frequencies (total captures), $y_i = \sum_k y_{ik}$, have a
 60 binomial distribution based on a sample of size K . That is

$$y_i = \sum_k y_{ik} \sim \text{Bin}(p, K)$$

61 for every individual in the population. This is a remarkably simple model
 62 that forms the cornerstone of almost all of classical capture-recapture mod-
 63 els, including most spatial capture-recapture models discussed throughout this
 64 book. Evidently, the basic capture-recapture model structure is precisely a
 65 simplistic version of a logistic-regression model with only an intercept term
 66 ($\text{logit}(p) = \text{constant}$). To say that all capture-recapture models are just logistic
 67 regressions is only slightly inaccurate. In fact, we are proceeding here “condi-
 68 tional on N ”, i.e., as if we knew N . In practice we don’t, of course, and that
 69 is kind of the point of capture-recapture models as estimating N is the central
 70 objective. But, by proceeding conditional on N , we can specify a simple model
 71 and then deal with the fact that N is unknown using standard methods that
 72 you are already familiar with (i.e., GLMs - see chapter 2).

Table 3.1: a capture-recapture data set with $n = 6$ observed individuals and $K = 5$ samples.

indiv i	Sample occasion					y_i
	1	2	3	4	5	
1	1	0	0	1	0	2
2	0	1	0	0	1	2
3	1	0	0	1	0	2
4	1	0	1	0	1	3
5	0	1	0	0	0	1
$n = 6$	1	0	0	0	0	1

Assuming individuals of the population are observed independently, the joint probability distribution of the observations is the product of N binomials

$$\begin{aligned} \Pr(y_1, \dots, y_N | p) &= \prod_{i=1}^N \text{Bin}(y_i | K, p) \\ &= \prod_{k=0}^K \pi(k)^{n_k} \end{aligned}$$

where $\pi(k) = \text{Bin}(k | K, p)$ and where $n_k = \sum_{i=1}^N I(y_i = k)$ denotes the number of individuals captured k times in K surveys. We emphasize that this is conditional on N , in which case we get to observe the $y = 0$ observations and the resulting data are just *iid* binomial counts. Because this is a binomial regression model of the variety described in chapter 2, fitting this model using a BUGS engine poses no difficulty.

The essential problem in capture-recapture, however, is that N is not known because the number of uncaptured/missing individuals (i.e., those in the zero cell that occur with probability $\pi(0)$) is unknown. Consequently, the observed capture frequencies n_k are no longer independent. Instead, their joint distribution is multinomial (e.g., see ?, p. xyz):

$$n_1, n_2, \dots, n_K \sim \text{Multin}(N, \pi(1), \pi(2), \dots, \pi(K)) \quad (3.1)$$

Note that in our notation the number of uncaptured/missing individuals is denoted by $n_0 = N - n$, where $n = \sum_{k=1}^K n_k$ denotes the total number of distinct individuals seen in the K samples.

To fit the model in which N is *unknown*, we can regard N as a parameter and maximize the multinomial likelihood directly. While direct likelihood analysis of the multinomial model is straightforward, that does not prove to be too useful in practice because we seldom are concerned with models for the aggregated encounter history frequencies. In many instances, including for spatial capture-recapture (SCR) models, we require a formulation of the model that can accommodate individual level covariates which we address subsequently in this chapter.

3.1.1 The Spatial Context of Capture-Recapture

A common assumption made is that of population “closure” which is really just a colloquial way of saying (in part) the Bernoulli assumptions stated explicitly above. In the biological context, closure means, strictly, no additions or subtractions from the population during study. This is manifest by the statement that the encounters are independent and identically distributed (iid) Bernoulli trials. In practice, closure is usually interpreted by the manner in which potential violations of that assumption arise. In particular, two important elements of the closure assumption are “demographic” and “geographic” closure. If an individual dies then subsequent values of y_{ik} are clearly no longer Bernoulli trials with the same parameter p . If there is no mortality or recruitment in the population, then we say that demographic closure is satisfied. Similarly, animals may emigrate or immigrate. If they do not, then geographic closure is satisfied. Sometimes a distinction is made between temporary and permanent emigration or immigration. That is a relevant distinction in spatial capture-recapture models, because SCR models explicitly accommodate “temporary emigration” of a certain type, due to individuals moving about their home range. The demographic closure assumption can also be relaxed using SCR models, but we will save that discussion for chapter 4.

3.1.2 Conditional likelihood

We saw that a basic closed population model is a simple logistic regression model if N is known and, when N is unknown, the model is multinomial with index or sample size parameter N . This multinomial model, being conditional on N , is sometimes referred to as the “joint likelihood” the “full likelihood” or the “unconditional likelihood” (or model in place of likelihood). This formulation differs from the so-called “conditional likelihood” approach in which the likelihood of the observed encounter histories is devised conditional on the event that an individual is captured at least once. To construct this likelihood, we have to recognize that individuals appear or not in the sample based on the value of the random variable y_i , that is, we capture them if and only if $y_i > 0$. The observation model is therefore based on $\Pr(y|y > 0)$. For the simple case of Model M0, the resulting conditional distribution is a “zero truncated” binomial distribution which accounts for the fact that we cannot observe the value $y = 0$ in the data set (see ?, section XYZ). Both the conditional or unconditional models are legitimate modes of analysis in all capture-recapture types of studies, and they provide equally valid descriptions of the data and for many practical purposes provide equivalent inferences, at least in large sample sizes (?).

In this book we emphasize Bayesian analysis of capture-recapture models using data augmentation (discussed subsequently), which produces yet a third distinct formulation of capture recapture-models based on the zero-*inflated* binomial distribution that we describe in the next section. Thus, there are 3 distinct formulations of the model – or models of analysis – for analyzing all capture-recapture models based on the (1) binomial model for the joint or un-

Mode of analysis	parameters in model	statistical model
Joint likelihood	p, N	multinomial with index N
Conditional likelihood	p	zero-truncated binomial
Data augmentation	p, ψ	zero-inflated binomial

Table 3.2: Modes of analysis of capture-recapture models.

conditional specification; (2) zero-truncated binomial that arises “conditional on n ”; and (3) the zero-inflated binomial that arises under data augmentation. Each formulation has a distinct complement of model parameters (shown in Table 3.2 for Model M0).

3.2 Data Augmentation

We consider a method of analyzing closed population models using data augmentation (DA) which is useful for Bayesian analysis and, in particular, analysis of models using the various BUGS engines and other software. Data augmentation is a general statistical concept that is widely used in statistics in many different settings. The classical reference is ? but see also ?. Data augmentation can be adapted to provide a very generic framework for Bayesian analysis of capture-recapture models with unknown N . This idea was introduced for closed populations by ?, and has subsequently been applied to a number of different contexts including individual covariate models (?), open population models (???), spatial capture-recapture models (???), and many others.

Conceptually, data augmentation takes the data you wish you had - that is, the data set with N rows - the known- N data set - and embeds that data set into a larger data set having $M > N$ rows.¹ It is always possible, in practice, to choose M pretty easily for a given problem and context. Then, under data augmentation, analysis is focused on the “augmented data set.” That is, we analyze the bigger data set - the one having M rows - with an appropriate model that accounts for the augmentation. Inference is focused directly on estimating the proportion $\psi = E[N]/M$, instead of directly on N , where ψ is the “data augmentation parameter.”

3.2.1 DA links occupancy models and closed population models

We provide a heuristic description of data augmentation based on the close correspondence between so-called “occupancy” models and closed population models following ?, sec. xyz.

In occupancy models (??) the sampling situation is that M sites, or patches, are sampled multiple times to assess whether a species occurs at each site. This

¹ RC: Might be just me, but I find that formulation a little confusing... I think it’s the ‘data you wish you had because that’s effectively data you don’t have. I think it might be easier to grasp if this were explained with the data you do have - based on n .

171 yields encounter data such as that illustrated in the left panel of Table 3.3. The
 172 important problem is that a species may occur at a site, but go undetected,
 173 yielding the “all-zero” encounter histories which are observed. However, some
 174 of the all-zeros may well correspond to sites where the species in fact *does*
 175 *not* occur. Thus, while the zeros are observed, there are too many of them
 176 and, in a sense, the inference problem is to allocate the zeros into “structural”
 177 (fixed) and “sampling” (or stochastic) zeros. More formally, inference is focused
 178 on the parameter ψ , the probability that a site is occupied. In contrast, in
 179 classical closed population studies, we observe a data set as in the middle panel
 180 of Table 3.3 where *no* zeros are observed. The inference problem is, essentially,
 181 to estimate how many sampling zeros there are - or should be - in a “complete”
 182 data set. The inference objective (how many sampling zeros?) is precisely the
 183 same for both types of problems if an upper limit M is specified for the closed
 184 population model. The only distinction being that, in occupancy models, M is
 185 set by design (i.e., the number of sites to visit) whereas a natural choice of M for
 186 capture-recapture models may not be obvious. However, by assuming a uniform
 187 prior for N on the integers $[0, M]$, this upper bound is induced (?). Then,
 188 one can analyze capture-recapture models by adding $M - n$ all-zero encounter
 189 histories to the data set and regarding the augmented data set, essentially, as a
 190 site-occupancy data set.

191 Thus, the heuristic motivation of data augmentation is to fix the size of the
 192 data set by adding *too many* all-zero encounter histories to create the data set
 193 shown in the right panel of Table 3.3 - and then analyze the augmented data
 194 set using an occupancy type model which includes both “unoccupied sites” as
 195 well as “occupied sites” at which detections did not occur. We call these $M - n$
 196 all-zero histories “potential individuals” because they exist to be recruited (in
 197 a non-biological sense) into the population, for example during an analysis by
 198 MCMC.

199 To analyze the augmented data set, we recognize that it is a zero-inflated
 200 version of the known- N data set. That is, some of the augmented all-zeros are
 201 sampling zeros (corresponding to actual individuals that were missed) and some
 202 are “structural” zeros, which do not correspond to individuals in the population.
 203 For a basic closed-population model, the resulting likelihood under data aug-
 204 mentation - that is, for the data set of size M - is a simple zero-inflated binomial
 205 likelihood. The zero-inflated binomial model can be described “hierarchically”,
 206 by introducing a set of binary latent variables, z_1, z_2, \dots, z_M , to indicate whether
 207 each individual i is ($z_i = 1$) or is not ($z_i = 0$) a member of the population of
 208 N individuals exposed to sampling. We assume that $z_i \sim \text{Bern}(\psi)$ where ψ is
 209 the probability that an individual in the data set of size M is a member of the
 210 sampled population - in the sense that $1 - \psi$ is the probability of realizing a
 211 “structural zero” in the augmented data set. The zero-inflated binomial model
 212 which arises under data augmentation can be formally expressed by the following
 213 set of assumptions:

$$\begin{aligned}
y_i|z_i = 1 &\sim \text{Bin}(K, p) \\
y_i|z_i = 0 &\sim \delta(0) \\
z_i &\stackrel{iid}{\sim} \text{Bern}(\psi) \\
\psi &\sim \text{Unif}(0, 1) \\
p &\sim \text{Unif}(0, 1)
\end{aligned}$$

for $i = 1, \dots, M$, where $\delta(0)$ is a point mass at $y = 0$.

We note that N is no longer an explicit parameter of this model. Instead, we estimate ψ and functions of the latent variables. In particular, under the assumptions of the zero-inflated model, $z_i \stackrel{iid}{\sim} \text{Bern}(\psi)$; therefore, N is a function of these latent variables:

$$N = \sum_{i=1}^M z_i.$$

Further, we note that the latent z_i parameters can be removed from the model by integration, in which case the joint probability of the data is

$$\Pr(y_1, \dots, y_M | p, \psi) = \prod_{i=1}^M \psi \text{Bin}(y_i | K, p) + I(y_i = 0)(1 - \psi) \quad (3.2)$$

Which can be maximized directly to obtain the MLEs of the structural parameters ψ and p or those of other more complex models (e.g., see ?). We could estimate these parameters and then use them to obtain an estimator of N using the so-called “Best unbiased predictor” (see ?).

3.2.2 Model M_0 in BUGS

For model M_0 in which we can aggregate the encounter data to individual-specific encounter frequencies, the augmented data are given by the vector of frequencies $(y_1, \dots, y_n, 0, 0, \dots, 0)$. The zero-inflated model of the augmented data combines the model of the latent variables, $z_i \sim \text{Bern}(\psi)$ with the conditional-on- z binomial model:

$$\begin{aligned}
y_i|z_i = 0 &\sim \delta(0) \\
y_i|z_i = 1 &\sim \text{Bin}(K, p)
\end{aligned}$$

It is convenient to express the conditional-on- z observation model concisely as:

$$y_i|z_i \sim \text{Bin}(K, pz_i)$$

Thus, if $z_i = 0$ then the success probability of the binomial distribution is identically 0 whereas, if $z_i = 1$, then the success probability is p . This is useful in describing the model in the **BUGS** language, as shown below. Note the last line of the model specification here provides the expression for computing N from the data augmentation variables z_i .

Table 3.3: Hypothetical occupancy data set (left), capture-recapture data in standard form (center), and capture-recapture data augmented with all-zero capture histories (right).

Occupancy data				Capture-recapture				Augmented C-R			
site	k=1	k=2	k=3	ind	k=1	k=2	k=3	ind	k=1	k=2	k=3
1	0	1	0	1	0	1	0	1	0	1	0
2	1	0	1	2	1	0	1	2	1	0	1
3	0	1	0	.	0	1	0	3	1	0	1
4	1	0	1	.	1	0	1	4	1	0	1
5	0	1	1	.	0	1	1	5	1	0	1
.	0	1	1	.	0	1	1	.	0	1	1
.	1	1	1	.	1	1	1	.	0	1	1
.	1	1	1	.	1	1	1	.	1	1	1
.	1	1	1	.	1	1	1	.	1	1	1
n	1	1	1	n	1	1	1	n	1	1	1
.	0	0	0					.	0	0	0
.	0	0	0					.	0	0	0
	0	0	0						0	0	0
	0	0	0						0	0	0
	0	0	0						0	0	0
	0	0	0					N	0	0	0
.	0	0	0					.	0	0	0
.	0	0	0					.	0	0	0
M	0	0	0					.	0	0	0
							
							
							
								M	0	0	0

```

237 p ~ dunif(0,1)
238 psi~dunif(0,1)
239
240 # nind = number of individuals captured at least once
241 # nz = number of uncaptured individuals added for PX-DA
242 for(i in 1:(nind+nz)) {
243   z[i]~dbern(psi)
244   mu[i]<-z[i]*p
245   y[i]~dbin(mu[i],K)
246 }
247
248 N<-sum(z[1:(nind+nz)])

```

249 Specification of a more general model in terms of the individual encounter
 250 observations y_{ik} is not much more difficult than for the individual encounter
 251 frequencies. We define the observation model by a double loop and change the
 252 indexing of things accordingly, i.e.,

```

253 for(i in 1:(nind+nz)) {
254   z[i]~dbern(psi)
255   for(k in 1:K){
256     mu[i,k]<-z[i]*p
257     y[i,k]~dbin(mu[i,k],1)
258   }
259 }

```

260 In this manner, it is straightforward to incorporate covariates on p (see discus-
 261 sion of this below and also chapt. 8 (REF XYZ) and consider other extensions.

262 3.2.3 Formal development of data augmentation

263 Use of DA for solving inference problems with unknown N can be justified as
 264 originating from the choice of uniform prior on N . The $\text{Unif}(0, M)$ prior for N
 265 is innocuous in the sense that the posterior associated with this prior is equal
 266 to the likelihood for sufficiently large M . One way of inducing the $\text{Unif}(0, M)$
 267 prior on N is by assuming the following hierarchical prior:

$$\begin{aligned}
 N &\sim \text{Bin}(M, \psi) \\
 \psi &\sim \text{Unif}(0, 1)
 \end{aligned}
 \tag{3.3}$$

268 which includes a new model parameter ψ . This parameter denotes the prob-
 269 ability that an individual in the super-population of size M is a member of
 270 the population of N individuals exposed to sampling. The model assumptions,
 271 specifically the multinomial model (eq. XYZ) and eq. 3.3, may be combined to
 272 yield a reparameterization of the conventional model that is appropriate for the
 273 augmented data set of known size M :

$$(n_1, n_2, \dots, n_K) \sim \text{Multin}(M, \psi\pi(1), \psi\pi(2), \dots, \psi\pi(K))
 \tag{3.4}$$

274 This arises by removing N from Eq. multinomial XYZ by integrating over the
 275 binomial prior distribution for N . Thus, the models we analyze under data
 276 augmentation arise formally by removing the parameter N from the ordinary
 277 model - the model conditional on N - by integrating over a binomial prior
 278 distribution for N .

279 Note that the $M - n$ unobserved individuals in the augmented data set
 280 have probability $\psi\pi(0) + (1 - \psi)$, indicating that these unobserved individuals
 281 are a mixture of individuals that are sampling zeros ($\psi\pi_0$, and belong to the
 282 population of size N) and others that are “structural zeros” (occurring in the
 283 augmented data set with probability $1 - \psi$). In Eq. 3.4 N has been eliminated as
 284 a formal parameter of the model by marginalization (integration) and replaced
 285 with the new parameter ψ , which we will call the “data augmentation param-
 286 eter.” However, the full likelihood containing both N and ψ can be analyzed
 287 (see ?).

288 3.2.4 Remarks on Data Augmentation

289 Data augmentation may seem like a strange and mysterious black-box, and
 290 likely it is unfamiliar to most people even those with extensive experience with
 291 capture-recapture models. However, it really is a formal reparameterization of
 292 capture-recapture models in which N is removed from the ordinary (conditional-
 293 on- N) model by integration. In the case of Model M0, data augmentation pro-
 294 duces the zero-inflated binomial which is distinct from the original observation
 295 model, but only in the sense that it embodies, explicitly, the $\text{Unif}(0, M)$ prior
 296 for N . Choice of M might be cause for some concern related to potential sen-
 297 sitivity to choice of M . The guiding principle is that it should be chosen large
 298 enough so that the posterior for N is not truncated, but no larger because large
 299 values entail more computational burden. It seems likely that the properties of
 300 the Markov chains should be affected by M and so some optimality might exist
 301 (?), as in occupancy models (?). Formal analysis of this is required.

302 We emphasize the motivation for data augmentation being that it produces a
 303 data set of fixed size, so that the parameter dimension in any capture-recapture
 304 model is also fixed. As a result, MCMC is a relatively simple proposition us-
 305 ing standard Gibbs Sampling. Consider the simplest context - analyzing Model
 306 M0 using the occupancy model. In this case, DA converts Model M0 to a ba-
 307 sic occupancy model and the parameters p and ψ have known full-conditional
 308 distributions (in fact, beta distributions) that can be sampled from directly.
 309 Furthermore, the data augmentation variables - the latent data augmentation
 310 variables z , can be sampled from Bernoulli full conditionals. MCMC is not
 311 too much more difficult for complicated models - sometimes the hyperparam-
 312 eters need to be sampled using a Metropolis-Hastings step, but nothing more
 313 sophisticated than that is required.

314 There are other approaches to analyzing models with unknown N , using re-
 315 versible jump MCMC (RJMCMC) or other so-called “trans-dimensional” (TD)

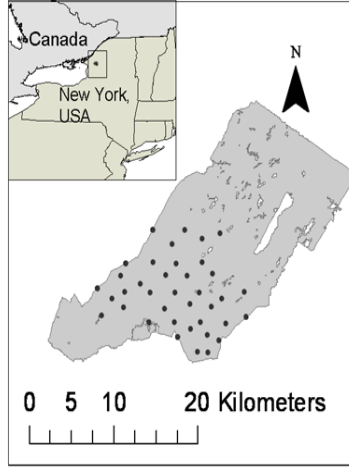


Figure 3.1: Fort Drum study area and hair snare locations.

algorithms² (???). What distinguishes DA from RJMCMC and related TD methods is that DA is used to create a distinctly new model that is unconditional on N and we (usually) analyze the unconditional model. The various TD/RJMCMC approaches seek to analyze the conditional-on- N model in which the dimensional of the parameter space is a variable function of N . TD/RJMCMC approaches might appear to have the advantage that one can model N explicitly or consider alternative priors for N . However, despite that N is removed as an explicit parameter in DA, it is possible to develop hierarchical models that involve structure on N (??) which we consider in chapt. XYZ.

3.2.5 Example: Black Bear Study on Fort Drum

To illustrate the analysis of Model M0 using data augmentation, we use a data set collected at Fort Drum Military Installation in upstate New York by the Department of Defense, Cornell University and colleagues. These data have been analyzed in various forms by ??, and ?. The specific data used here are encounter histories on 47 individuals obtained from an array of 38 baited “hair snares” (Fig. 3.1) during June and July 2006. Barbed wire traps were baited and checked for hair samples each week for eight weeks, thus we have $K = 8$ sample intervals. The data are provided on the Web Supplement and the analysis can be set up and run as follows. Here, the data were augmented with $M - n = 128$ ($M = 175$) all-zero encounter histories.

```
# Consider adding comments to your code.
## Good idea. This will be done in final draft
```

²Look these citations up in Royle-Dorazio EURING paper

```

339 trapmat<-read.csv("FDtrapmat.csv")
340 bearArray<-source("FDbeararray.R")$value
341 nind<-dim(bearArray)[1]
342 K<-dim(bearArray)[3]
343 ntraps<-dim(bearArray)[2]
344
345 M=175
346 nz<-M-nind
347
348 Xaug <- array(0, dim=c(M,ntraps,K))
349 Xaug[1:nind,,]<-bearArray
350 y<- apply(Xaug,c(1,3),sum)
351 y[y>1]<-1
352 ytot<-apply(y,1,sum) # total encounters out of K

```

Note that the raw data, \mathbf{y} , is an $M \times K$ array of individual encounter events (i.e., $y_{ik} = 1$ if individual i was encountered in any trap and 0 otherwise). For $i = 48, \dots, 175$, $y_{ik} = 0$ as these are augmented observations. For Model M0 it is sufficient to reduce the data to individual encounter frequencies which we have labeled \mathbf{y}_{tot} above. The BUGS model file along with commands to fit the model are as follows:

```

359 set.seed(2013) # to obtain the same results each time
360 data0<-list(y=y,M=M,K=K)
361 params0<-list('psi','p','N')
362 zst=c(rep(1,nind),rbinom(M-nind, 1, .5))
363 inits = function() {list(z=zst, psi=runif(1), p=runif(1)) }
364
365 cat("
366 model {
367
368   psi~dunif(0, 1)
369   p~dunif(0,1)
370
371   for (i in 1:M){
372     z[i]~dbern(psi)
373     for(k in 1:K){
374       tmp[i,k]<-p*z[i]
375       y[i,k]~dbin(tmp[i,k],1)
376     }
377   }
378   N<-sum(z[1:M])
379 }
380 ",file="modelM0.txt")
381
382 fit0 = bugs(data0, inits, params0, model.file="modelM0.txt",
383             n.chains=3, n.iter=2000, n.burnin=1000, n.thin=1,
384             debug=TRUE,working.directory=getwd())

```

The posterior summary statistics from this analysis are as follows:


```

386 > print(fit0,digits=2)
387 Inference for Bugs model at "modelM0.txt", fit using WinBUGS,
388 3 chains, each with 2000 iterations (first 1000 discarded)
389 n.sims = 3000 iterations saved
390      mean      sd   2.5%    25%    50%    75%   97.5% Rhat n.eff
391 psi      0.29  0.04   0.22   0.26   0.29   0.31   0.36    1  3000
392 p        0.30  0.03   0.25   0.28   0.30   0.32   0.35    1  3000
393 N        49.94 1.99  47.00  48.00  50.00  51.00  54.00    1  3000
394 deviance 489.05 11.28 471.00 480.45 488.80 495.40 513.70    1  3000
395
396 [... some output deleted ...]

```

WinBUGS did well in choosing an MCMC algorithm for this model – we have $\hat{R} = 1$ for each parameter, and an effective sample size of 3000, equal to the total number of posterior samples. We see that the posterior mean of N under this model is 49.94 and a 95% posterior interval is (48, 54). We revisit these data later in the context of more complex models.

In order to obtain an estimate of density, D , we need an area to associate with the estimate of N , and commonly used procedures to conjure up such an area include buffering the trap array by the home range radius, often estimated by the mean maximum distance moved (MMDM)³, 1/2 MMDM (?) or directly from telemetry data (REF XXX NEED REF HERE XXXXX). Typically, the trap array is defined by the convex hull around the trap locations, and this is what we applied a buffer to. We computed the buffer by using an estimate of the mean female home range radius (2.19 km) estimated from telemetry studies (?) instead of using an estimate based on our relatively more sparse recapture data⁴. For the Fort Drum study, the convex hull has area 157.135 km^2 , and the buffered convex hull has area 277.011 km^2 . To create this we used functions contained in the **R** package **rgeos** and created a utility function **bcharea** which is in our **R** package **scrbook**. The commands are as follows:

```

415 library("rgeos")
416
417 bcharea<-function(buff,traplocs){
418   p1<-Polygon(rbind(traplocs,traplocs[1,]))
419   p2<-Polygons(list(p1=p1),ID=1)
420   p3<-SpatialPolygons(list(p2=p2))
421   p1ch<-gConvexHull(p3)
422   bp1<-gBuffer(p1ch, width=buff)
423   plot(bp1, col='gray')
424   plot(p1ch, border='black', lwd=2, add=TRUE)
425   gArea(bp1)
426 }
427
428 bcharea(2.19,traplocs=trapmat)

```

³really MMDM? How can this be an estimate of the home range radius? Reference for this?

⁴BETH: Why?

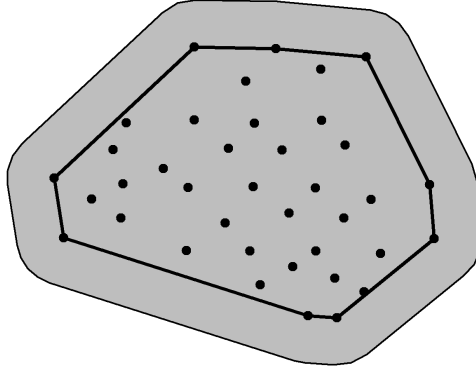


Figure 3.2: buffered convex hull of the bear hair snare array

429 The resulting buffered convex hull is shown in Fig. 3.2.

430 To conjure up a density estimate under model M_0 , we compute the appro-
 431 priate posterior summary of N and the prescribed area (277.011 km^2):

```

432 > summary(fit0$sims.list$N/277.011)
433   Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
434 0.1697 0.1733 0.1805 0.1803 0.1841 0.2130
435
436 > quantile(fit0$sims.list$N/277.011,c(0.025,0.975))
437      2.5%      97.5%
438 0.1696684 0.1949381
```

439 which yields a density estimate of about 0.18 ind/km^2 , and a 95% Bayesian
 440 confidence interval of $(0.170, 0.195)$.

441 The obvious limitation of this estimate and, indeed, of the whole process, is
 442 that our choice of “area” is completely subjective - which area should we use?
 443 MMDM? One-half MMDM? Estimated from telemetry data? And, furthermore,
 444 how certain are we of this area? Can we quantify our uncertainty about this
 445 quantity? More important, what exactly is the meaning of this area and, in this
 446 context, how do we gauge bias and/or variance of “estimators” of it? (i.e., what
 447 is it estimating?).

3.3 Temporally varying and behavioral effects

The purpose of this chapter is mainly to emphasize the central importance of the binomial model in capture-recapture and so we have considered models for individual encounter frequencies - the number of times individuals are captured out of K samples. Sometimes it is not acceptable to aggregate the encounter data for each individual - such as when encounter probability varies over time among samples. A type of time-varying response that seems relevant in most capture-recapture studies is “effort” such as amount of search time, number of observers, or trap effort or when p depends on date (??). A common situation is that in which there exists a “behavioral response” to trapping (even if the animal is not physically trapped).

Behavioral response is an important concept in carnivore studies because individuals might learn to come to baited traps or avoid traps due to trauma related to being encountered. There are a number of ways to parameterize a behavioral response to encounter. The distinction between persistent and ephemeral was made by ? who considered a general behavioral response model of the form:

$$\text{logit}(p_{ik}) = \alpha_0 + \alpha_1 * y_{i,k-1} + \alpha_2 x_{ik}$$

where x_{ik} is a covariate indicator variable of previous capture (i.e., $x_{ik} = 1$ if captured in any previous period). Therefore, encounter probability changes depending on whether an individual was captured in the immediate previous period (ephemeral behavioral response) or in any previous period (persistent behavioral response). The former probably models a behavioral response due to individuals moving around their territory relatively slowly over time and the latter probably accommodates trap happiness due to baiting or shyness due to trauma. In spatial capture-recapture models it makes sense to consider a local behavioral response that is trap-specific (?) - that is, the encounter probability is modified for individual traps depending on previous capture in specific traps.

Models with temporal effects are easy to describe in the **BUGS** language and analyze and we provide a number of examples in chapt. 8. XXXXX ??
XXXXX

3.4 Models with individual heterogeneity

Here we consider models with individual-specific encounter probability parameters, say p_i , which we model according to some probability distribution, $g(\theta)$. We denote this basic model assumption as $p_i \sim g(\theta)$. This type of model is similar in concept to extending a GLM to a GLMM but in the capture-recapture context N is unknown. The basic class of models is often referred to as “Model M_h ” but really this is a broad class of models, each being distinguished by the specific distribution assumed for p_i . There are many different varieties of Model M_h including parametric and various putatively non-parametric approaches (???). One important practical matter is that estimates of N can be extremely sensitive to the choice of heterogeneity model (???). Indeed, ? showed that in some

cases it's possible to find models that yield precisely the same expected data, yet produce wildly different estimates of N . In that sense, N for most practical purposes is not identifiable across classes of mixture models, and this should be understood before fitting any such model. One solution to this problem is to seek to model explicit factors that contribute to heterogeneity, e.g., using individual covariate models (See 3.5 below). Indeed, spatial capture-recapture models seek to do just that, by modeling heterogeneity due to the spatial organization of individuals in relation to traps or other encounter mechanism. For additional background and applications of Model M_h see ?, chapt. 6 and ?, chapt. 6.

Model M_h has important historical relevance to spatial capture-recapture situations (?) because investigators recognized that the juxtaposition of individuals with the array of trap locations should yield heterogeneity in encounter probability, and thus it became common to use some version of Model M_h in spatial trapping arrays to estimate N . While this doesn't resolve the problem of not knowing the area relevant to N , it does yield an estimator that accommodates the heterogeneity in p induced by the spatial aspect of capture-recapture studies.

To see how this juxtaposition induces heterogeneity, we have to understand the relevance of movement in capture-recapture models. Imagine a quadrat that can be uniformly searched by a crew of biologists for some species of reptile (see ?). Figure 3.3 shows a sample quadrat searched repeatedly over a period of time. Further, suppose that species exhibits some sense of spatial fidelity in the form of a home range or territory, and individuals move about their home range (home range centroids are given by the blue dots) in some kind of random fashion. It is natural to think about it in terms of a movement process and sometimes that movement process can be modeled explicitly using hierarchical models (??). Heuristically, we imagine that each individual in the vicinity of the study area is liable to experience variable exposure to encounter due to the overlap of its home range with the sampled area - essentially the long-run proportion of times the individual is within the sample plot boundaries, say ϕ . We might model the exposure of an individual to capture by supposing that $z_i = 1$ if individual i is available to be captured (i.e., within the survey plot) during any sample, and 0 otherwise. Then, $\Pr(z_i = 1) = \phi$. In the context of spatial studies, it is natural that ϕ should depend on *where* an individual lives, i.e., it should be individual-specific ϕ_i (?). This system describes, precisely, that of "random temporary emigration" (?) where ϕ_i is the individual-specific probability of being "available" for capture.

Conceptually, SCR models aim to deal with this problem of variable exposure to sampling due to movement in the proximity of the trapping array explicitly and formally with auxiliary spatial information. If individuals are detected with probability p_0 , *conditional* on $z_i = 1$, then the marginal probability of detection of individual i is

$$p_i = p_0 \phi_i$$

so we see clearly that individual heterogeneity in encounter probability is in-

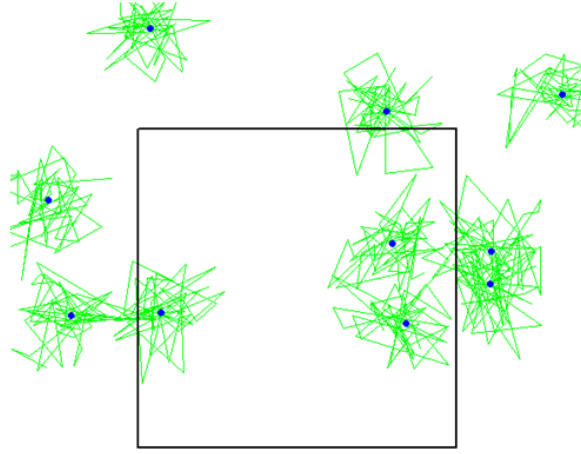


Figure 3.3: A quadrat searched for lizards and the locations of each lizard over some period of time.

533 duced as a result of the juxtaposition of individuals (i.e., their home ranges)
 534 with the sample apparatus and the movement of individuals about their home
 535 range.

536 We will work with a specific type of Model M_h here, that in which we extend
 537 the basic binomial observation model of Model M_0 so that

$$\text{logit}(p_i) = \mu + \eta_i$$

538 where

$$\eta_i \sim \text{Normal}(0, \sigma_p^2)$$

539 We could as well write

$$\text{logit}(p_i) \sim \text{Normal}(\mu, \sigma_p^2)$$

540 This “logit-normal mixture” was analyzed by ? and elsewhere. It is a natural
 541 extension of the basic model with constant p , as a mixed GLMM, and similar
 542 models occur throughout statistics. It is also natural to consider a beta prior
 543 distribution for p_i (?) and so-called “finite-mixture” models are also popular
 544 (??).

545 3.4.1 Analysis of Model M_h

546 If N is known, it is worth taking note of the essential simplicity of Model M_h
 547 as a binomial GLMM. This is a type of model that is widely applied in just

about every scientific discipline and using standard methods of inference based either on integrated likelihood (??) which we discuss in chapt. 6 or standard Bayesian methods. However, because N is not known, inference is somewhat more challenging. We address that here using Bayesian analysis based on data augmentation (DA). Although we use data augmentation in the context of Bayesian methods here, we note that heterogeneity models formulated under DA are easily analyzed by conventional likelihood methods as zero-inflated binomial mixtures (?) and more traditional analysis of model M_h based on integrated likelihood, without using data augmentation, has been considered by ?, ?, and others.

As with model M_0 , we have the Bernoulli model for the zero-inflation variables: $z_i \sim \text{Bern}(\psi)$ and the model of the observations expressed conditional on the latent variables z_i . For $z_i = 1$, we have a binomial model with individual-specific p_i :

$$y_i|z_i=1 \sim \text{Bin}(K, p_i)$$

and otherwise $y_i|z_i=0 \sim \delta(0)$. Further, we prescribe a distribution for p_i . Here we assume

$$\text{logit}(p_i) \sim \text{Normal}(\mu, \sigma^2)$$

The basic **BUGS** description for this model, assuming a $\text{Unif}(0, 1)$ prior for $p_0 = \text{logit}^{-1}(\mu)$, is given as follows:

```

model{
  p0 ~ dunif(0,1)      # prior distributions
  mup<- log(p0/(1-p0))
  taup~dgamma(.1,.1)
  psi~dunif(0,1)
  for(i in 1:(nind+nz)){
    z[i]~dbern(psi)    # zero inflation variables
    lp[i] ~ dnorm(mup,taup) # individual effect
    logit(p[i])<-lp[i]
    mu[i]<-z[i]*p[i]
    y[i]~dbin(mu[i],J) # observation model
  }
  N<-sum(z[1:(nind+nz)]) # N is a derived parameter
}
```

3.4.2 Analysis of the Fort Drum data

The logit-normal heterogeneity model was fitted to the bear data from the Fort Drum study, and we used data augmentation to produce a data set of $M = 500$ individuals. We ran the model using **JAGS** with the instructions given as follows⁵.

⁵For WinBUGS, should provide starts for lp and sigma or sometimes WinBUGS breaks

```

588 [... get data as before ....]
589
590 set.seed(2013)
591
592 cat("
593 model{
594   p0 ~ dunif(0,1)          # prior distributions
595   mup<- log(p0/(1-p0))
596   taup~dgamma(.1,.1)
597   sigmap<-sqrt(1/taup)
598   psi~dunif(0,1)
599
600   for(i in 1:(nind+nz)){
601     z[i]~dbern(psi)        # zero inflation variables
602     lp[i] ~ dnorm(mup,taup) # individual effect
603     logit(p[i])<-lp[i]
604     mu[i]<-z[i]*p[i]
605     y[i]~dbin(mu[i],K)    # observation model
606   }
607
608   N<-sum(z[1:(nind+nz)])
609 }
610 ",file="modelMh.txt")
611
612 library("rjags")
613 jm<- jags.model("modelMh.txt", data=data1, inits=inits, n.chains=4,
614                n.adapt=1000)
615 jout<- coda.samples(jm, params1, n.iter=50000, thin=1)

```

CHANGE THIS TO RUN SIGMA DUNIF(0,5) PRIOR INSTEAD OF
TAUY

**ANDY IS WORKING THIS SECTION RIGHT NOW. KEY IS-
SUE IS THAT BEAR DATA HAVE VERY LONG RIGHT TAIL.
PSSIBLY NOT EVEN IDENTIFIABLE FOR LOGIT-NORMAL MODEL.
NEED TO RUN WINBUGS AND JAGS FOR M=500 AND RUN
A 200K RUN AND THEN MAYBE A 500K RUN TO SEE HOW
THINGS LOOK. THEN RUN MY R CODE BELOW FOR 5 MIL-
LION ITTERS OR SOME bs like that. I'm not sure if this is a teaching
moment (Link 2003) or if we need a different example here!**

This produces the posterior distribution for N shown in Fig. 3.4. Posterior summaries of parameters are given as follows:

```

628 > summary(jout)
629 Iterations = 1001:201000
630 Thinning interval = 1
631 Number of chains = 4
632 Sample size per chain = 2e+05
633
634 1. Empirical mean and standard deviation for each variable,
635    plus standard error of the mean:

```

636						
637		Mean	SD	Naive SE	Time-series SE	
638	N	108.63259	52.53176	5.873e-02	2.077726	
639	p0	0.08615	0.05919	6.618e-05	0.001950	
640	psi	0.21841	0.10615	1.187e-04	0.004141	
641	sigmap	1.94096	0.51014	5.703e-04	0.018244	
642						
643	2. Quantiles for each variable:					
644						
645		2.5%	25%	50%	75%	97.5%
646	N	59.00000	77.00000	93.00000	121.0000	261.0000
647	p0	0.00418	0.03852	0.07657	0.1240	0.2210
648	psi	0.11230	0.15373	0.18920	0.2457	0.5241
649	sigmap	1.11906	1.57643	1.87752	2.2386	3.1166

650 We used $M = 500$ for this analysis and we note that while the posterior
651 mass of N is concentrated away from this upper bound (Fig. 3.4), the posterior
652 has an extremely long right tail, with some posterior values at the upper bound
653 $N = 500$. Maybe or maybe not sufficient data augmentation. The model runs
654 effectively in **WinBUGS** but sometimes with apparently inefficient mixing for
655 reasons that may be related to bad starting values. In some cases this was
656 resolved if we supplied starting values for the $\text{logit}(p_i)$ parameters and τ .

657 **to do:** insert final results. longer run. more data augmentation. compare
658 with winbugs.

659 The posterior mode compares well with the MLE which we obtained using
660 the **R** code contained in Panel 6.1 of ?. The MLE of $\log(n_0)$, the logarithm of
661 the number of uncaptured individuals, is $\log(n_0) = 3.86$ and therefore the MLE
662 is $\hat{N} = \exp(3.86) + 47 = 94.47$ consistent with the apparent mode in Fig. 3.4.
663 ⁶ To convert this to density we use the buffered area as computed above (255.3
664 km^2)⁷ and perform the required summary analysis on the posterior samples
665 of N , which results in about 0.37 individuals/ km^2 . The reader should carry
666 out this analysis to confirm the estimates, and also obtain the 95% confidence
667 interval.

668 3.4.3 Building your own MCMC algorithm

669 For fun, we construct our own MCMC algorithm using a Metropolized Gibbs
670 sampler for Model M_h . In chapter 7 we devise MCMC algorithms for spatial
671 capture-recapture models and the basic conceptual and technical considerations
672 are entirely analogous to Model M_h .

673 To begin, we first collect all of our model components which are as follows:
674 $[y_i|p_i, z_i]$, $[p_i|\mu_p, \sigma_p]$, and $[z_i|\psi]$ for $each\ i = 1, 2, \dots, M$ and then prior dis-
675 tributions $[\mu_p]$, $[\sigma_p]$ and $[\psi]$. The joint posterior distribution of all unknown

⁶We note that the result is inconsistent with Gardner et al. (2009) who reported an MLE of 104.1 ($\text{density} = 0.437\text{inds}/\text{km}^2$) although we do not know the reason for this at the present time.

⁷WRONG #

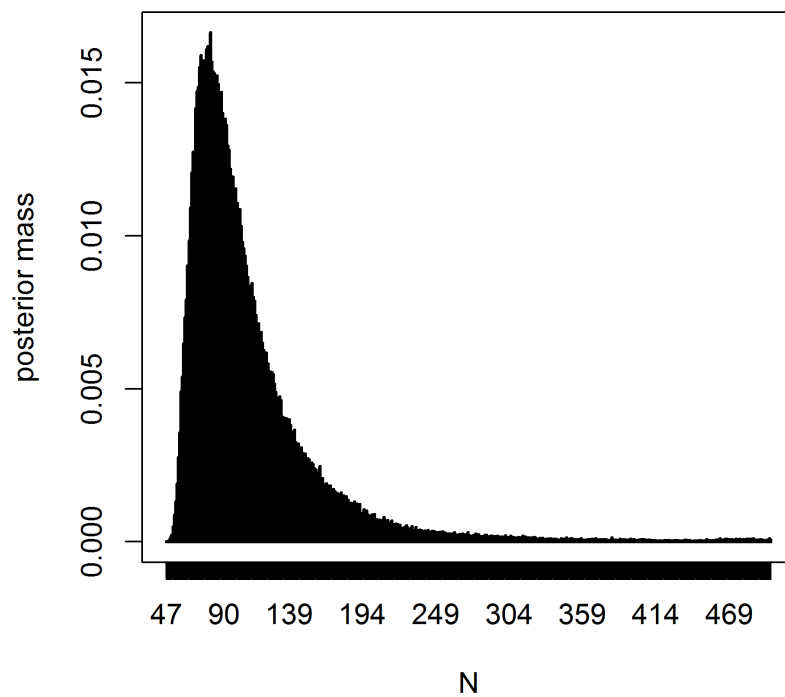


Figure 3.4: Posterior of N for Fort Drum bear study data under the logit-normal version of model M_h . From WinBUGS output. 200k samples.

quantities in the model is proportional to the joint distribution of all elements y_i, p_i, z_i and also the prior distributions of the prior parameters:

$$\left\{ \prod_{i=1}^M [y_i | p_i, z_i] [p_i | \mu_p, \sigma_p] [z_i | \psi] \right\} [\mu_p, \sigma_p, \psi]$$

For prior distributions, we assume that μ_p, σ_p, ψ are mutually independent and for μ_p and σ_p we use improper uniform priors, and $\psi \sim \text{Unif}(0, 1)$. Note that the likelihood contribution for each individual, when conditioned on p_i and z_i , does not depend on ψ, μ_p , or σ_p . As such, the full-conditionals for the structural parameters ψ only depends on the collection of data augmentation variables z_i , and that for μ_p and σ_p will only depends on the collection of latent variables $p_i; i = 1, 2, \dots, M$. The full conditionals for all the unknowns are as follows:

(1) For p_i :

$$[p_i | y_i, \mu_p, \sigma_p, z_i = 1] \propto [y_i | p_i] [p_i | \mu_p, \sigma_p^2] \text{ if } z_i = 1 \\ [p_i | \mu_p, \sigma_p] \text{ if } z_i = 0$$

(2) for z_i :

$$z_i | \cdot \propto [y_i | z_i * p_i] \text{Bern}(z_i | \psi)$$

(3) For μ_p :

$$[\mu_p | \cdot] \sim \prod_i [p_i | \cdot] * \text{const}$$

(4) For σ_p :

$$[\sigma_p | \cdot] \sim \prod_i [p_i | \cdot] * \text{const}$$

(5) For ψ :

$$\psi | \cdot \sim \text{Beta}(1 + \sum z_i, 1 + M - \sum z_i)$$

What we've done here is identify each of the full conditional distributions in sufficient detail to toss them into our Metropolis-Hastings algorithm. With the exception of ψ which has a convenient analytic solution – it is a beta distribution which we can easily sample directly. In truth, we could also sample μ_p and σ_p^2 directly with certain choices of prior distributions. For example, if $\mu_p \sim \text{Normal}(0, 1000)$ then the full conditional for μ_p is also normal, etc.. We implement an MCMC algorithm for this model in the following block of **R** code. The basic structure is: initialize the parameters and create any required output or intermediate “holders”, and then begin the main MCMC loop which, in this case, generates 100000 samples.

```
## obtain the bear data by executing the previous data grabbing
## function
temp<-getdata()
```

```

705 M<-temp$M
706 K<-temp$K
707 ytot<-temp$ytot
708
709
710 ###
711 ### MCMC algorithm for Model Mh
712
713 out<-matrix(NA,nrow=100000,ncol=4)
714 dimnames(out)<-list(NULL,c("mu","sigma","psi","N"))
715 lp<- rnorm(M,-1,1)
716 p<-expit(lp)
717 mu<- -1
718 p0<-exp(mu)/(1+exp(mu))
719 sigma<- 1
720 psi<- .5
721 z<-rbinom(M,1,psi)
722 z[ytot>0]<-1
723
724 for(i in 1:100000){
725
726   ### update the logit(p) parameters
727   lpc<- rnorm(M,lp,1) # 0.5 is a tuning parameter
728   pc<-expit(lpc)
729   lik.curr<-log(dbinom(ytot,K,z*p)*dnorm(lp,mu,sigma))
730   lik.cand<-log(dbinom(ytot,K,z*pc)*dnorm(lpc,mu,sigma))
731   kp<- runif(M) < exp(lik.cand-lik.curr)
732   p[kp]<-pc[kp]
733   lp[kp]<-lpc[kp]
734
735   p0c<- rnorm(1,p0,.05)
736   if(p0c>0 & p0c<1){
737     muc<-log(p0c/(1-p0c))
738     lik.curr<-sum(dnorm(lp,mu,sigma,log=TRUE))
739     lik.cand<-sum(dnorm(lp,muc,sigma,log=TRUE))
740     if(runif(1)<exp(lik.cand-lik.curr)) {
741       mu<-muc
742       p0<-p0c
743     }
744   }
745
746   sigmac<-rnorm(1,sigma,.5)
747   if(sigmac>0){
748     lik.curr<-sum(dnorm(lp,mu,sigma,log=TRUE))
749     lik.cand<-sum(dnorm(lp,mu,sigmac,log=TRUE))
750     if(runif(1)<exp(lik.cand-lik.curr))

```

```

751   sigma<-sigmac
752 }
753
754 ### update the z[i] variables
755 zc<- ifelse(z==1,0,1) # candidate is 0 if current = 1, etc..
756 lik.curr<- dbinom(ytot,K,z*p)*dbinom(z,1,psi)
757 lik.cand<- dbinom(ytot,K,zc*p)*dbinom(zc,1,psi)
758 kp<- runif(M) < (lik.cand/lik.curr)
759 z[kp]<- zc[kp]
760
761 psi<-rbeta(1, sum(z) + 1, M-sum(z) + 1)
762
763 out[i,]<- c(mu,sigma,psi,sum(z))
764 }

```

765 **Remarks:** (1) for parameters with bounded support, i.e., σ_p and p_0 , we
766 are using a random walk candidate generator but rejecting draws outside of the
767 parameter space. (2) We mostly use Metropolis-Hastings except for the data
768 augmentation parameter ψ which we sample directly from its full-conditional
769 distribution which is a beta distribution. (3) Even the latent data augmentation
770 variables z_i are updated using Metropolis-Hastings although they too can be
771 updated directly from their full-conditional.

772 3.4.4 Exercises related to model Mh

- 773 (1) Enclose the MCMC algorithm in an R function and provide arguments for
774 some of the parameters of the function that a user might wish to modify.
- 775 (2) Execute the function and compare the results to those generated from
776 WinBUGS in the previous section
- 777 (3) Note that the prior distribution for the “mean” parameter is given on
778 $p_0 = \exp(\mu)/(1 + \exp(\mu))$. Reformulate the algorithm with a flat prior on
779 μ and see what happens. Contemplate this.
- 780 (4) Using Bayes rule, figure out the full conditional for z_i so that you don’t
781 have to use MH for that one. It might be more efficient. Is it?

782 3.5 Individual Covariate Models: Toward Spa- 783 tial Capture-Recapture

784 A standard situation in capture-recapture models is when an individual covariate is measured, and this covariate is thought to influence encounter probability. As with other closed population models, we begin with the basic binomial observation model:

$$y_i \sim \text{Bin}(K, p_i)$$

and we assume also a model for encounter probability according to:

$$\text{logit}(p_i) = \alpha_0 + \alpha_1 x_i$$

Classical examples of covariates influencing detection probability are type of animal (juvenile/adult or male/female), a continuous covariate such as body mass (? , chapt. 6), or a discrete covariate such as group or cluster size. For example, in models of aerial survey data, it is natural to model detection probabilities as a function of the observation-level individual covariate, “group size” (???) .

Such “individual covariate models” are similar in structure to Model M_h , except that the individual effects are *observed* for the n individuals that appear in the sample. These models are important here because spatial capture-recapture models are precisely a form of individual covariate model, an idea that we will develop here and elsewhere. Specifically, they are such models, but where the individual covariate is a partially observed latent variable similar.. That is, unlike Model M_h , we do have some direct information about the latent variable, which comes from the spatial locations/distribution of individual recaptures. More on that later.

Traditionally, estimation of N in individual covariate models is achieved using methods based on ideas of unequal probability sampling (i.e., Horwitz-Thompson estimation), see ? and ?. An estimator of N is

$$\hat{N} = \sum_i \frac{1}{\tilde{p}_i}$$

where \tilde{p}_i is the probability that individual i appeared in the sample. That is, $\tilde{p}_i = \Pr(y_i > 0)$. In practice, \tilde{p}_i is estimated from the conditional-likelihood formed by the encounter histories. Namely,

$$\Pr(y_i | y_i > 0) = \Pr(y_i) / \Pr(y_i > 0)$$

where we substitute

$$\Pr(y_i > 0) = (1 - (1 - p_i)^K)$$

with

$$\text{logit}(p_i) = \alpha_0 + \alpha_1 x_i$$

Here we take a formal model-based approach to Bayesian analysis of such models using data augmentation (?). Classical likelihood analysis of the so-called “full likelihood” is covered in some detail by ?. For Bayesian analysis of individual covariate models, because the individual covariate is unobserved for the $N - n$ uncaptured individuals, we require a model to describe variation among individuals, essentially allowing the sample to be extrapolated to the population. For our present purposes, we consider a continuous covariate and we assume that it has a normal distribution:

$$x_i \sim \text{Normal}(\mu, \sigma^2)$$

Data augmentation can be applied directly to this class of models. In particular, reformulation of the model under DA yields a basic zero-inflated binomial model of the form:

$$\begin{aligned} z_i &\sim \text{Bern}(\psi) \\ y_i|z_i=1 &\sim \text{Bin}(K, p_i) \\ y_i|z_i=0 &\sim \delta(0) \end{aligned}$$

In addition, we assume that p_i is functionally related to a covariate x_i , e.g., by the logit model given above, and we assume a distribution for x_i appropriate for the context.

Fully spatial capture-recapture models essentially use this formulation with a latent covariate that is directly related to the individual detection probability (see next Section). As with the previous models, implementation is trivial in the BUGS language. The BUGS specification is very similar to that for model M_h , but we require the distribution of the covariate to be specified, along with priors for the parameters of that distribution.

3.5.1 Example: Location of capture as a covariate.

If we had a regular grid of traps over some closed geographic system then we imagine that the average location of capture would be a decent estimate (heuristically) of an individual's home range center. Intuitively some measure of typical distance from home range center to traps for an individual should be a decent covariate to explain heterogeneity in encounter probability, i.e., individuals with more exposure to traps should have higher encounter probabilities and vice versa. A version of this idea was put forth by ? (see also ?), but using the Huggins-Alho estimator and with covariate "distance to edge" of the trapping array. A limitation of this basic approach is that it does not provide a solution to the problem that the trap area is fundamentally ill-defined, nor does it readily accommodate the inherent and heterogeneous variation in this measured covariate. Here, we provide an example of this type of heuristically motivated approach using the fully model-based individual covariate model described above analyzed by data augmentation. We take a slightly different approach than that adopted by ?. By analyzing the full likelihood and placing a prior distribution on the individual covariate, we resolve the problem of having an ill-defined area over which the population size is distributed. After you read later chapters of this book, it will be apparent that SCR models represent a formalization of this heuristic procedure.

For our purposes here, we define $x_i = ||s_i - x_0||$ where s_i is the average encounter location of individual i and x_0 is the centroid of the trap array. Conceptually, individuals in the middle of the array should have higher probability of encounter and, as x_i increases, p_i should therefore decrease. We note that we have defined s_i in terms of a sample quantity - the observed mean - which is

ad hoc but maybe satisfactory under the circumstances. That said, for an expansive, dense trapping grid then we might expect the sample mean encounter location to be a good estimate of home range center but, clearly this is biased for individuals that live around the edge (or off) the trapping array. Regardless, it should be good enough for our present purposes of demonstrating this heuristically appealing application of an individual covariate model. A key point is that s_i is missing for each individual that is not encountered and thus so is x_i . Thus, it is a latent variable, or random effect, and we need therefore to specify a probability distribution for it. As a measurement of distance we know it must be positive-valued. Suppose further than we imagine no individual could have a home range radius larger than D_{max} . As such, we think a reasonable distribution for this individual covariate is

$$x_i \sim \text{uniform}(0, D_{max})$$

where D_{max} is a specified constant. In practice, people have used distance from edge of the trap array but that is less easy to define and compute.

Fort Drum Bear Study

We have to do a little bit of data processing to fit this individual covariate model to the Fort Drum data. To compute the average location of capture for each individual and the distance from the centroid of the trap array, we execute the following R instructions:

```
avg.s<-matrix(NA,nrow=nind,ncol=2)
for(i in 1:nind){
  tmp<-NULL
  for(j in 1:T){
    aa<-bearArray[i,,j]
    if(sum(aa)>0){
      aa<- trapmat[aa>0,]
      tmp<-rbind(tmp,aa)
    }
  }
  avg.s[i,]<-c(mean(tmp[,1]),mean(tmp[,2]))
}
Cx<-mean(trapmat[,1])
Cy<-mean(trapmat[,2])
avg.s<-rbind(avg.s,matrix(NA,nrow=nz,ncol=2))
xcent<- sqrt( (avg.s[,1]-Cx)^2 + (avg.s[,2]-Cy)^2)
```

To define the maximum distance (maxD) from the centroid, we use that of the farthest trap, and so maxD is computed as follows:

```
minx<- min(trapmat[,1]-Cx)
maxx<-max(trapmat[,1]-Cx)
```

```

895 miny<- min(trapmat[,2]-Cy)
896 maxy<- max(trapmat[,2]-Cy)
897 # most extreme point determines maxD
898 ul<- c(minx,maxy)
899 maxD<- sqrt( (ul[1]-0)^2 + (ul[2]-0)^2)

```

For the bear data the maxD was about 11.5 km. As such, the model described above will produce an estimate of the population size of bears within 11.5 units of the trap centroid⁸. The BUGS model specification and R commands to package the data and fit the model are as follows:

```

904 cat("
905 model{
906   p0 ~ dunif(0,1)          # prior distributions
907   mup<- log(p0/(1-p0))
908   psi~dunif(0,1)
909   beta~dnorm(0,.01)
910
911   for(i in 1:(nind+nz)){
912     xcent[i]~dunif(0,maxD)
913     z[i]~dbern(psi)        # DA variables
914     lp[i] <- mup + beta*xcent[i] # individual effect
915     logit(p[i])<-lp[i]
916     mu[i]<-z[i]*p[i]
917     y[i]~dbin(mu[i],K)    # observation model
918   }
919   N<-sum(z[1:(nind+nz)])
920 }
921 ",file="modelMcov.txt")
922 data2<-list(y=ytot,nz=nz,nind=nind,K=T,xcent=xcent,maxD=11.5)
923 params2<-list('p0','psi','N','beta')
924 inits = function() {list(z=z, psi=psi, p0=runif(1),beta=rnorm(1) ) }
925 fit2 = bugs(data2, inits, params2, model.file="modelMcov.txt",working.directory=getwd(),
926             debug=T, n.chains=3, n.iter=4000, n.burnin=1000, n.thin=4)

```

Posterior summaries are given in Table ?? XYZ, and the posterior distribution of N is given in Figure XYZ. It might be perplexing that the estimated N is much lower than obtained by model Mh but there is a good explanation for this, discussed subsequently. That issue notwithstanding, it is worth pondering how this model could be an improvement (conceptually or technically) over some other model/estimator including M0 and Mh considered previously. Well, for one, we have accounted formally for heterogeneity due to spatial location of individuals relative to exposure to the trap array, characterized by the centroid of the array. Moreover, we have done so using a model that is based on an explicit mechanism, as opposed to a phenomenological one such as Model Mh.

⁸To be convincing this might need a little bit of hand-holding

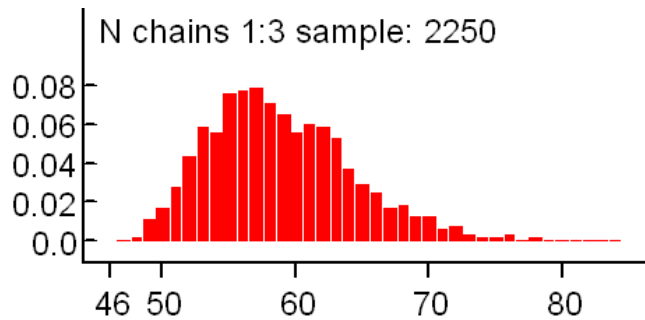


Figure 3.5: Needs a caption

Moreover, importantly, using our new model, *the estimated N applies to an explicit area which is defined by our prescribed value of $\max D$* . That is, this area is a fixed component of the model and the parameter N therefore has explicit spatial context, as the number of individuals with home range centers less than $\max D$ from the centroid of the trap array. As such, the implied “effective trap area”⁹ for any $\max D$ is that of a circle with radius $\max D$.

```
%% Not sure whether this should be a table or verbatim print-out
\begin{table}
\tabular{ccccccccc}
Node statistics
node mean sd MC error 2.5% median 97.5% start sample
N 58.89 5.483 0.2199 50.0 58.0 71.0 251 2250
beta -0.246 0.06087 0.003892 -0.3592 -0.2457 -0.126 251 2250
deviance 459.4 13.29 0.4496 435.7 458.4 487.8 251 2250
p0 0.5409 0.06817 0.004052 0.4072 0.544 0.6678 251 2250
psi 0.1706 0.02572 7.759E-4 0.1247 0.1692 0.2242 251 2250
\end{tabular}
\caption{..... xyz .....}
\end{table}
\label{tab.maxD}
```

We’ll remake this figure in R. For now, insert it as is.

3.5.2 Extension of the Model

One important issue in understanding the meaning of estimates produced under the individual covariate model is that the uniform distribution on $\max D$ implies that density is *not constant* over space. In particular, this model implies that it *decreases* as we move away from the centroid of the trap array. This is one reason

⁹This is a bad use of this term. We have never defined ETA or ESA. What is it, exactly?

we have a lower estimate of density than that obtained previously and also why, if we were to increase maxD , we would see density continue to decrease: $x[i] \sim \text{Uniform}(0, \text{maxD})$ implies constant N in each distance band from the centroid but obviously the *area* of each distance band is increasing. The reader can verify this as a homework exercise. Obviously, the use of an individual covariate model is *not* restricted to use of this specific distribution for the individual covariate. Clearly, it is a bad choice and, therefore, we should think about whether we can choose a better distribution for maxD - one that doesn't imply a decreasing density as distance from the centroid increases. Conceptually, what we want to do is impose a prior on distance from the centroid, x , such that density is proportional to the amount of area in each successive distance band as you move farther away from the centroid. In fact, there is theory that exists which tells us what the correct distribution of x is $2x/\text{maxD}^2$. This can be derived by noting that $F(x) = \text{Pr}(X < x) = \pi \cdot x \cdot x / \pi \cdot \text{maxD} \cdot \text{maxD}$. Then, $f(x) = dF/dx = 2 \cdot x / (\text{maxD} \cdot \text{maxD})$. This might be called a triangular distribution, I think, which makes sense because the incremental area in each additional distance band increases linearly with radius (i.e., distance from centroid). It is sometimes comforting to verify things empirically:

```

981 > u<-runif(10000,-1,1)
982 > v<-runif(10000,-1,1)
983 > d<- sqrt(u*u+v*v)
984 > hist(d[d<1])
985 > hist(d[d<1],100)
986 > hist(d[d<1],100,probability=TRUE)
987 > abline(0,2)

```

It would be useful if we could describe this distribution in *BUGS but there is not a built-in way to do this. One possibility is to use a discrete version of the pdf. We might also be able to use what is referred to in WinBUGS jargon as the “zeros trick” (see Advanced BUGS tricks) although we haven't pursued this approach. Instead, we consider using a discrete version and break D_{max} into L distance classes of width δ , with probabilities proportional to $2 \cdot x$. In particular, if the cut-points are $xg[1] = 0, xg[2], \dots, xg[L+1] = D_{\text{max}}$ and the interval midpoints are $xm[i] = xg[i+1] - \delta$. Then, the interval probabilities are $p[i] = 2 \cdot xm[i] \cdot \delta / (D_{\text{max}} \cdot D_{\text{max}})$, which we can compute once and then send them to WinBUGS as data.

The R script is as follows. In the model description the variable x (observed home range center) has been rounded so that the discrete version of the $f(x)$ can be used as described previously. The new variable labeled **xround** is actually then the integer category label in units of δ from 0. Thus, to convert back to distance in the expression for $lp[i]$, **xround[i]** has to be multiplied by δ .

```

1003 delta<-.2
1004 xround<-xcent%%delta + 1
1005 Dgrid<- seq(delta,maxD,delta)
1006 xprobs<- delta*(2*Dgrid/(maxD*maxD))

```

Table 3.4: Table: Analysis of Fort Drum bear hair snare data using the individual covariate model, for different values of D_{\max} , the upper limit of the uniform distribution of ‘distance from centroid of the trap array’

maxD mn SD [1,] 12 0.230 0.038 [2,] 15 0.244 0.041 [3,] 17 0.249 0.044 [4,] 18 0.249 0.043 [5,] 19 0.250 0.043 [6,] 20

```

1007 xprobs<-xprobs/sum(xprobs)
1008
1009 cat("
1010 model{
1011   p0 ~ dunif(0,1)           # prior distributions
1012   mup<- log(p0/(1-p0))
1013   psi~dunif(0,1)
1014   beta~dnorm(0,.01)
1015
1016   for(i in 1:(nind+nz)){
1017     xround[i]~dcat(xprobs[])
1018     z[i]~dbern(psi)          # zero inflation variables
1019     lp[i] <- mup + beta*xround[i]*delta # individual effect
1020     logit(p[i])<-lp[i]
1021     mu[i]<-z[i]*p[i]
1022     y[i]~dbin(mu[i],K)      # observation model
1023   }
1024
1025   N<-sum(z[1:(nind+nz)])
1026 }
1027 ",file="modelMcov.txt")

```

To fit the model we do this - keeping in mind that the data objects required below have been defined in previous analyses of this chapter:

```

1030 data2<-list(y=ytot,nz=nz,nind=nind,K=T,xround=xround,xprobs=xprobs,delta=delta)
1031 params2<-list('p0','psi','N','beta')
1032 inits = function() {list(z=z, psi=psi, p0=runif(1),beta=rnorm(1) ) }
1033 fit = bugs(data2, inits, params2, model.file="modelMcov.txt",working.directory=getwd(),
1034           debug=FALSE, n.chains=3, n.iter=11000, n.burnin=1000, n.thin=2)

```

This is a useful model because it induces a clear definition of area in which the population of N individuals reside. Under this model, that area is defined by specification of $\max D$. We can apply the model for different values of $\max D$ and observe that the estimated N varies with $\max D$. Fortunately, we see empirically, that while N seems highly sensitive to the prescribed value of $\max D$, density seems to be invariant to $\max D$ as long as it is chosen to be sufficiently large. We fit the model for $\max D = 12$ (points in close proximity to the trap arra) to 20 for and the results are given in Table ??.

We see that the posterior mean and SD of density (individuals per square km) appear insensitive to choice of $\max D$ once we get a slight ways away from

the maximum observed value of about 11.5. The estimated density of 0.250 per km² is actually quite a bit lower than we reported using model Mh (0.37, see section XYZ above) for which sample area is not an explicit feature of the model. On the other hand it is higher than that reported from Model M0 using the buffered area (0.195). There is no basis really for comparing or contrasting these various estimates and it would be a useful philosophical exercise for the reader to discuss this matter. In particular, application of model M0 and Mh are distinctly *not* spatially explicit models – the area within which the population¹⁰ resides is not defined under either model. There is therefore no reason at all to think that the estimates produced under either model, using a buffered area, are justifiable based on any theory. In fact, we would get exactly the same estimate of N no matter what we declare the area to be. On the other hand, the individual covariate model explicitly describes a distribution for “distance from centroid” that is a reasonable and standard null model - it posits, in the absence of direct information, that individual home range centers are randomly distributed in space and that probability of detection depends on the distance between home range center and the centroid of the trap array. Under this definition of the system, we see that density is invariant to the choice of sample area which seems like a desirable feature. The individual covariate model is not ideal, however, because it does not make full use of the spatial information in the data set, i.e., the trap locations and the locations of each individual encounter.

3.5.3 Invariance of density to maxD

Under the model above, and also under models that we consider in later chapters, a general property of the estimators is that while N increases with the prescribed trap area (equivalent to maxD in this case), we expect that density estimators should be invariant to this area. In the model used above, we note that $Area(maxD) = \pi * maxD * maxD$ and $E[N(maxD)] = \lambda * A(maxD)$ and thus $E[Density(maxD)] = \lambda$ which is constant. This should be interpreted as the *prior* density. Absent data, then realizations under the model will have density λ regardless of what $maxD$ is prescribed to be. As we verified empirically above, the posterior density is also invariant if $maxD$ as long as the implied area (implied by maxD) is large enough so that the data no longer provide information about density (i.e., “far away”), then our estimator of density should become insensitive.

3.5.4 Toward Fully Spatial Capture-recapture Models

We developed this model for the average observed location and equated it to home range center s_i . Intuitively, taking the average encounter location as an estimate of home range center makes sense but more so when the trapping grid is dense and expansive relative to typical home range sizes. However, our approach also ignored the variable precision with which each $s[i]$ is estimated and also, as

¹⁰We need to look back at Chapter 1 and make sure we quit calling this “sample area” - it really isn’t that at all, but rather the area within which N resides.

noted previously, estimates of $s[i]$ around the “edge” (however we define that) are biased because the observations are truncated (we can only observe locations within the trap array). In the next Chapter we provide a further extension of this individual covariate model that definitively resolves the ad hoc nature of the individual covariate approach we took here. In that model we build a model in which $s[i]$ are regarded as latent variables and the observation locations (i.e., trap specific encounters) are linked to those latent variables with an explicit model. We note that the model fitted previously could be adapted easily to deal with s_i as a latent variable, simply by adding a prior distribution for s_i . The reader should contemplate how to do this in WinBUGS.

3.6 DISTANCE SAMPLING: A primitive Spatial Capture-Recapture Model

Distance sampling is one of the most popular methods for estimating animal abundance. One of the great benefits of distance sampling is that it provides explicit estimates of *density*. The distance sampling model is a special case of a closed population model with a covariate. The covariate in this case, x_i , is the distance between an individual’s location “ u ” and the observation location or transect. In fact, the model underlying distance sampling is precisely the same model as that which applies to the individual-covariate models, except that observations are made at only $K = 1$ sampling occasion. In a sense, distance sampling is a spatial capture-recapture model, but without the “recapture.” This first and most basic spatial capture-recapture model has been used routinely for decades and, formally, it is a spatially-explicit model in the sense that it describes, explicitly, the spatial organization of individual locations (although this is not always stated explicitly) and, as a result, somewhat general models of how individuals are distributed in space can be specified (???). As before, the distance sampling model, under data augmentation, includes a set of M zero-inflation variables z_i and the binomial model expressed conditional on z (binomial for $z = 1$, and fixed zeros for $z = 0$). In distance sampling we pay for having only a single sample (i.e., $K = 1$) by requiring constraints on the model of detection probability. A standard model is

$$\log(p_i) = b * x_i^2$$

for $b < 0$, where x_i denotes the distance at which the i th individual is detected relative to some reference location where perfect detectability ($p = 1$) is assumed. This function corresponds to the “half-normal” detection function (i.e., with $b = 1/\sigma^2$). If $K > 1$ then the intercept alpha is identifiable and such models are usually called “capture-recapture distance sampling” (?) and others XYZ????).

As with previous examples, we require a distribution for the individual covariate x_i . The customary choice is

$$x_i \sim \text{Uniform}(0, B)$$

wherein $B > 0$ is a known constant, being the upper limit of data recording by the observer (i.e., the point count radius, or transect half-width). In practice, this is sometimes asserted to be infinity, but in such cases the distance data are usually truncated. Specification of this distance sampling model in the BUGS language is shown in Panel 3.1. ?, p. xyz) provide a distance sampling example analyzed by DA using the famous Impala data.

```

b~dunif(0,10)
psi~dunif(0,1)

for(i in 1:(nind+nz)){
  z[i]~dbern(psi)      # DA Variables
  x[i]~dunif(0,B)      # B=strip width
  p[i]<-exp(logp[i])    # DETECTION MODEL
  logp[i]<- -((x[i]*x[i])*b)
  mu[i]<-z[i]*p[i]
  y[i]~dbern(mu[i])    # OBSERVATION MODEL
}
N<-sum(z[1:(nind+nz)])
D<- N/striparea      # area of transects

```

Panel 3.1: Distance sampling model in WinBUGS, using a “half-normal” detection function.

As with the individual covariate model in the previous section, the distance sampling model can be equivalently specified by putting a prior distribution on individual *location* instead of distance between individual and observation point (or transect). Thus we can write the general distance sampling model as

$$\text{logit}(p[i]) = \alpha + \beta * ||u[i] - x_0||$$

Along with

$$\mathbf{u}_i \sim \text{Uniform}(\mathcal{S})$$

where x_0 is a fixed point (or line) and $u[i]$ is the individual’s location which is observable for n individuals. In practice it is easier to record distance instead of location. Basic math can be used to argue that if individuals have a uniform distribution in space, then the distribution of Euclidean distance is also uniform. In particular, if a transect of length L is used and x is distance to the transect then $F(x) = \Pr(X \leq x) = L * x / L * B = x/B$ and $f(x) = dF/dx = (1/B)$. For measurements of radial distance, see the previous section.

In the context of our general characterization of SCR models (chapter 1.XYZ), we suggested that every SCR model can be described, conceptually, by a hierarchical model of the form:

$$[y|u][u|s][s].$$

Distance sampling ignores s , and treats u as observed data¹¹. Thus, we are left with

$$[y|u][u].$$

In contrast, as we will see in the next chapters, basic SCR models (chapter 4) ignore u and condition on s , which is not observed:

$$[y|s][s]$$

Since $[u]$ and $[s]$ are both assumed to be uniformly distributed, these are structurally equivalent models! The main differences have to do with interpretation of model components and whether or not the latent variables are observable (in distance sampling they are).

So why bother with SCR models when distance sampling yields density estimates and accounts for spatial heterogeneity in detection? For one, imagine try to collect distance sampling data on tigers! Clearly, distance sampling requires that one can collect large quantities of distance data, which is not always possible. For tigers, it is much easier, efficient, and safer to employ camera traps or tracking plates and then apply SCR models. Furthermore, as we will see in Ch XYZ, SCR models can use distance data to estimate all the parameters of our enchilada, allowing us to study distribution, movement, and density. Thus, SCR models are much more flexible than distance sampling models, and can accommodate data from virtually all animal survey designs.

3.6.1 Example: Muntjac deer survey from Nagarahole, India

Here we fit distance sampling models to distance sampling data on the muntjac deer (*Muntiacus muntjak*) collected in the year 2004 from Nagarahole National Park in southern India (?) (Kumar et al. unpublished data). The muntjac is a solitary species and distance measurements were made on 57 groups that were largely singletons with XYZ pairs of individuals. Commands for reading in and organizing the data for WinBUGS, followed by writing the model to a text file. Note that the total sampled area of the transects is fed in as “striparea” which is 708 (km of transect) multiplied by the strip width ($B=150 = 0.15$ km) multiplied by 2.

```
library("R2WinBUGS")
data<- read.csv("Muntjac.csv")
nind<-nrow(data)
y<-rep(1,nind)
nz<-400
y<-c(y,rep(0,nz))
x<-data[,3]
x<-c(x,rep(NA,nz))
z<-y
```

¹¹Formally we could also say that $[u] = \int [y|s][s]ds$

```

1183 data<-list(y=y,x=x,nz=nz,nind=nind,B=150,striparea=708*.15*2)
1184
1185 cat("
1186 model{
1187   b~dunif(0,10)
1188   psi~dunif(0,1)
1189
1190   for(i in 1:(nind+nz)){
1191     z[i]~dbern(psi)      # DA Variables
1192     x[i]~dunif(0,B)      # B=strip width
1193     p[i]<-exp(logp[i])    # DETECTION MODEL
1194     logp[i]<- -((x[i]*x[i])*b)
1195     #logp[i]<- -b*log(x[i]+1)
1196     mu[i]<-z[i]*p[i]
1197     y[i]~dbern(mu[i])    # OBSERVATION MODEL
1198   }
1199   N<-sum(z[1:(nind+nz)])
1200   D<- N/striparea      # area of transects
1201 }
1202 ",file="dsamp.txt")

```

Next, we provide inits, indicate which parameters to monitor, and then pass those things to WinBUGS:

```

1205 params<-list('b','N','D','psi')
1206 inits = function() {list(z=z, psi=runif(1), b=runif(1,0,.02) )}
1207 fit = bugs(data, inits, params, model.file="dsamp.txt",
1208 working.directory=getwd(),debug=T, n.chains=3, n.iter=4000, n.burnin=1000, n.thin=2)

```

Posterior summaries are provided in the following table. Estimated density is pretty low, 1.1 individuals per sq. km.¹²

```

1211 node mean sd MC error 2.5% median 97.5% start sample
1212 D 1.096 0.1694 0.009122 0.8098 1.078 1.474 501 4500
1213 N 232.8 35.99 1.938 172.0 229.0 313.0 501 4500
1214 b 5.678E-4 1.05E-4 4.129E-6 3.867E-4 5.616E-4 7.949E-4 501 4500
1215 deviance 681.2 16.72 0.7536 650.8 680.6 716.6 501 4500
1216 psi 0.5099 0.08238 0.004442 0.3681 0.5033 0.6918 501 4500

```

3.7 Summary and Outlook

Traditional closed population capture-recapture models are closely related to binomial generalized linear models. Indeed, the only real distinction is that in capture-recapture models, the population size parameter N (corresponding also

¹² much lower than Samba's : Observers walked about 708 km from 39 transects in Nagarhole and the muntjac density is about 3 per sq km.. I need to get to the bottom of this.

1221 to the size of a hypothetical “complete” data set) is unknown. This requires
1222 special consideration in the analysis of capture-recapture models. The classi-
1223 cal approach to inference recognizes that the observations don’t have a stan-
1224 dard binomial distribution but, rather, a truncated binomial (from which which
1225 the so-called “conditional likelihood” derives) since we only have encounter fre-
1226 quency data on observed individuals. If instead we analyze the models using
1227 data augmentation, the observations can be modeled using a zero-inflated bino-
1228 mial distribution. In short, when we deal with the unknown-N problem using
1229 data augmentation then we are left with zero-inflated GLM and GLMMs in-
1230 stead of ordinary GLM or GLMMs. The analysis of such zero-inflated models is
1231 practically convenient, especially using the various Bayesian analysis packages
1232 that use the BUGS language.

1233 Spatial capture-recapture models that we will consider in the rest of the
1234 chapters of this book are closely related to what have been called individual co-
1235 variate models. Heuristically, spatial capture-recapture models arise by defining
1236 individual covariates based on observed locations of individuals – we can think of
1237 using some function of mean encounter location as an individual covariate. We
1238 did this in a novel way, by using distance to the centroid of the trapping array
1239 as a covariate. We analyzed the “full likelihood” using data augmentation, and
1240 placed a prior distribution on the individual covariate which was derived from
1241 an assumption that individual locations are, a priori, uniformly distributed in
1242 space. This assumption provides for invariance of the density estimator to the
1243 choice of population size area (induced by maximum distance from the centroid
1244 of the). The model addressed some important problems in the use of closed pop-
1245 ulation models: it allows for heterogeneity in encounter probability due to the
1246 spatial context of the problem and it also provides a direct estimate of density
1247 because area is a feature of the model (via the prior on the individual covariate).
1248 The model is still not completely general because the model does not make use
1249 of the fully spatial encounter histories, which provide direct information about
1250 the locations and density of individuals. A specific individual covariate model
1251 that is in widespread use is classical “distance sampling.” The model underlying
1252 distance sampling is precisely a special kind of SCR model - but one without
1253 replicate samples. Understanding distance sampling and individual covariate
1254 models more broadly provides a solid basis for understanding and analyzing
1255 spatial capture-recapture models.

1256 Chapter 4

1257 Fully Spatial
1258 Capture-Recapture Models

1259 Chapter 5

1260 Other observation models

1261 Chapter 6

1262 Maximum likelihood 1263 estimation

1264 **Chapter 7**

1265 **MCMC details**

1266 Chapter 8

1267 Goodness of Fit and stuff

1268 Chapter 9

1269 Covariate models

1270 Chapter 10

1271 Inhomogeneous Point 1272 Process

1273 Chapter 11

1274 Open models

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